Evolutionary Psychology

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Evolutionary Perspectives on Infancy

Springer

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Evolutionary Perspectives on Infancy

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In memory of my parents Pola and Pincus
Sybil L. Hart

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Part I
Introduction

Chapter 1
Infancy Through the Lens of Evolutionary Developmental Science

David F. Bjorklund and Sybil L. Hart

Natural selection has acted to shape the evolution of human form and function at all stages of the lifespan, but not necessarily equally. Natural selection has operated more strongly at the earlier stages of life than the latter. Although it is adults who must make a living in an often-hostile environment and who do the reproducing vital for continuation of the species, they must first survive infancy, childhood, and adolescence before making it to full maturity. Infancy, in particular, can be thought of as the *crucible of natural selection*, with approximately a quarter of ancestral infants failing to see their first birthdays (Volk & Atkinson, 2013; McDowell & Volk, Chap. 5, this volume).

Life is perilous for all infant mammals to varying degrees, and mammal infants (along with their parents, mostly their mothers) have evolved adaptations to increase their chances of survival. Human babies, however, remain immature and dependent on their mothers longer than other primates, and this necessitated extraordinary adjustments to the typical primate developmental pattern for *Homo sapiens* infants to stay alive and thrive. Compared to their chimpanzees cousins, human infants are slower to attain physical developmental milestones such as walking, require more effort on the part of their mothers for care (human infants cannot cling to their mothers, but rather must be carried by their mothers), and are born “early” compared to other primates (with respect to proportion of eventual brain size), with the result that their brains grow rapidly while experiencing a richer sensory and social environment than they would have had they followed the typical primate developmental course (e.g., Portman, 1990/1944; see Bjorklund, Chap. 2; DeSilva, Chap. 4; Locke

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& Bogin, Chap. 6, this volume). Although mammals all begin life as infants, the evolved nature of human infancy is in some ways substantially different from that of other mammals, beginning with a developmental process that transformed *Homo sapiens'* social and cognitive abilities to be qualitatively (or at least massively quantitatively) different than those of all other species.

1.1 What Evolved and What Develops?

Central to any evolutionary perspective is that individuals with features that promote survival in local environments pass on those features to their offspring, and that, over many generations and in some contexts, changes at a species level can occur. Thus, our ancestors evolved, but, during their lifetimes, they each developed (de Beer, 1958). In fact, because organisms display a high level of *plasticity* (ability to change) early in development, it was modifications in patterns of development in our forechildren that provided the variation upon which natural selection operated. According to West-Eberhard (2003, p. 139): "Adaptive evolution [improvement in a species due to selection] is a two-step process: first the generation of variation by development, then the screening of that variation by selection."

1.1.1 The Emergence of Adaptations

Contemporary evolutionary developmental scientists assume that development is a natural consequence of species-typical behavior emerging in a species-typical environment that evolved to solve problems associated with survival for one's ancestors. What, then evolved? The short answer is *adaptations*, alterations in the structure or function of an organism that provided a survival or reproductive benefit. In some cases, adaptations involved changes in physical morphology, such as a bigger brain or enhanced fine-motor coordination. However, both brains and fine-motor coordination go through lengthy development before they can be used to solve physically complex problems or to use tools efficiently. Other adaptations are related to behavior, emotions, or cognition – psychological adaptations – that also promoted survival. However, sophisticated, adult-level behavior or cognitive abilities do not arise fully formed in adults but emerge from skeletal psychological mechanisms through interaction with the environment over the course of development. From this perspective, adaptations not only evolved but also develop (Bjorklund, 2015). This is reflected by the field of *evolutionary developmental psychology*, defined as "the study of the genetic and ecological mechanisms that govern the development of social and cognitive competencies common to all human beings and the epigenetic (gene-environment interactions) processes that adapt these competencies to local conditions" (Geary & Bjorklund, 2000, p. 57).

With respect to psychological adaptations, evolutionary developmental scientists have proposed that infants and young children are biologically prepared to develop a suite of social and cognitive skills that, in interaction with their cultural environment, produce a unique type of human cognition and sociality. More specifically, infants are born with sets of low-level perceptual or cognitive "primitives" related to a variety of domains, such as understanding the physical world (e.g., objects fall when not supported), processing numbers ("more" vs. "less" relations), and understanding the biological and social world. Concepts such as *core knowledge* (e.g., Spelker & Kinzler, 2007), *starting-state nativism* (Gopnik & Meltzoff, 1997), *skeletal competencies* (Geary, 1995), and *evolved probabilistic cognitive mechanisms* (Bjorklund et al., 2007) have been proposed to capture the idea that infants are born with perceptual or cognitive biases that prompt them to pay attention to or process information in some domains more effectively than others. Abilities associated with these domains (e.g., tool use or social relations) become more sophisticated as they are fleshed out over ontogeny through exploration, play, and social interaction. Thus, what evolved are not fully articulated abilities, but low-level mechanisms that emerge in a species-typical way when infants and children are exposed to a species-typical environment.

As an example of how adaptations develop, consider vision. All typically developing mammals are born with a portion of their cortex devoted to vision. However, research with nonhuman animals clearly shows that the visual systems of animals reared in species-*atypical* conditions (e.g., in darkness or seeing only vertical lines) develop in atypical ways (Crabtree & Riesen, 1979; Hubel & Wiesel, 1962). Similarly, human babies born with cataracts develop normal vision if cataracts are removed within the first 2 or 3 months of life; vision is impaired, however, when cataracts are not removed until later in development (Le Grand et al., 2001; Maurer et al., 2007; see Maurer & Lewis, 2013, for a review). Visual experience is needed for neurons in the visual cortex to become properly organized, permitting normal "sight."

For developmentally typical infants, vision is limited at birth, yet even newborns will orient to what is perhaps the most important visual stimuli in their lives, faces (particularly of their mothers). For example, neonates attend to face-like stimuli (e.g., Mondloch et al., 1999); are especially attentive to eyes open and gazing at them (e.g., Farroni et al., 2002); and look longer at right-side-up versus inverted faces, but only when they can see the eyes (Gava et al., 2008). Yet, such early orientation seems not to be to faces, per se, but to perceptual features associated with faces. For instance, young infants are attentive to movement (Haith, 1966), areas of high contrast, such as eyes (Salapatek & Kessen, 1966), curvilinear (versus linear) stimuli (Ruff & Birch, 1974), vertically symmetrical stimuli (i.e., the right and left sides of a stimulus are alike) (e.g., Griffey & Little, 2014), and to "top-heavy" stimuli (i.e., up-down asymmetry, such as two eyes over one mouth) (Macchi Cassia et al., 2004). With experience, infants become increasingly skilled at identifying and processing faces. For example, 3-month-old babies are able to discriminate equally well among faces of different species (e.g., among monkeys and among humans), among faces of both men and women, and among faces of people from different races. However, by 9 months of age infants' abilities to tell the difference between faces from nonhuman species (e.g., monkeys; Pascalis et al., 2002) and races other than their own (e.g., Asian faces for Caucasian infants; Kelly et al., 2009) decline, while improving in their ability to discriminate among faces from their own race (e.g., Kelly et al., 2009; Quinn et al., 2002), a phenomenon called *perceptual narrowing* (Lewkowicz, 2014; Werker & Tees, 1984). This pattern makes good adaptive sense, in that infants should become skilled at differentiating among types of faces that they see often in their lives, with the ability to discriminate among types of faces they rarely or never see (e.g., different species, different races) being less important. This pattern is not inevitable, however. If children receive species-*atypical* experiences (e.g., frequently seeing monkey faces, [Pascalis et al., 2005], faces from other races [Anzures et al., 2012; Tham et al., 2017], or if their fathers are their primary caregivers [Quinn et al., 2002]), they retain the ability to discriminate efficiently among different members of these groups.

Although infants seem to begin life with a bias to attend to and process faces, this does not seem to involve complex "instincts" for faces, but rather a bias to attend to a suite of low-level perceptual features that faces happen to possess (movement, curvilinearity, top-heavy asymmetry) along with some processing biases (e.g., efficient processing of vertically symmetrical stimuli; better ability to discriminate among top-heavy than bottom-heavy stimuli). Thus, even for so basic a capacity as vision and infants' abilities to discriminate among critically important visual stimuli (i.e., faces), natural selection has achieved adaptive end states through the interaction of inherited low-level perceptual and cognitive dispositions interacting with a (usually) species-typical environment. Neural structures and functions emerge as a result of dynamic interactions between brain systems and "expected" environments (i.e., environments that most members of a species can expect to experience, given the natural history of the species) to produce species-typical patterns of development. Infants have enough plasticity, however, to modify their developmental trajectory to be consistent with local environments (e.g., seeing faces from one's own racial group), although substantial deviations from a species-typical environment can interfere with the "choreographed dance between gene-influenced neural maturation and perceptual experience," resulting is species-atypical outcomes (Bjorklund et al., 2007, p. 13).

1.1.2 Deferred Adaptations

The ability to process faces efficiently emerges from the interaction of a species-typical nervous system and a species-typical environment. Moreover, these emergent abilities serve as the basis of more sophisticated processing later in development. These can be thought of as *deferred adaptations*, serving to adapt individuals not only to their immediate environment, but also to future ones.

Perhaps the most important suite of deferred adaptations in infancy are related to social cognition. For example, when adults have conversations with babies, they often talk about and point out things to their young conversation partners, and beginning about 9 months of age infants start to understand what the adults are talking about, looking, for example, at the object the adult is pointing to and possibly expressing some emotion while doing so (Carpenter et al., 1998; Tomasello & Carpenter, 2007). Although such *shared* (or *joint*) *attention* may not appear to reflect a major cognitive milestone, it represents a significant change in how infants understand their social world and serves as the foundation for all subsequent higher-order forms of social cognition (e.g., theory of mind, see Buttelmann, Chap. 13, this volume). Infants are now treating others as *intentional agents*, people who do things intentionally, or "on purpose." Shared attention increases over the second year of life. Twelve- and 18-month-old infants will point to objects to direct adults' attention to something they are searching for, will point to adults to inform them about things the adults don't know, will use others' eye gaze as a cue to direct their own attention (Brooks & Meltzoff, 2002; Liszkowski et al., 2006, 2007), and will engage in *social referencing*, using a parent's facial expression, gesture, or tone of voice to interpret an ambiguous situation, such as falling off a chair (should I cry or not?) (Hornik et al., 1987; Vaish & Striano, 2004). This developmental pattern is found universally, even in cultures in which adults direct little attention to young infants (Callaghan et al., 2011).

Other research has shown that infants between the ages of 12 and 14 months show "egocentric empathic distress," responding to another's distress as if they themselves were in distress (Hoffman, 2000), display sympathy for the distress of others in the first year of life (Davidov et al., 2020), and toddlers in a wide range of cultures show greater happiness giving away treats than receiving treats (Aknin et al., 2015). Each of these behaviors is likely to promote future prosocial behavior with conspecifics (see Vaish & Grossmann, Chap. 16, this volume).

Tomasello (2019) has proposed that children develop what he calls *collective intentionality* and the ability to establish a *group-minded "we"* with other people beginning around the age of 3, reflected by, among other things, in-group favoritism, conformity to social norms, and collaboration to achieve a joint goal. Yet, forerunners of these abilities can be found in infancy. For example, 9-month-olds associate faces from their own race with happy music and other-race faces with sad music (Xiao et al., 2018), and 11- and 14-month-old infants are more likely to imitate the gestures of a native speaker than a foreign speaker (with associated differences in brain activity) (Buttelmann et al., 2013; de Klerk et al., 2019). Slightly older toddlers (18- to 20-months) associate sex-stereotypic toys with the "appropriate" gender (for instance, dolls for girls; toy cars and trucks for boys), and 2-year-olds selectively imitate same-sex stereotypic behavior (for example, caring for a baby for girls; building a house for boys) (Bauer, 1993; Martin et al., 2002). With respect to collaboration, although it is not until 3 years of age that children who work together to attain a goal will share treats equally, again the roots of cooperative behavior can be found in infancy. For instance, 18-month-olds will coordinate their actions with an adult to play a social game and protest when the adult suddenly stops, even when they can continue the game without the help of the adult, demonstrating that it is the social interaction that they are trying to reinstate not merely the completion of the game (Warneken et al., 2006, 2012). Thus, infants and toddlers seem to have the cognitive capacity to make in-group versus out-group distinctions early, as well as the foundation for collaboration, setting the stage for more sophisticated social-cognitive processes.

1.1.3 Ontogenetic Adaptations

In contrast to deferred adaptations, other adaptations seem not to develop into full-blown adult abilities, but rather serve to adapt infants to their current environment and disappear when they are no longer needed. These are referred to as *ontogenetic adaptations* (Bjorklund, 1997, 2015; Oppenheim, 1981). Consider, for example, the umbilical cord. It serves a universal function for all members of the species, supplying oxygen and nutrition to a fetus, but is useless after birth, as an entirely new set of physiological systems become operative. After birth, babies possess a suite of reflexes, some of which, such as the sucking reflex, are critical for nursing. With maturation of the nervous systems, control is shifted from subcortical to cortical brain areas, and infants no longer need a reflex to facilitate nursing, as they gain increasing intentional control over their behavior.

Ontogenetic adaptations can occur in the behavioral and psychological realms as well. For example, one candidate for a psychological ontogenetic adaptation is *neonatal imitation*. Under some conditions, newborns will match the facial gestures (e.g., tongue protrusion or lip pursing) of an adult model (e.g., Meltzoff & Moore, 1977). More recent research has suggested that babies may not actually match the facial gesture they see modeled, but nonetheless make some facial response to the model, even if it is not the one demonstrated (Oostenbroek et al., 2016; Redshaw et al., 2019). Meltzoff and Moore (1977) originally proposed that neonatal imitation reflects a form of social learning, although subsequent research questioned this interpretation. An alternative perspective is that neonatal imitation serves to motivate caretakers to interact with an infant during a time when babies cannot control their own behavior (Bjorklund, 1987, 2018). Consistent with this interpretation is research that showed that newborns who displayed high levels of neonatal imitation demonstrated higher levels of social interactions with their mothers three months later than newborns who showed lower levels of neonatal imitation (Heimann, 1989), and that neonatal imitation disappears by about 2 months of age when higher-cortical brain areas are able to influence infants' intentional actions (see Periss & Bjorklund, 2011).

1.1.4 Infant Adaptations as Emergent Properties

Infants are born with perceptual and cognitive biases to attend to and process some information more readily than others. Because of infants' high degree of plasticity, these biases can result in a range of outcomes, dependent on an infant's specific experiences; however, most will result in species-typical behavior assuming exposure to a species-typical environment. According to Bjorklund (2015, p. 30), "evolutionary adaptations are not so much inherited as they are emergent properties, arising from early developing perceptual and cognitive biases, in interaction with species-typical environments, to produce individuals that are adapted to their local environment."

1.2 Who Is an Infant?

Most researchers who study human infants specify who exactly they are talking about, i.e., who is an infant. The problem is, they often differ in their definition.

Perhaps the most common definition of infancy, for both scholars and laypeople alike, is children in their first year of postnatal life. There is good justification for identifying infancy as the time between birth and 12 months, for this is a period in which humans show perhaps the greatest amount of motor, social, and cognitive change than any other time in life. Babies are born with limited control over their physical actions, but over the course of the first year most infants can sit unsupported, crawl, and even walk. Although babies in their first weeks of life may be oriented toward social stimuli (e.g., attending to biological motion and face-like stimuli), over the course of the first year the social lives of infants change drastically, most importantly in forming attachments to their caregivers (see Locke & Bogin, Chap. 6; Hart, Chap.7; Hrdy & Burkhart, Chap. 8; Salmon & Hehman, Chap. 9; Henry & Morelli, Chap. 10; Simpson & Jaeger, Chap. 11, all in this volume). Changes may be equally substantial in cognition. For example, Piaget described infant cognition over the first year of life as a gradual change in representation and problem-solving, with infants between 8 and 12 months showing the first signs of goal-directed behavior (i.e., need preceding action, coordination of secondary circular reactions). As discussed earlier in this chapter, this corresponds to the time when infants first engage in shared attention, understanding that they and another person can share a single experience (e.g., baby and mother both seeing a third object). Coupled with this is infants seeing others as intentional agents, who cause things to happen, and the ability to take the perspective of other people (e.g., Tomasello, 2019). Although shared attention might seem to be a minor intellectual accomplishment, it serves as the basis for all subsequent social-cognitive abilities (see Buttelmann, Chap. 13; Hart, Chap. 15, both in this volume).

Other researchers recognize the continuity of development between the first and second years of life and consider what others would call toddlerhood as part of infancy, extending to 18–24 months. Major changes during this time include, from a Piagetian perspective, the transition from a mostly sensorimotor to symbolic form of representation, with perhaps the onset of language being the most obvious change (see Doi & Masataka, Chap. 12, this volume). Rate of brain development also slows down beginning around 18 months (Marchetto et al., 2019; see Wilder & Semendeferi, Chap. 3, this volume). Extending infancy to well into the second year of life is in keeping with the origin of the word, *infans*, from the Latin meaning "unable to speak" or "speechless."

For others still, especially comparative biologists and psychologists, infancy extends to weaning, 2.5–3 years of age in hunter-gatherers (see Hart, Chap. 15, this volume). From this perspective, infancy encompasses the period that is often referred to as toddlerhood and is one of three life stages of all mammals. The other two stages include the juvenile period, the time following weaning to sexual maturity (called middle childhood by psychologists and educators) and adulthood. (Bogin [2021] has suggested that humans have added two additional stages, not found in other mammals, *childhood*, the 3 or 4 years following weaning when children are no longer nursing but still require substantial support from adults, and *adolescence*, the several-year period of rapid growth and the onset of sexual maturity.) Following this definition, attainment of developmental milestones in humans can be directly compared with those of other animals, particularly primates. For example, although human babies' motor development lags that of chimpanzees, they are weaned a year or two earlier than chimpanzees, reducing the inter-birth interval in humans relative to chimps (Bründl et al., 2020; see DeSilva, Chap. 4; Locke & Bogin, Chap. 6, this volume). Some major changes in cognition are also seen beginning around 3 years of age; for example, as mentioned earlier in this chapter, Tomasello (2019) proposed that beginning around 3 years children start to form a *group-minded "we"* with other people (collective intentionality), resulting in the identification of in- and out-group members, social norms, and the ability to collaborate effectively.

It should not be surprising that each of these definitions of "who is an infant" can be found, implicitly or explicitly, in the chapters in this volume, given the variety of disciplines represented by the contributors. Authors of the chapters self-identify as coming from the fields of developmental psychology, evolutionary psychology, biological psychology, primatology, paleoanthropology, biological anthropology, neuroscience, linguistics, and human biology. Despite differences in who, exactly, is considered an infant, each discipline and author shares the view that infancy is a unique and important time in human ontogeny.

1.3 Overview of the Book

The first part of this volume devotes attention to some of the key physical parameters that governed processes which played a role in shaping the modern human infant's mind. In his chapter on *Human Evolution and the Neotenous Infant*, David F. Bjorklund discusses genetic-based differences in the timing and rates of attaining developmental milestones along the pathway toward physical and psychological maturity. He explains how different patterns of change enhanced neural plasticity that expanded capacities for cognitive and social functioning, and adaptations that fostered survival. In Chap. 3, Linnea Wilder and Katerina Semendeferi discuss modifications in infant brain development that arose following the split from the last common ancestor of hominins. The authors show how advances in *Homo sapiens'* brain function were augmented by accelerated rate of growth that occurred prenatally as well as prolonged development that took place postnatally. The next chapter, *Childbirth and Infant Care in Early Human Ancestors: What the Bones Tell Us* by Jeremy DeSilva, explores circumstances that drove major evolutionary shifts in the ways that human birth and infant care were carried out. Drawing on the human fossil record and findings on comparative skeletal anatomy, he illuminates changes that came about with upright posture, bipedalism, and the demands of transporting infants. The final chapter in this part, by Hannah McDowell and Anthony Volk, focuses on the first year of life as a period that was unique for being characterized by exceptionally by high rates of mortality. The authors present data on common causes of infant mortality and discuss implications of the high infant mortality rate in terms of its function as a filter that was responsible for potent evolutionary selective pressures.

Part II addresses various social attributes of the environments where humans evolved and the ways in which the infant's mind was formed by social encounters within those environments. In Chap. 6, *An Unusually Human Time: Effects of The Most Social Stage on the Most Social Species* by John Locke and Barry Bogin, the social nature of humans is addressed in light of infant altriciality, the demands of infant care, and social pressures related to group living that compelled psychological adaptations, including intentionality and theory of mind. Next, Sybil Hart presents evolutionary developmental psychology models of maternal caregiving and infant-maternal attachment. Following an interpretation of breastfeeding as a species-wide parenting behavior, she describes its practice by ancestral mothers and explains how it satisfied infants' physical and psychological needs in a manner and to a degree that gave rise to the infant-maternal bond forming uniquely as a species-wide phenomenon. In their chapter, *How Reliance on Allomaternal Care Shapes Primate Development with Special Reference to the* Genus *Homo,* Sarah Hrdy and Judith Burkart discuss the exceptional degree to which hominins reared young with the help of alloparents. They propose that transformations arose in offspring due to social pressures that favored those who were motivated to be found appealing by alloparents and were best at monitoring others' intentions, mental states, and preferences.

Chapter 9, *Evolutionary Perspectives on Infant-Mother Conflict* by Catherine Salmon and Jessica Hehman, discusses issues that presented as maternal resources were allocated among offspring, each of whom was more closely related to themselves than to their siblings. In particular, the chapter focuses on maternal-fetal conflict and weaning conflict. The next chapter, by Paula Ivey Henry and Gilda Morelli, discusses the biology, behavior, and sociocultural experience of Efe infants.

Evidence of resilience, such as lower mortality, high positive affect, and high rates of social engagement and food exchange, is considered in light of risk factors, including small size and slow growth, toward insight into ancestral conditions and forager infant variation. The final chapter in this part, by Jeffry Simpson and Margaret Jaeger, discusses the evolutionary foundations of attachment theory. The authors address features of the physical and social environments that shaped the attachment behavioral system and detail evolutionary-grounded, attachment-based models of social development toward understanding development as it occurs in individuals across the lifespan.

Part III focuses on the evolved basis of various components of infants' cognitive and social-cognitive capacities. In Chap. 12, Hirokazu Doi and Nobuo Masataka consider how language acquisition in prelinguistic infants is underpinned by perceptual capacities for processing features of music, such as pitch contour and rhythmic structure. They highlight parallels between infants' musical and linguistic abilities and consider how these abilities could have originated in non-human species. In the next chapter, *What is Unique in Infant Thinking About Others? Infant Social Cognition from an Evolutionary Perspective,* David Buttelmann presents findings on infants' understanding of others' mental states, such as others' desires, intentions and beliefs. He then compares these capacities in infants with those of nonhuman great apes toward identifying features that are uniquely human. Chapter 14, *Fear Learning in Infancy: An Evolutionary Developmental Perspective* by David Rakison, describes traditional and non-associative theories of fear acquisition. The chapter then focuses on the prepared-learning model, which is explained as a privileged associative-learning mechanism that orients infants to threats that were significant in ancestral environments. In her chapter, *Jealousy and the Terrible Twos*, Sybil Hart interprets the need for exclusivity as an outcome of infant dependence on mothers who suckled only one infant at a time. She explains that by representing a recurrent, life-threatening event, usurpation by a newborn sibling compelled advances in socio-emotional, cognitive, and motor development that enabled jealousy protest, a behavioral mechanism that helped prepare infants for the challenge of managing usurpation as they entered toddlerhood. In the final chapter, *Caring for Others: The Early Emergence of Sympathy and Guilt* by Amrisha Vaish and Tobias Grossmann, sympathy and guilt are construed as psychological mechanisms that were compelled by the need to ensure the wellbeing of individuals who were potential sources of support. The authors discuss evidence of their early emergence and discuss the functionality of reparative and prosocial behaviors that help establish and repair ruptures in cooperative relationships.

Throughout these chapters, this volume stands out for its attention to infancy as a discrete stage during which particular types of adaptations arose, and did so as a consequence of particular types of environmental pressures. They are offered with hope for their potential to illuminate basic understanding of the human brain and the environment that was responsible for shaping that brain.

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Part II
Foundations

Chapter 2
Human Evolution and the Neotenous Infant

David F. Bjorklund

All mammal infants are dependent and helpless, but to varying degrees. Newborns of precocial species such as horses, mountain goats, and gazelles have all of their senses working and can stand and walk on wobbly legs just hours after birth. Neonates of more altricial species such as cats, rats, and dogs are born effectively blind and deaf (although their senses of touch and olfaction are much better developed) and can locomote just enough to make their ways to their mothers' nipples. Primates, in general, have relatively well-developed senses and large brains at birth, but limited motor abilities. For example, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), humans' closest genetic relatives, don't sit up on their own until 3–4 months and don't walk until 6 or 7 months (Bründl et al., 2020; Kuroda, 1989). Humans follow a similar developmental trajectory, with all senses functioning to some degree at birth (although visual acuity is poor and improves over the first year in both humans and chimpanzees, Bard et al., 1995), although they take even longer to reach milestones of gross motor development (Bründl et al., 2020). The great apes in general follow a slow life history course. Parents (especially mothers) invest heavily in few offspring, who reach maturity relatively late in life. This trend is exaggerated in *Homo sapiens*, whose females reach sexual maturity at 16.5 years of age (on average among traditional groups), compared to 6.5 years for gorillas (*Gorilla gorilla*), 7.0 years for orangutans (*Pongo pygmaeus*), and 9.8 years for chimpanzees (Harvey & Clutton-Brock, 1985). Taking so long to reach adulthood and sexual maturity has its obvious shortcomings, particularly death before reproducing, and must therefore have some adaptive benefit, lest it would have been eliminated by natural selection. Most scholars argue that extending immaturity affords large-brained animals with opportunities to develop their survival skills and

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learn the complexities of their physical or social environments (Alexander, 1989; Bjorklund, 2021; Dunbar, 2003; Whiten & Erdal, 2014). Humans represent the extreme of slow primate development, and this process begins in the earliest stages of life.

2.1 Heterochrony as an Engine of Evolutionary Change

Homo sapiens' slow road to maturity begins early, in infancy, with human infants taking longer to achieve many developmental milestones than their simian relatives, and presumably than their *hominin* (group consisting of modern humans and their bipedal ancestors) predecessors. The retention of infantile or juvenile traits, including the rate of development into later life, is referred to as *neoteny*. Neoteny is a form of *heterochrony*, genetic-based differences in developmental timing, which is a central concept in the field of *evolutionary developmental biology*, or *Evo Devo* (Carroll, 2005, 2017; Raff, 1996). Evo devo explores how different developmental mechanisms affect evolutionary change. In general, aspects of development can be accelerated or retarded relative to that of an ancestor (McKinney & McNamara, 1991). Moreover, different parts, or modules, of an animal are relatively independent from one another, such that natural selection can operate independently on different modules at different times. This is often accomplished through the expression of *regulatory genes*, which, unlike structural genes, do not code for proteins but rather determine when and whether structural genes are activated and how much protein they produce. According to Carroll (2005), "It is the switches [regulatory genes] that encode instructions unique to individual species and that enable different animals to be made using essentially the same tool kit" (p. 211).

Although humans have often been described as a neotenous species (e.g., Bjorklund, 2021, in press; Bolk, 1926; Gould, 1977; Montagu, 1989), human evolution has clearly involved aspects of both acceleration and retardation of development relative to our ancestors. For example, although human infants are slower to develop gross motor abilities than chimpanzees (and presumably our last common ancestor with chimpanzees), they tend to be weaned earlier than chimps (between 2.5 and 3 years versus 4.5 and 5 years, Bogin, 2006), which results in a shortened inter-birth interval for human mothers. Moreover, as I'll discuss in greater detail later in this chapter, brain development is faster (accelerated) during the prenatal period in human fetuses relative to other primates, with this rapid rate of growth being maintained postnatally in humans relative to the other great apes (a form of retardation). Thus, human evolution reflects a mosaic pattern of different traits arising at different times, often associated with heterochronic changes, some reflecting acceleration and others retardation of ancestral rates and characteristics.

2.2 Neoteny in Human Evolution

Although human evolution has clearly involved both acceleration and retardation of ancestral traits, my focus in this chapter will be on the former, neoteny, especially its role in human infancy.[1] It may sound counterintuitive that evolutionary advances can sometimes be achieved by retaining infantile or juvenile traits into later development. Yet, neoteny can be a source of evolutionary innovation. According to Gould (1977), "the early stages of ontogeny are a storehouse of potential adaptations, for they contain countless shapes and structures that are lost through later allometries. When development is retarded, a mechanism is provided (via retention of fetal growth rates and proportions) for bringing these features forward to later ontogenetic stages" (p. 375).

As an example of neoteny in action, consider the work of the Russian zoologists Dmitry Belyayev and Lyudimila Trut, who bred wild red foxes (*Vulpes vulpes*) attempting to replicate the process that had converted wolves into domesticated dogs (Trut, 1999; Trut et al., 2009). The researchers selectively bred foxes for tameability, mating the most human-receptive females with the most human-receptive males. After 20 generations 35% of the foxes were classified as "domesticated elites," acting more like domesticated puppies than wild foxes. This domestication unexpectedly produced a suite of immature physical features, including floppy ears, wider and shorter heads, and shortened tails, snouts, legs, and upper jaws. Trut and her colleagues commented that, "The shifts in the timing of development brought about by selection of foxes for tameability have a neotenic-like tendency: the development of individual somatic traits is decelerated, while sexual maturation is accelerated" (Trut et al., 2009, p. 354). Along a similar vein, some scholars have suggested that humans are a *self-domesticated species*, in which neotenous traits were selected for decreased reactive aggression and increased prosociality and cooperativeness (Bjorklund, 2021, in press; Hare, 2017; Hood, 2014; Wrangham, 2019).

Let me provide an example more directly relevant to human evolution. In most adult mammals the backbone connects to the opening in the back of the skull (the *foramen magnum*) so that the angle at which the spine connects to the skull (called the *cranial flexure*) is such that the animal is facing forward when walking. This position was different in the fetal period, with the head sitting more or less on top of the spine. During prenatal development, the cranial flexure shifts in most mammals, producing the adult quadrupedal orientation. This shift does not occur as substantially in humans, however, so that the head of *Homo sapiens* is looking forward

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[1] Technical note: Following McKinney and McNamara (1991), there are three types of heterochronic retardation: (1) *progenesis*, or earlier onset of some aspect of development; (2) *neoteny*, or reduced rate of development; and (3) *post-displacement*, or delayed onset of development. For ease of reading, I do not differentiate between these three types of retardation here, often using the term neoteny to refer to retardation of development in general. McKinney and McNamara also identified three forms of heterochronic acceleration: (1) *hypermorphosis*, or delayed offset of development; (2) *acceleration*, or increased rate of development; and (3) *pre-displacement*, or earlier onset of growth (from Bjorklund, 2007, p. 44).

when standing on two legs. Thus, by retaining the embryonic relation between the skull and the spine, human heads sit atop their spines, permitting bipedal locomotion (see Gould, 1977; Montagu, 1989). Table 2.1 provides a list of some human neotenous traits.

My focus in the remainder of this chapter will be on neotenous features of infancy and early childhood that promoted adaptation to local environments, promoting survival, and can be seen in present day human babies and toddlers. I begin looking at motor and physical features, followed by an examination of the role of neoteny in human brain evolution, and finally aspects of "cognitive neoteny," immature features of infants' neural and cognitive processing that help babies adjust to their current ecological niche or serve as the basis for more advanced cognition.

2.3 Neotenous Motor and Physical Features and Their Consequences for Infant Survival

Human infants' extended period of physical dependency is a problem. Although all mammal infants are dependent on their mothers for nutrition, nurturing, and protection, this dependency is exaggerated in *Homo sapiens*. Human babies cannot cling to their mothers' fur or grasp around their mothers' necks, but must be carried and supported by their mothers for an extended period of time. Even once walking, human infants lack the physical dexterity and mental capacities to be left alone for any length of time. In fact, this dependency extends into childhood, a period between weaning and the eruption of permanent teeth (between about 3 and 7 years), which

Table 2.1 Some neotenous functional traits in humans

Rapid growth of brain well into third year
Low birth weight
External gestation (postnatal brain growth that would normally occur prenatally in other primates)
Prolonged immaturity
Prolonged dependency
Infant's great need of fluids (150 ml per day)
Fetal rate of bodily growth, weight, and length during first year
Prolonged growth period
Ends of long and finger/toe bones remain cartilaginous for years
Late development of reproductive maturity
Small nose
Longer legs than arms
Absence of baculum (penis bone)
How the spine connects to the base of the skull, permitting bipedal locomotion
Orientation of the vagina

Adapted from Bjorklund (2021), Bolk (1926), Montagu (1989), and Skulachev et al. (2017)

Bogin (2021) contends is a stage unique to humans between infancy and the juvenile stages (between about 7 years and puberty, called *middle childhood* by psychologists and educators). Thus, ancestral infants and toddlers required near-constant and extended care, and this factor may have been responsible, in part, for male-female pair bonding (a mother cannot adequately care for a child alone, necessitating help from the father) and for humans' adoption of *cooperative breeding*, with a host of mostly female relatives assisting in the care of infants and young children (Hrdy, 1999; see DeSilva, Chap. 4; Locke & Bogin, Chap. 6; Hrdy & Burkart, Chap. 8, this volume).

2.3.1 The Effects of Kindchenschema

Infants' extended period of dependency and motor immaturity may necessitate that they receive care from adults, but other aspects of physical immaturity increase the likelihood that they will receive that care. John Bowlby (1969), the father of attachment theory, observed that infant-parent attachment, critical for the survival of a helpless, long-dependent baby, is fostered by a number of infant features, including cries, smiles, movements, and immature facial features. The Nobel Prize-winning ethologist Konrad Lorenz (1943) noted a suite of facial features possessed by infants that promote feelings of affection and caregiving in adults, particularly mothers. Lorenz referred to these features as *kindchenschema* or *baby schema.* Compared to adult faces, infant faces have flat noses, fat cheeks, rounded heads that are large relative to body size, small chins, and large eyes relative to head size (e.g., Almanza-Sepúlveda et al., 2018). Everything else being equal, adults are more attentive to baby faces than to those of adults (e.g., Brosch et al., 2007; see Kringelbach et al., 2016 and Lucion et al., 2017 for reviews). One possible reason for adults' preference for babyness is that these cues are relatively honest signs of fitness and health of infants.

The effects of the baby schema have been investigated in more than 100 studies over the last 70 years, and although there is some variability in the findings, most studies confirm Lorenz's hypothesis that kindchenschema evolved to promote attachment to and nurturance from adults, all in the quest of surviving the perilous stage of infancy. Using a variety of measures, babies with cuter faces (i.e., faces with greater degrees of babyness) are associated with increased interest and caring from adults than less-cute infants. For example, adults evaluate infants with high levels of baby schema as friendlier, more sociable, more attractive, and easier to care for than less-baby-faced infants (e.g., Alley, 1981; Leibenluft et al., 2004; Senese et al., 2013; Sprengelmeyer et al., 2009). Adults display greater empathy for and have more affectionate interactions with cuter than less-cute babies (e.g., Langlois et al., 1995; Glocker et al., 2009a; Machluf & Bjorklund, 2016); they also express greater motivation to care for, and make favorable hypothetical adoption decisions toward, cuter than less-cute infants (e.g., Aradhye et al., 2015; Volk et al., 2007; Waller et al., 2004; see Franklin & Volk, 2018 for a review). This preference for baby-faced infants extends to members of different races (e.g., Caucasian adults respond similarly to cues of cuteness in Caucasian, African, and Asian infants), and, as any puppy or kitten owner knows, we even respond to cuteness cues in other species (e.g., Esposito et al., 2014; Golle et al., 2013). Consistent with the idea that baby-faced features promote affection and caregiving, premature infants, who display fewer of the kindchenschema features, are more apt to be abused at points during childhood than full-term infants (see Martin et al., 1974).

The effects of the baby schema have been documented in neuroimaging studies. For example, viewing infant faces typically produces faster neural responses involving more brain regions than when viewing adult faces (Glocker et al., 2009b; Hahn & Perrett, 2014; Leibenluft et al., 2004). Viewing infant faces elicits greater reactions in brain areas associated with processing emotion (Baeken et al., 2010; Glocker et al., 2009b; Nitschke et al., 2004), with Luo et al. (2015) concluding that "overall infant faces evoke [from adults] both stronger arousal and enhanced responses to both positive and negative cues from the infant" (p. 10). Research has also found that viewing baby faces is associated with greater activity in brain regions associated with empathy (e.g., Glocker et al., 2009b; Leibenluft et al., 2004), reward and attachment (e.g., Leibenluft et al., 2004; Nitschke et al., 2004), and motor behavior (Glocker et al., 2009b). The increased neural activation in motor areas when viewing baby faces may result in adults being extra careful when interacting with babies, as suggested by studies in which adults improved their fine-motor abilities, as well as expressions of tenderness and calmness, after viewing cute infant faces (or faces of puppies and kittens) (Sherman et al., 2009, 2013). Overall, looking at infant faces with high baby schema produces greater activation in brain areas associated with processing faces, emotion, and attention than viewing low-baby-schema faces (Luo et al., 2015).

One might think that the effects of babyness would be strongest at birth, when infants are most vulnerable and in need to care. This clearly makes good evolutionary sense from the infant's perspective, but research has shown that babies are viewed as most cute between 3 and 6 months of age. Many newborns have misshapen heads from their trip through the birth canal, and babies born prematurely have more atypical features and lower body weight than full-term infants. In studies by Franklin and her colleagues (2018), adults were asked to rate photographs of newborns, 3-month-olds, and 6-month-olds in terms of cuteness, health, and happiness, and to make hypothetical adoption decisions about the babies. Although babies of all ages were rated relatively high on these dimensions (average ratings ranged from 3.06 for happiness to 4.08 for adoption decisions on a five-point scale), adults rated the 3- and 6-month-old infants higher than the newborns on each measure. One explanation for this finding is that, although it may be in the infant's best interest to garner as much attention and caring from adults as soon as possible, it may not be in the best interest of the parents. Ancestral parents, especially mothers, often had to evaluate whether and how much to invest in a newborn. In situations where resources are scarce and parents have other offspring to care for, it may be in the mother's best interest to abandon a sickly child. So whereas it may not have been a benefit to neonates for their parents to objectively evaluate the health and fitness of an infant, it likely was to the parents' advantage (see Salmon & Hehman, Chap. 9, this volume).

Although the benefits of babyness may be greatest in the first year of life, they persist into early childhood. For example, in one study adults recommended less-severe punishment for more baby-faced 4-year-olds than for children with more mature faces (Zebrowitz et al., 1991). However, the positive effects of baby schema extend only to 4 or 5 years of age, after which adults' judgments of attractiveness and likeability are similar to their judgments for adult faces (Luo et al., 2011). Other research has shown that neurological responses to faces vary as a function of the age of the person shown in the photograph, with images of infants having the greatest activation, followed by photos of prepubescent children, and the least activation for photos of adults (Proverbio et al., 2011).

2.3.2 Sex Differences in the Effects of Kindchenschema

The effects of the baby schema are found in both men and women, but they are greater in women, who historically (and surely prehistorically) have done the bulk of the infant care (e.g., Cárdenas et al., 2013; Sprengelmeyer et al., 2009; Yamamoto et al., 2009; see Hart, Chap. 7; Simpson & Jaeger, Chap. 11, this volume). For instance, in a series of experiments, Sprengelmeyer et al. (2009) varied the kindchenshema features of infants' faces and asked men and women to select which of two infant faces (one having more babyness features than the other) was cuter. Although women, overall, were more sensitive to subtle differences in cuteness than men, women's selections varied with their age. Figure 2.1 shows the judgments of cuteness (selecting the photo with the higher cuteness value) for men and women of different ages. Women between 19 and 26 years of age were the most sensitive to

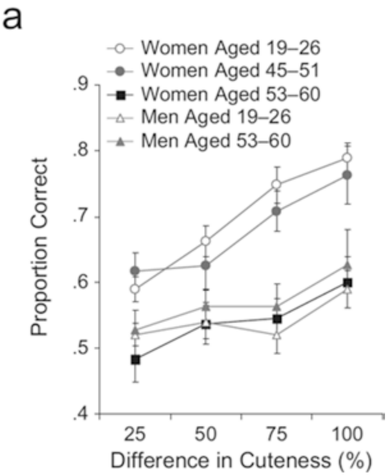

Fig. 2.1 Mean accuracy (±1 SE) in cuteness-discrimination task as a function of the difference in cuteness between the faces for men and women of different ages (Study 1). (From Sprengelmeyer et al., 2009)

cuteness cues, followed closely by women 45–51 years of age. In contrast, older women, 53–60 years of age, were less able to distinguish the high-baby-schema faces and were comparable in their performance to both younger and older men. That these results were linked to hormone levels was supported by subsequent findings that age-matched premenopausal women were more accurate at selecting the cuter faces than postmenopausal women, and that women using hormonal contraception were better able to distinguish the cuter baby than women not on hormonal birth control (Sprengelmeyer et al., 2009).

Other research has found that sex differences in sensitivity to babyness is first seen in early adolescence, consistent with the hypothesis that it is related to changes in hormone levels (e.g., Borgi et al., 2014; Fullard & Reiling, 1976; Goldberg et al., 1982; Gross, 1997). For example, Goldberg et al. (1982) showed 12- and 13-year-old girls and same-age boys slides of infant and adult faces and asked them to choose which faces they preferred. Half of the girls had had their first period (postmenarcheal) and half had not (premenarcheal). The postmenarcheal girls preferred the infant faces significantly more often than both the premenarcheal girls and the boys, who did not differ from one another. This pattern is consistent with idea that a strong preference for baby-faced features, especially in girls, may reflect a preparation for parenthood, or at least did for our ancestors.

2.4 Neoteny and Brain Development

Infants' immature, or neotenous, physical features helped keep ancestral babies alive by endearing them to adults and promoting attachment. This, of course, requires adaptations in adults (chiefly mothers) to be responsive to infants' cues of dependency, which serve to benefit the inclusive fitness of both parents and offspring. As critical as these features are to survival, they are not unique to humans, as other species have evolved biparental families, cooperative breeding, and respond positively to immature features of their infants. What *is* special about humans is their cognition and social acumen. *Homo sapiens* possess symbolic representation, language, and tool-using and problem-solving abilities that, while possibly not unique in the animal kingdom, are far more advanced than those shown by any other creature. And although *Homo sapiens* surely evolved from other social primates, humans' degree of social sophistication – abilities to learn from and cooperate and compete with social others – qualifies them as a *hypersocial*, or *eusocial*, species, analogous in some ways to the social insects (e.g., Tomasello, 2014, 2019; Wilson, 2013). One currently popular theory of human evolution is the *social brain hypothesis*, the idea that increased social cognition was a (perhaps *the*) driving force in human evolution and necessitated a large brain to handle the variety and complexity of human communities (e.g., Alexander, 1989; Bjorklund & Bering, 2003; Dunbar, 2003). The building of such a brain was achieved, in large part, by heterochronic changes in the timing and rate of development, beginning prenatally and continuing through infancy.

The adult human brain is about three times the size of chimpanzee and bonobo brains, as well as the brains of our early hominin ancestors, both in absolute size and in relation to body size (Jerison, 2000; see Wilder & Semendeferi, Chap. 3, this volume, for an excellent summary of infant brain development and evolution). The human brain got that large in part by producing more neurons and accelerating growth prenatally (forms of heterochronic acceleration) and by retaining the prenatal rate of brain growth postnatally (a form of heterochronic deceleration, or neoteny).

Although natural selection favored increased brain size in the hominin line eventuating in humans, there were morphological limits in how large a neonate's skull (and thus brain) could be and still fit through the birth canal of a bipedal female. (Bipedality evolved prior to increased brain size in hominin evolution.) This is referred to as the *obstetrical dilemma* (Washburn, 1960). As a result, at birth human infants' brains, while absolutely large in size compared to their simian relatives, are smaller relative to their eventual adult size than those of other primates. In most primates, babies are born when their brains are on average 47% of their eventual adult weight (DeSilva, 2016; Trevathan & Rosenberg, 2016). In contrast, human babies are born when their brains are about 28% of their eventual weight (DeSilva, 2016; see DeSilva, Chap. 4, this volume).[2]

Following birth, human infants retain the rapid, prenatal rate of brain growth in terms of size of neurons, formation of dendritic connections, and myelination (Liu et al., 2012; Marchetto et al., 2019; Miller et al., 2012). By 6 months of age, infants' brains achieve about 50% of their adult weight. This increases to 75% at 2 years, 90% at 5 years, 95% at 10 years, with the final 5% of growth not being completed until late adolescence or early adulthood. Chimpanzees, in comparison, attain adult brain size by about 5 years of age (Bogin, 2006). Thus, even when humans develop "more brain" than other primates, they do it, in part, by retaining fetal growth rates long after birth.

Despite the "early" birth, human infants' brains – that are still large in an absolute sense – were surely a risk for our hominin ancestors. Death in childbirth, for both the mother and infant, was a real possibility for most of human history and prehistory, and likely because of this, women in most hunter-gatherer cultures give birth with the assistance of other women (e.g., Trevathan, 1987; See DeSilva, Chap. 4, this volume). Given the risk associated with giving birth to such a large-brained baby, there must have been substantial benefits, or it would have been eliminated by natural selection.

The benefits were surely in what larger and more complex brains can achieve in terms of technical and social abilities. But brains not only evolved but also develop, and the particular pattern of infant brain development set the stage for the many

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[2] Many of the assumptions of Washburn's obstetrical-dilemma hypothesis have recently been challenged (e.g., Dunsworth, 2016; see DeSilva, Chap. 4, this volume). However, regardless of the validity of Washburn's original claims, human newborns' brains are smaller relative to their eventual adult size than those of other primates, with more development occurring in postnatal environments relative to apes.

abilities that characterize human adult brains. By extending brain growth that would normally occur in the protective wombs of their mothers following the typical primate developmental pattern, human infants are exposed to a vastly different set of experiences. Their brains continue to develop rapidly while receiving visual, auditory, tactile, olfactory, vestibular, and social stimulation that a typical primate would not receive until its brain was substantially more developed. Scholars have long proposed that human infants' gestation is essentially extended into postnatal life and have referred to this period by a number of terms, including *extrauterine spring*, *exterior gestation, exterogestation,* and *the fourth trimester* (e.g., Konner, 2010; Montagu, 1989; Portmann, 1944/1990; Trevathan & Rosenberg, 2016). As a result of experiencing the external world at a time when their brains are going through a rapid period of change, human infants develop very differently than they would if they remained in the protective warmth of their mothers' wombs, causing some theorists to argue that this extended period of brain development is responsible for the extraordinary features of *Homo sapiens'* technical and social skills. Imagine, German zoologist Adolf Portmann (1944/1990) asks us, "the developing human spending the important maturation period of its first year in the dark, moist, uniform warmth of its mother's womb… It will gradually become clear that world-open behavior of the mature form is directly related to early contact with the richness of the world, an opportunity available only to humans" (p. 93).

Although 1-year-old infants are hardly mental giants, some early-acquired developmental milestones serve as the basis of later essential social-cognitive accomplishments. For example, starting around 9-months of age, infants begin to display *shared attention* (e.g., mother and infant sharing attention about a third object), begin to see others as intentional agents, and are able to take the perspective of other people. In his *shared intentionality theory*, Tomasello (2019) refers to these early-developing abilities as *joint intentionality*, defined as "the cognitive capacity to create a joint agent 'we' with other individuals, creating the possibility of taking the perspective of others" (p. 305). The abilities underlying joint intentionality, particularly viewing others as intentional agents, are the basis for all more sophisticated social-cognitive accomplishments, and they would likely not have had the opportunity to evolve were infants born following the typical primate schedule.

Tomasello (2019) argues that, "if we wish to explain how uniquely human psychology is created, we must focus our attention on ontogeny, and especially on how great ape ontogeny in general has been transformed into human ontogeny in particular" (p. 6). One important way that great ape and human ontogeny differ is in the rate of brain development, with humans' extension of the rapid prenatal rate of brain growth altering the very nature of infancy and the social-cognitive accomplishments of the species. Consistent with the social brain hypothesis that posits that changes in social cognition may be especially important in human psychological evolution is evidence that 2-year-old chimpanzees and human children display comparable levels of physical cognition (e.g., tasks dealing with space, quantities, and tools), although 2-year-old children out-perform chimps on tasks of social cognition (e.g., imitation, nonverbal communication, and reading the intentions of others). Moreover, whereas children continue to improve on both physical- and social-cognitive tasks for the next few years, chimpanzees do not, essentially attaining adult levels by 2 years of age (Wobber et al., 2014).

Neoteny apparently not only played a role in extending the rate of brain development but also affected the development of individual neurons and neuronal plasticity. *Synaptogenesis*, the process of forming new synapses, is responsible in large part for human behavioral and cognitive plasticity, and such plasticity is greatest early in life. Neuronal metabolism and synaptic activity peak later in humans than in other primates (see, e.g., Bufill et al., 2011; Liu et al., 2012; Petanjek et al., 2011; Somel et al., 2009), as does the process of myelination (Miller et al., 2012), thus extending neural plasticity into adulthood. Humans and chimpanzees possess similar genes associated with synapse formation in the cerebral cortex, with the expression of these genes peaking earlier in chimpanzees (before 1 year) than in humans (about 5 years) (Liu et al., 2012). Also, levels of gene expression associated with cortical synaptogenesis are similar in adolescent and adult humans to that observed in juvenile chimpanzees (see Bufill et al., 2011; Somel et al., 2009), causing Bufill et al. (2011, p. 735) to state that "human neurons belonging to particular association areas retain juvenile characteristic throughout adulthood, which suggests that a neuronal neoteny has occurred in *H. sapiens*, which allows the human brain to function, to a certain degree, like a juvenile brain during adult life… Neuronal neoteny contributes to increasing information storage and processing capacity throughout life, which is why it was selected during primate evolution and, to a much greater extent, during the evolution of the genus *Homo*."

Human brains are substantially larger than those of the great apes and those of their hominin antecedents. Although there is no single cause for this brain expansion, much of it was due to variation of growth rates relative to *Homo sapiens'* ancestors, some due to accelerations and others due to retention of rapid prenatal growth rates into infancy, as well as retention of plasticity of individual neurons well into adulthood. Infants' brains grow rapidly at a time when, if they followed a typical primate schedule, they would be tucked securely within their mothers' wombs. Instead, because of their "early" birth, they experience a world of lights, sounds, smells, social others, and artifacts, which changes the nature of their cognition, and, in many ways, were responsible for the evolution of the modern human mind.

2.5 Cognitive Neoteny: The Benefit of Neural and Cognitive Inefficiency

It is hard to underestimate the impact on the evolution of the human mind of having lots of neurons that retain their plasticity well past infancy. However, the brains of human infants are still immature and inefficient compared to those of older children and adults, with synaptogenesis not peaking until childhood and many areas of the brain, particularly the prefrontal cortex, having little or no myelin. Thus, infants and young children process information more slowly than older children and adults, such that their processing is *effortful* in that it uses substantial portions of their limited mental resources (Hasher & Zacks, 1979). In contrast, the cognitive processing of older children and adults is more apt to be *automatic*, in that it requires little or none of one's limited capacity. Despite the obvious disadvantages to infants' inefficient neural processing, there are some benefits. According to Bjorklund and Green (1992, pp. 49–50):

> Because little in the way of cognitive processing can be automatized early, presumably because of children's incomplete myelination, they are better prepared to adapt, cognitively, to later environments. If experiences early in a life yielded automatization, the child would lose the flexibility necessary for adult life. Processes automatized in response to the demands of early childhood may be useless and likely detrimental for coping with the very different cognitive demands faced by adults. Cognitive flexibility in the species is maintained by an immature nervous system that gradually permits the automatization of more mental operations, increasing the likelihood that lessons learned as a young child will not interfere with the qualitatively different tasks required of the adult.

2.5.1 The Adaptive Value of Neural Inefficiency

Perhaps the greatest benefit of neural inefficiency in early development is in terms of *plasticity*, the ability to change. As we saw in the previous section, human neurons retain their ability to change well into adulthood (neuronal neoteny). However, this does not mean that plasticity is infinite. Rather, experiences early in life result in strengthening connections among some sets of neurons and weakening or eliminating connections among others. The end result is a reduction of plasticity. However, because neuronal processing is relatively inefficient during the first 2 years of life, high levels of plasticity are retained. Because of this, the effects of a deleterious early environment can be reversed should circumstances change.

Such plasticity has been repeatedly demonstrated in nonhuman animals (e.g., Suomi & Harlow, 1972) and human children (e.g., Beckett et al., 2010; Nelson et al., 2007; Troller-Renferee et al., 2018). For example, children who spend their early months in understaffed, neglectful institutions display signs of neurological, social, and intellectual deficits that tend to persist into adolescence (e.g., Beckett et al., 2010; Mackes et al., 2020; Merz et al., 2016). Such psychological effects are mirrored by differences in brain functioning. According to developmental neuroscientist Charles Nelson (2007), "many forms of institutional rearing lack most elements of a mental-health-promoting environment. As a result, the young nervous system, which actively awaits and seeks out environmental input, is robbed of such input … institutionalization appears to lead to a reduction in cortical brain activity … and to dysregulation of neuroendocrine systems that mediate social behavior" (p. 16). However, if children are removed from such institutions before 18–24 months, they often display substantial recovery of social, emotional, and intellectual functioning. In contrast, children who remain in institutions much past their second birthdays are less apt to show recovery of typical psychological functioning (e.g., Beckett et al., 2010; Merz & McCall, 2010; Nelson et al., 2007).

The results of institutionalization studies clearly show that children can rebound from the negative effects of social deprivation if they experience a supportive environment beginning around 18 or 24 months of age. Some researchers have proposed that human development is highly *canalized* during the first 18 or 24 months of life, meaning that children follow the species-typical path "under a wide range of diverse environments and exhibit strong self-righting tendencies following exposure to severely atypical environments" (McCall, 1981, p. 5). Although infants may be negatively affected by early neglectful environments, there is a tendency to return to a course of normalcy when they experience more supportive conditions. As infants' brains mature, the degree of plasticity reduces, making it more difficult to reverse the effects of a maladaptive environment. Eighteen to 24 months also corresponds to a time when the rate of brain growth begins to slow (Leigh, 2004; Matsuzawa, 2001) and when children's cognitive abilities undergo substantial changes (e.g., the onset of language and the transition from Piaget's sensorimotor to preoperational periods), further suggesting that maturational-based changes in brain development and organization are responsible, in part, for the reduction in plasticity at this time.

2.5.2 The Adaptive Value of Poor Memory

At the core of cognition is memory, and there is an extensive literature demonstrating age-related differences in memory from infancy through adulthood (see, e.g., Bauer & Fivush, 2014). Young infants demonstrate memory mainly through perceptual phenomena (e.g., showing dishabituation to novel stimuli) or conditioning. For example, Rovee-Collier and her colleagues developed the *conjugate reinforcement procedure*, in which a ribbon is tied to an infant's ankle and then to a mobile over the infant's head while in a crib. Infants learn that their leg movements cause the mobile to move, and demonstrate this by kicking their legs when, after initially learning the connection between kicking and the movement of the mobile, they later kick their leg when placed in the crib when the ribbon is *not* tied to the mobile (see Rovee-Collier & Cuevas, 2009). In one set of experiments, Rovee-Collier and her colleagues (1992) showed that 2-month-old infants remembered the connection between kicking and the movement of the mobile but only when the crib liner was the same during both acquisition and testing. Rovee-Collier and Shyi (1992) proposed that this reflects an extreme dependency on context for young infants that may prevent them from retrieving memories in "inappropriate" situations. Given infants' poor inhibitory abilities (e.g., Baird et al., 2002; Diamond, 1985; Holmboe et al., 2008), such dependency on context may prevent infants from retrieving previously learned memories (actions) in inappropriate situations. As infants gain more experience with their physical and social worlds over the course of the first year, they become less dependent on the context in remembering (Learmonth et al., 2004; Rovee-Collier & Cuevas, 2009), such that experiences in one context can be usefully applied in similar contexts. According to Hartshorn and her colleagues (2004, p. 76), “As the physical world of the developing infant progressively expands and the infant’s niche also changes, the behavioral solutions to problems that characterized the relatively static habitat and niche of the younger infant must also change or lose their adaptive utility.”

As children acquire language, they begin to recall information according to *scripts*, schematic organizations with real-world events organized in terms of their causal and temporal characteristics (Nelson, 1996). Children learn what usually happens in a situation (e.g., eating breakfast in the morning) and remember novel information in the context of these familiar events (see Bauer, 2007; Fivush et al., 1992). However, 2-year-old children often show an over-reliance on scripts, remembering only script-consistent facts and failing to remember novel experiences (e.g., Fivush & Hamond, 1990). Rather than being maladaptive, Nelson (1996, 2005) suggested that young children’s reliance on scripts helps them predict the probability of events in the future. According to Nelson (1996, p. 174):

> Memory for a single, one-time occurrence of some event, if the event were not traumatic or life-threatening, would not be especially useful, given its low probability. Thus, a memory system might be optimally designed to retain information about frequent and recurrent events—and to discard information about unrepeated events—and to integrate new information about variations in recurrent events into a general knowledge system.

Similarly, Rovee-Collier and Giles (2010) argued that infants’ generally poor long-term memory reflects “*rapid forgetting… an evolutionarily selected survival-related strategy* that facilitates young infants’ adaptation to their rapidly changing niche and enables them to shed the excessive number of recent, rapidly formed associations that are potentially useless, irrelevant, or inappropriate” (p. 203) (cf., Bjorklund & Green, 1992). Rovee-Collier proposed that the first 9- or 10-months of life is a time of “exuberant learning” accompanied by rapid synaptogenesis and pruning.

There has also been some speculation that young children’s limited working memories may facilitate the initial acquisition of language. For example, some researchers have shown that the different sensory systems develop at different times, coordinated with sensory experiences, so that the development of one sensory system does not interfere with the development of other sensory systems (Turkewitz & Kenny, 1982). Newport (1991) made an analogous argument for the early stages of language acquisition, proposing that young children’s limited working memories simplify the body of language they process, which makes the complicated syntactical system of any human language easier to learn. Newport developed a computer simulation that varied how much the computer program could keep in memory at any one time, equivalent to varying the size of a child’s short-term store. She reported that restricting the computer program’s memory resulted in early deficits in language learning (for instance, whole words were often lost), but that word endings that denote verb tense and plurals were more likely to be retained. Newport concluded, “overall, then, a learning mechanism with a restricted input filter [smaller short-term memory] more successfully acquired a morphology [syntactic structure];

the same learning mechanism with a less restricted filter [larger short-term memory], or with no filter at all, entertains too many alternative analyses and cannot uniquely determine which is the better one" (p. 127). (See also Elman [1994], who reached a similar conclusion using a very different type of computer simulation.) Experimental support for Newport's and Elman's hypotheses comes from research demonstrating that adults learn an artificial grammar faster when presented with smaller rather than larger units of the language (Kersten & Earles, 2001).

The research examined in this section may not reflect neoteny in a literal sense. Inefficient neural processing or limited memory abilities do not reflect features of juvenile ancestors that have been retained in modern adults. They do reflect the consequences of prolonging neural maturation, and they are examples of what are usually thought of as immature or poor cognition that actually may have an adaptive value for infants and children at a particular time in development. Natural selection has made use of infants' immaturity to help them develop into children and later adults who can function well in their communities (Bjorklund & Green, 1992).

2.6 Conclusion

Our ancient ancestors evolved to become the species we are today. But each of our ancestors also developed, and the forces of natural selection operated as potently, if not more so, on the early stages of development as on later stages. Modifications of development, including changes in rate and timing of developmental milestones (heterochrony), had an enormous impact on the evolution of many species, with humans being no exception. Although there is ample evidence of both heterochronic acceleration and retardation in *Homo sapiens*, neoteny can be seen as the source of many of our species' unique features. This may be most clearly seen in infancy, from birth to weaning, with neotenic changes in infants' physical characteristics, rate of brain growth, and enhanced neural plasticity fostering babies' survival and transforming the nature of their cognitive and social functioning to serve as the foundation for the modern human mind.

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Chapter 3
Infant Brain Development and Plasticity from an Evolutionary Perspective

Linnea Wilder and Katerina Semendeferi

The evolution of the human brain following the split from the last common ancestor of hominins and *Pan* (*Pan troglodytes* and *Pan paniscus*) has involved a substantial increase in size as well as modifications to the internal, cellular organization. These changes were likely achieved through modifications in the timing and rate of development during hominin evolution. The result of those changes is a uniquely derived developmental trajectory of the brain in humans compared to non-human primates, which includes an accelerated rate of growth prenatally and in infancy, prolonged development, and substantial postnatal plasticity.

The outcome of these evolutionary modifications is significant brain growth and development occurring postnatally. This allows the brain to be shaped by the physical and social environment outside of the uterus to a greater degree than is seen in non-human primates, contributing to the cognitive flexibility, intelligence, and brain plasticity of humans (Leigh & Park, 1998; Neubauer & Hublin, 2012; Piantadosi & Kidd, 2016).

3.1 Brain Development in Infancy

3.1.1 General Primate Development

Brain development in primates begins with the formation of the neural tube, the first structure of the central nervous system to arise in primate embryos, which develops to form the brain and spinal cord. In humans, neural tube formation is complete by the end of the third week of gestation. A region of the interior of the neural tube known as the ventricular zone is lined with neural progenitor cells. Initially, these

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cells divide symmetrically, with each cell producing two progenitor cells. This increases the pool of progenitor cells and thus the number of neurons that can be produced. They later gradually shift to asymmetric division, producing one neural progenitor and one neuron. The progenitor cells remain in the ventricular zone producing more neurons, which then migrate out of the ventricular zone (Stiles & Jernigan, 2010).

Newly born cortical neurons migrate to the emerging cortical plate, where they will form the laminar structure of the cortex in an inside-out manner, with the earliest born neurons populating the deeper cortical layers (V/VI), and later born neurons populating more superficial layers (II/III) (Cooper, 2008). Neural proliferation occurs almost exclusively prenatally, with a peak in neuron density in the second half of gestation. This is followed by a period of *apoptosis*, where approximately half of all neurons produced undergo programmed cell death, resulting in neuron numbers at birth that are near adult values (Rabinowicz et al., 1996; Stiles & Jernigan, 2010). Proliferation and migration of glial cells begin prenatally after the onset of neurogenesis, first with astrocytes, then oligodendrocytes (Lee et al., 2000). Neurogenesis continues throughout life in primates in only two regions, the dentate gyrus of the hippocampus and the olfactory bulb (Kornack & Rakic, 2001; Taupin & Gage, 2002). There is no reliable evidence of postnatal neurogenesis in the primate neocortex, but the production of glial cells continues throughout life (Gage, 2019; Lee et al., 2000).

As neurons reach their target destinations, they begin to extend axons, and dendrites form synapses with other cells. This begins prenatally and continues after birth. This initial cell growth and *synaptogenesis* is followed by a period of pruning unnecessary or unused connections. This activity-dependent fine-tuning of connections allows the brain to be modified in response to the environment (Buss et al., 2006; Oppenheim, 1989). Following *gliogenesis*, oligodendrocytes begin to form myelin sheaths around axons, aiding in the transmission of neural signals.

The microstructural changes described above are reflected in changes to the gross anatomy of the brain. Dendritic growth causes an increase in gray matter (mostly neurons and glial cells) volume early in life, followed by a later decline. This is paralleled by changes in cortical thickness, which initially increases, then thins as synapses and dendrites are pruned (Brown et al., 2012; Lyall et al., 2015). Myelination causes the growth of white matter (mostly myelinated axons), which begins slowly prenatally and continues steadily until reaching maximum volume (Sakai et al., 2011). In some primates, these changes occur at different times (i.e., are heterochronous) across different regions of the brain (Bianchi et al., 2013). Generally, primary processing regions develop first, and association regions such as the prefrontal cortex (PFC), which serves higher order cognitive and emotional functions, develop later (Petanjek et al., 2011; Bianchi et al., 2013).

Less is known about the development of subcortical structures in primates, but there are data available for amygdala development in humans and non-human primates (Payne et al., 2010; Ulfig et al., 2006). The amygdala is known to play an important role in primate behavior and typical development in the production and processing of social and emotional behavior (Gabard-Durnam et al., 2018). The amygdala is of particular interest to human evolution as it shows evidence for reorganization in humans relative to non-human apes. The human amygdala has a larger lateral nucleus, with a greater number of neurons than expected for an ape brain of its size. This expansion of the lateral nucleus may contribute to enhanced social cognition in humans (Barger et al., 2007, 2012). The primate amygdala emerges early in prenatal development but is immature at birth, allowing the postnatal experience to shape its development (Payne et al., 2010; Ulfig et al., 2006).

Although all primates follow the same general pattern of brain development, there are differences in the timing of these events, which have been best studied in macaques (*Macaca mulatta)*, common chimpanzees (*Pan troglodytes*), and humans.

3.1.1.1 Macaque

The majority of growth in total brain volume in macaques, approximately 60%, occurs prenatally, with slower growth postnatally (Leigh, 2004; Malkova et al., 2006). Total brain volume, as well as both gray and white matter volume, increase for the first five postnatal months. This is followed by a slight decline in gray matter volume by the end of infancy after which it stabilizes. White matter volume continues to increase through infancy and into the juvenile period, with both gray matter and white matter volumes reaching adult values by the onset of puberty (Kim et al., 2020; Knickmeyer et al., 2010). Postnatal growth of the amygdala is greatest in the first 2 weeks, with growth slowing and finally stabilizing around 8 months of age, near the end of infancy, when the adult volume is reached (Payne et al., 2010).

At the cellular level, neurogenesis in macaques begins on embryonic day 40, with synaptogenesis starting by embryonic day 65 (average gestation length = 167 days) (Bourgeois & Rakic, 1993). Across the macaque cortex, there is a rapid increase in density of synapses in the last two prenatal months that takes place concurrently in all cortical layers. This increase continues throughout the first six postnatal months, the majority of the infancy period, after which the density of synapses begins to decline as unused connections are pruned (Bourgeois et al., 1994; Rakic et al., 1986, 1994).

3.1.1.2 Chimpanzee

Combining longitudinal magnetic resonance imaging (MRI) data with cross-sectional measures of brain volume at death allows the rate of chimpanzee brain growth to be described throughout the prenatal and infant period. As shown in MRI studies, the rate of brain growth in chimpanzees accelerates in utero until it reaches its peak growth of approximately 12 cc/week at gestation week (GW) 22, after which the rate of brain growth gradually slows, reaching 4.1 cc/week at the end of gestation (see Fig. 3.1). At birth, the neonatal chimpanzee brain is approximately 150 cc, 40% of its adult volume (Sakai et al., 2012). Shown through measures of brain size at death, postnatally, the rate of brain growth continues to slow until

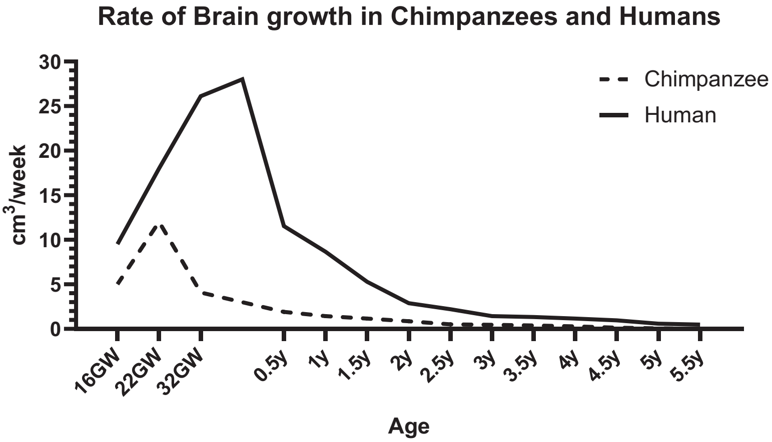

Fig. 3.1 Approximate rate of total brain volume growth by week in chimpanzees and humans. (Adapted from Leigh, 2004 and Sakai et al., 2012)

around 5 years of age, when adult brain volume, 380 cc, is achieved (Herndon et al., 1999; Leigh, 2004).

Gray matter volume in chimpanzees increases throughout infancy. In non-prefrontal regions, gray matter volume reaches its peak at the end of infancy, 3 years of age. After 3 years of age gray matter volume in non-prefrontal regions declines until reaching adult values. Gray matter growth is prolonged in prefrontal regions, with gray matter volume continuing to increase past infancy before eventually declining. White matter growth occurs throughout infancy, growing 173% and 62% of the volume at birth in the prefrontal and non-prefrontal regions of the cerebrum, respectively. Cerebral white matter reaches 50% (prefrontal) and 64% (non-prefrontal) of adult volume by 3 years of age. This growth continues past infancy, only reaching adult volume after puberty (Sakai et al., 2011). The growth of white matter is largely the result of changes in myelin. Myelination begins prenatally, with 20% of neocortical myelination complete at birth, and continues throughout infancy and the juvenile period before reaching adult levels around the time of sexual maturity, with myelin growth in prefrontal regions slightly prolonged relative to other brain regions (Miller et al., 2012).

At the cellular level, brain development is described through postmortem histological studies of neural anatomy at different ages throughout life. Synaptogenesis in chimpanzees occurs concurrently across cortical areas, similar to macaques, with a peak density of synapses reached at 3–5 years of age, just after infancy ends (Bianchi et al., 2013). There is a growth of dendrites across the cortex in infancy, which appears to be prolonged in the prefrontal cortex. In adult primates, including macaques, chimpanzees, and humans, dendritic trees of pyramidal neurons in PFC are longer, and have more branches and spines than those of primary sensory areas (Jacobs, 2001; Hrvoj-Mihic et al., 2013). In infant chimpanzees, the dendritic trees and spine density in the PFC are not as elaborate as in other cortical areas, indicating continued development of pyramid neurons in the PFC past infancy (Bianchi et al., 2013).

3.1.1.3 Human

Prenatally, the rate of growth of the human brain accelerates from the period of GW 16 to GW 32, reaching a growth rate of 26.1 cc/week at GW 32, more than six times the rate of growth in a chimpanzee fetus of the same gestational age (Fig. 3.1). This rate of growth is maintained throughout the remainder of the fetal period, with brain size at birth being approximately 400 cc, about 30% of adult brain volume (Holland et al., 2014). The growth rate begins to decrease after birth.

Total brain volume increases dramatically in humans during infancy, doubling in size in the first year of life, to approximately 72% of adult volume (Fig. 3.2). This growth is largely due to increases in gray matter, which grows by 149%, while white matter increases by 11% at the same time. In the second year of life, there is a 15% increase in total brain volume, to approximately 83% of adult volume. In this period gray matter increases by 14%, while white matter increases by 19% (Knickmeyer et al., 2008). The dramatic increase in gray matter in the first year of life is in part

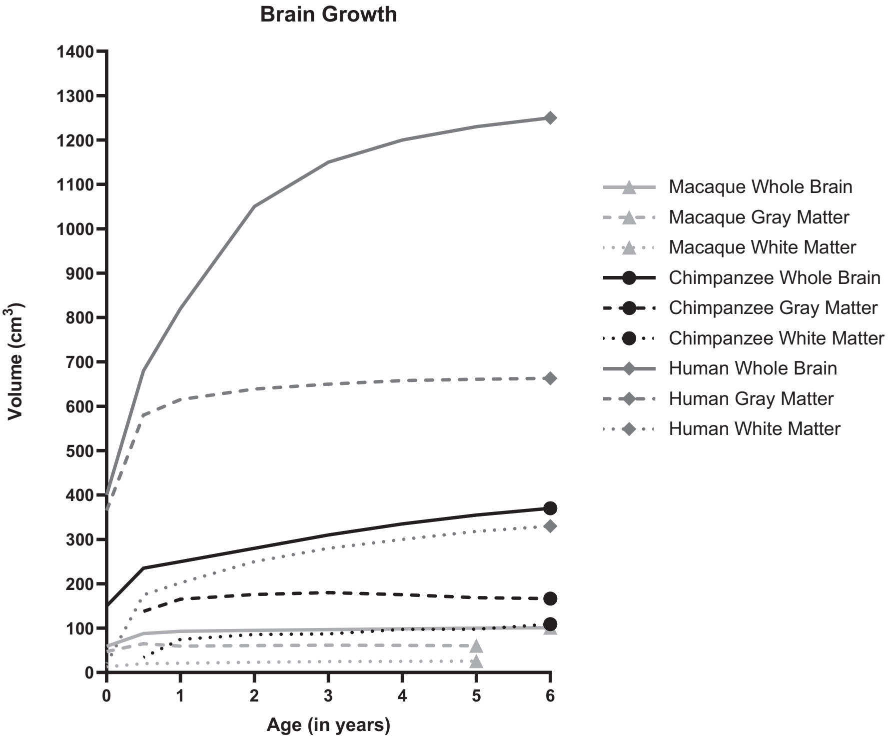

Fig. 3.2 Growth in total brain volume, cerebral gray matter and white matter in macaques, chimpanzees, and humans. (Adapted from Herndon et al., 1999, Kim et al., 2020, Leigh, 2004, Matsuzawa, 2001, and Sakai et al., 2011)

due to growth of the cerebellum, which doubles in volume in the first three postnatal months, and increasing another 70% from 3 months to 1 year (Holland et al., 2014; Knickmeyer et al., 2008). In the cerebral hemispheres both gray and white matter volume increase in infancy, with gray matter possibly peaking at age 4, while white matter continues to slowly increase (Fig. 3.2) (Matsuzawa, 2001; Pfefferbaum et al., 1994). In the first 2 years of life, cerebral gray matter growth is slowest in primary processing areas, with frontal association cortices (including portions of the PFC) growing more rapidly (Gilmore et al., 2012).

Throughout infancy cerebral white matter grows at a faster rate than cerebral gray matter, growing 185% in prefrontal regions from 1 to 6 years of age, reaching 76.2% of adult volume, and 80% in non-prefrontal regions in the same period, reaching 77.2% of adult volume (Matsuzawa, 2001). The growth in the white matter continues past infancy, particularly in prefrontal regions, due to prolonged myelin growth. Myelination begins prenatally. In the neocortex, this is restricted to postnatal development and continues beyond adolescence (Miller et al., 2012).

The amygdala in humans can be found as early as GW 8, and structural connectivity is present by GW 13 (Gabard-Durnam et al., 2018). Postnatally, there is a large increase in amygdala volume in the first 3 months of life, with continued growth until around 4 years of age (Holland et al., 2014; Tottenham, 2012). Development continues past this point, with mature amygdala-PFC connectivity emerging after 10 years of age in typical development (Gee et al., 2013a).

Neurogenesis begins at GW 6 in humans, with the number of neurons reaching a peak at GW 28 then declining due to cell death to adult values at the time of birth (Rabinowicz et al., 1996). Postnatal growth in gray matter is due to *neuropil* growth, which reflects cellular development, specifically the growth of dendrites and axons (Knickmeyer et al., 2008; Rabinowicz et al., 1996). Neuronal development in the PFC is prolonged relative to other cortical regions. At birth, the earlier generated layer V pyramidal neurons of the PFC have larger and more complex dendritic trees than those of the later generated layer III pyramidal neurons (see Fig. 3.3). In the first year of life, the dendritic trees of layer III pyramidal neurons grow more rapidly than those of layer V, with neurons in both layers reaching similar growth. This is followed by a period of minor dendritic growth, a "plateau" period, until 2 years of

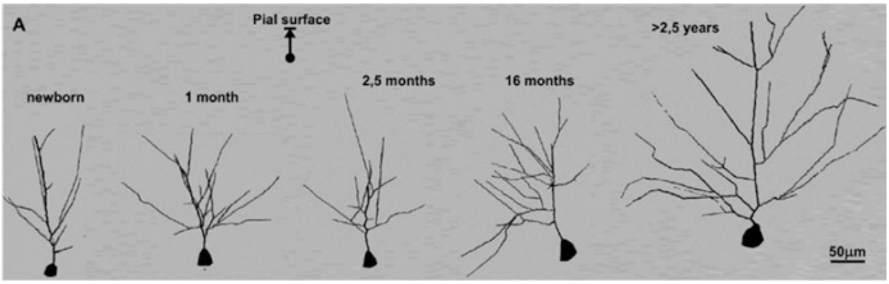

Fig. 3.3 Dendritic growth of human layer III pyramidal neurons in the PFC (Brodmann area 9). (From Sedmak et al., 2018)

age. Between the ages of 2 and 3 years, these neurons undergo a period of substantial dendritic elaboration, resulting in dendritic trees that are more extensive that those of layer V pyramidal neurons (Petanjek et al., 2008; Hrvoj-Mihic et al., 2013).

Synaptogenesis begins by GW 27 in humans and peaks around 5 years of age, with synaptic refinement and pruning continuing into adulthood (Huttenlocher & Dabholkar, 1997; Petanjek et al., 2011). Development of synapses is heterochronous in different cortical areas, with primary processing areas developing more rapidly, while the development of the PFC is prolonged (Huttenlocher & Dabholkar, 1997; Petanjek et al., 2011).

3.1.2 Uniquely Human Features of Infant Brain Development

Beginning prenatally, and continuing through early postnatal life, the rate of brain growth in humans is much greater than in chimpanzees (Fig. 3.1). In the prenatal period, this rate of growth is greater even relative to the greater volume of the human fetal brain. At birth, the human brain is approximately 2.5 times larger than a neonatal chimpanzee brain, and slightly larger than the average adult chimpanzee brain. However, humans achieve a smaller percentage of brain growth prenatally than chimpanzees, ≈30% compared to ≈40% of adult volume at birth, respectively (DeSilva, Chap. 4, this volume). Postnatally, humans and chimpanzees appear to share a derived pattern of a rapid rate of postnatal brain growth compared to Old World monkeys.

After 18 months of age, the rate of brain growth in humans and chimpanzees slows significantly, with both species reaching a similar growth rate at this time (Fig. 3.2). Brain growth duration does not vary substantially between species, suggesting that the change in the rate of growth during prenatal and early postnatal life is what allows the human brain to grow so large. This rapid growth is energetically costly. Approximately 87% of the resting metabolic rate of a newborn human is devoted to brain growth and function, while a chimpanzee of the same age only requires 45% of the resting metabolic rate to maintain brain growth and function (Bogin, 2007). In addition to a greater rate of overall brain growth, humans have more rapid growth of white matter in the brain than chimpanzees during infancy, particularly in prefrontal regions, and myelination is prolonged past sexual maturity well into adulthood.

At the cellular level, brain maturation follows the same overall pattern in humans as in non-human primates. There is a period of exuberant neuron production and synaptogenesis, with neurons and synapses later pruned in an activity-dependent manner, allowing the brain to be modified in response to the environment. Nevertheless, there are differences in the timing of these events in humans relative to non-human primates. Maturation of pyramidal neurons in humans appears prolonged compared to non-human primates. Human neurons display delayed growth in dendritic length and dendritic spine number, with the substantial developmental remodeling of synaptic spine density in the prefrontal cortex continuing until approximately 30 years of age (Petanjek et al., 2011). Novel experimental studies using induced pluripotent stem cells to directly compare human and chimpanzee neuronal development showed that human pyramidal neurons develop and migrate more slowly than chimpanzee pyramidal neurons. Even though the initial growth of dendrites and dendritic spines occurs earlier in chimpanzees, growth is prolonged in human neurons. This allows humans to have a greater total dendritic length and a greater number of dendritic spines (Marchetto et al., 2019).

Synaptogenesis in both humans and chimpanzees is prolonged compared to macaques. This is additionally prolonged in humans at least in the prefrontal cortex, and is reflected in changes in gene expression, with synaptic genes reaching peak expression in the prefrontal cortex before 1 year of age in chimpanzee and macaques, and 5 years of age in humans (Liu et al., 2012). Functionally important aspects of synaptic remodeling may occur during "plateau" periods, described for humans above. These occur in both humans and non-human primates later in development (Levitt, 2003). However, the early phase of limited growth in layer III of the PFC has only been observed in humans and may represent a specialization for enhanced cognition and cortico-cortical connectivity (Petanjek et al., 2008).

Brain development in human infancy is characterized by both rapid early growth and prolonged cellular maturation. Particularly interesting is the fact that regions with prolonged cellular maturation, such as the PFC, also exhibit the most rapid growth in the early postnatal period in humans (Gilmore et al., 2012). These features contribute to neuroplasticity in infancy, allowing the brain to be modified by the environment while the infant is in a critical period of social and cultural learning.

3.2 Neuroplasticity and Atypical Development

Typical neural development in primates relies on both experience-expectant and experience-dependent plasticity. *Experience-dependent plasticity* is idiosyncratic, knowledge that is unique to the individual, shaping them for their particular environment. *Experience-expectant plasticity* is associated with critical periods in development, when expected experiences shape the developing brain in a species-typical way (Greenough & Black, 1999). These expected experiences are required for typical neural development, and may be experienced atypically in individuals with some neurodevelopmental disorders.

In social primates, there is a critical period during infancy for the development of social behaviors. Both common marmosets and macaques deprived of social contact as infants display aberrant social behaviors, including increased fear and a lack of social play, which persist into adulthood (Dettling et al., 2002; Harlow & Harlow, 1962). This atypical development does not require complete social deprivation. Macaques raised without their mother, but with age-matched peers until 6 months of age, also displayed aberrant social behaviors (Spinelli et al., 2009). In common marmosets, typically in constant contact with their parents early after birth, separation from both parents for just 2 h per day in the first month of life is enough to induce stress and decreased social play (Dettling et al., 2002). This suggests that social contact with the parent(s) during infancy is required for species-typical development of social behavior to occur.

Early life stress in infancy has similar results in humans. Children who experience an early life neglect have higher levels of anxiety and depression that may be tied to altered connectivity between the amygdala and PFC (Tottenham, 2012). Early life stress in humans results in reduced integrity of white matter between frontal and limbic regions of the brain, as well as accelerated development of functional connectivity between the amygdala and medial PFC (Bick et al., 2015; Gee et al., 2013b). This accelerated development may be adaptive, as it does appear to provide greater resilience to stress. However, it also decreases early life plasticity and may prevent optimal neural development (Gee et al., 2013b). In the extreme case of institutionalization devoid of typical parental care, children show significant decreases in both cortical gray matter and white matter volumes. These negative effects can be partially ameliorated by providing a replacement parental figure, as long as this is done prior to 2 years of age (Nelson et al., 2009). Even less extreme stress can negatively impact brain development in infancy, as is the case with socioeconomic status, now known to positively correlate with cortical surface area (Noble et al., 2015).

Studies of brain development in neurodevelopmental disorders, in conjunction with studies of behavior and cognition in these disorders, shed light on the impact of *neuroplasticity*, which can be seen in autism spectrum disorder (ASD) and Williams syndrome (WS). ASD is complex and heterogenous, genetically and phenotypically, while WS has a known deletion of approximately 25–28 genes that underlies all typical WS cases, and a more consistent behavioral and cognitive profile (Bellugi et al., 2000; Strømme et al., 2002). Despite the differences in etiology, both ASD and WS involve altered social behavior, and both provide examples of alterations to typical development.

ASD is characterized by early overgrowth in the brain, likely the result of exuberant neurogenesis or reduced apoptosis prenatally, and impaired white matter tracts in infancy (Shen & Piven, 2017). The growth of axons and dendrites from an excessive number of neurons may accelerate the rate of brain growth in infancy. This is seen in the PFC, where children with ASD have 67% more neurons than typically developing controls (Courchesne et al., 2011). Young children with ASD experience early overgrowth of the amygdala so that in childhood they have enlarged amygdalas relative to controls. They do not show typical growth of the amygdala during childhood that occurs in controls, and by adolescence amygdala volume in ASD subjects is equal to that of controls (Schumann, 2004). Overall neuron number is decreased in the ASD amygdala, and serotonergic innervation is increased relative to controls (Lew et al., 2020; Schumann & Amaral, 2006). Alterations to brain growth and neural development during infancy are not limited to the area directly affected. During this critical period of development, while the brain is highly sensitive to external input, disruptions to development can alter functional connectivity across the brain, resulting in substantial cognitive and behavioral consequences. In ASD it is hypothesized that early life neural overgrowth may alter the course of typical development, resulting in overconnectivity of local circuits and underconnectivity of long-range networks, impacting neural function throughout life (Courchesne & Pierce, 2005).

In WS, alterations to the brain appear to be more consistent and genetically guided than in ASD. WS is characterized by hypersociability, a lack of social inhibition, along with high levels of anxiety (Bellugi et al., 2000). In adulthood, WS subjects have alterations in parts of the brain known to be involved in social behavior. They have reduced neuron density and higher glia density, along with relatively decreased dendritic trees in some regions of the PFC (Hrvoj-Mihic et al., 2017; Lew et al., 2017; Wilder et al., 2018). They also have a higher number of neurons, and decreased serotonergic innervation in the amygdala (Lew et al., 2018, 2020). There are very few studies on morphology of the infant and developing WS brain, but it appears that the alterations present in WS adults begin prenatally or in infancy. Increased neuron number in the lateral nucleus of the amygdala is present even in the youngest WS subject examined (<1 month of age), and increased glia density in the PFC is present at 8 months of age (Lew et al., 2018; Wilder et al., 2018). These early life alterations in WS may impact functional connectivity and future development within these brain regions, limiting neuroplasticity in some respects. This could be reflected in the behavioral profile of WS, which is consistent even cross-culturally (Zitzer-Comfort et al., 2007).

3.3 Brain Development in Human Evolution

As the brain does not fossilize, and development itself cannot be directly observed in extinct species, it is difficult to determine exactly when the *Homo sapiens* pattern of prolonged brain development, with rapid early growth, emerged during hominin evolution. However, by examining the fossil record and the timing of genetic changes, some inferences can be made (DeSilva, Chap. 4, this volume).

3.3.1 Extinct Hominins

In two early species of hominins, *Sahelanthropus tchadensis* and *Ardipithecus ramidus*, adult endocranial volume was under 400 cc, within the range of present-day chimpanzees. Brain growth in these species was likely relatively conserved and similar to the pattern that would have been present in the last common ancestor of the *Pan* genus and hominins (Zollikofer & de León, 2013).

The earliest evidence of possible changes to the brain in hominin evolution has been demonstrated in Australopithecines. Adult Australopithecine endocranial volume (410–550 cc) is slightly larger than that of chimpanzees (approximately 380 cc) (Falk et al., 2000). Estimated neonatal brain size in Australopithecines is also slightly larger than the average neonatal brain size in chimpanzees, 179.8 cc and

145.7 cc, respectively. Based on these estimates, Australopithecines would have completed a slightly lower percentage of brain growth prenatally than chimpanzees, 38% and 40% respectively (DeSilva & Lesnik, 2008). More direct evidence of brain ontogeny in Australopithecines comes from the endocasts of the Dikika child (*Austalopithecus afarensis*) and the Taung child (*Austalopithecus africanus*). The Dikika child, which dates to 3.3 million years ago, was approximately 3 years old at the time of death and had an estimated endocranial volume of 275-330 cc (Alemseged et al., 2006). The Taung child, dated to 2.5 million years ago, was approximately 3–4 years old at the time of death, with an estimated endocranial volume of 382–405 cc (Falk et al., 2000; Falk & Clarke, 2007). Relative to endocranial volume in adults of the same species, the values of both of these specimens fit within what would be expected for chimpanzees (Zollikofer & de León, 2013). Further evidence of brain ontogeny in the Taung child is found in its metopic suture, which had not completely fused at the time of death. In great apes, this occurs shortly after birth, while in *Homo sapiens* this suture fuses much later, possibly to accommodate a greater degree of brain growth. This delayed fusion of the metopic suture in the Taung child may indicate a higher rate of growth in the very early postnatal period in Australopithecines (Falk et al., 2012). Overall, brain growth in Australopithecines appears to be similar to that of chimpanzees, while possibly shifting very gradually to more prolonged postnatal growth, in the direction of the *Homo sapiens* growth pattern. Due to the limited number of juvenile fossils found from the various Australopithecine species, there is not enough evidence to conclusively identify a change from the ancestral pattern of brain growth.

Brain volume increased significantly in the *Homo* genus relative to earlier hominins, with endocranial volumes of nearly all *Homo habilis* specimens being greater than 580 cc. Estimates based on adult endocranial volume and pelvis size suggest neonatal brain size in early *Homo* species (*Homo habilis* and *Homo rudolfensis*) may have been approximately 225 cc, only 35% of average adult values (Falk et al., 2000). The lack of any infant or young juvenile specimens from either of these species makes these estimates somewhat speculative, however.

The earliest species in which brain growth trajectory has been thoroughly examined is *Homo erectus*, where there is evidence of a change in the rate of brain growth compared to chimpanzees and relative to earlier hominins. The skull cap of an infant *Homo* erectus was found in Mojokerto, Indonesia, and dated to 1.43–1.49 million years ago. The endocranial volume of the Mojokerto specimen is between 630 and 660 cc, approximately 70% of the adult cranial capacity in *Homo erectus* from this time period (Balzeau et al., 2005). The individual was most likely younger than 4 years of age at death and may have been as young as 0.5–1.5 years of age, although estimates of age range widely due to the lack of information on *Homo erectus* somatic growth (Coqueugniot et al., 2004). By 0.5–1.5 years of age, humans achieve an average of approximately 62% of their adult endocranial volume, while chimpanzees reach approximately 80% by the same age (Fig. 3.2 above). These values suggest an intermediate pattern of postnatal brain growth in *Homo erectus*, falling somewhere between *Homo sapiens*-like growth and non-human ape-like growth (O'Connell & DeSilva, 2013). This is supported by simulated annual growth rates of endocranial volume in *Homo erectus*, based on the Mojokerto specimen. These results suggest a rate of brain growth in *Homo erectus* that is on the lower end of the range of *Homo sapiens* growth from 0.5 to 1.5 years of age, falling below the human range after 2 years of age, and elevated above that of chimpanzees or gorillas for the entire period from 0.5 to 2 years of age (Cofran & DeSilva, 2015; Zollikofer & de León, 2010).

Rapid brain growth in the early postnatal period appears to have emerged at least 1.8 million years ago with *Homo erectus*. The rapid growth period is even more prolonged in later hominins, *Homo neanderthalensis* and *Homo sapiens*. In *Homo neanderthalensis*, this rate of growth was likely even greater than in *Homo sapiens*. This higher rate of growth resulted in a larger adult brain volume, despite a similar percentage of brain growth completed prenatally and a similar duration of brain growth (de León et al., 2008).

One feature of brain ontogeny that appears to be completely unique to *Homo sapiens* is *globularization* – developmental changes that result in a more rounded, globular braincase – that occurs in the perinatal, or immediate postnatal period. This postnatal change in brain shape is not seen in chimpanzees or in *Homo neanderthalensis*, likely only having evolved after *Homo sapiens* and *Homo neanderthalensis* diverged. It is achieved through parietal lobe expansion, expansion of posterior cranial fossa and basicranial flexion, which together result in a more rounded shape to the braincase (Neubauer et al., 2010). As this globularization takes place prior to complete ossification of the skull, while cranial sutures remain unfused, this change in the shape of the braincase is more likely the result of brain growth, suggesting possible subtle changes to the internal brain organization in early infancy that is unique to *Homo sapiens* (Neubauer et al., 2018).

3.3.2 Genetic Changes in the Human Lineage

There are many genes expressed in the brain that have undergone evolutionary modifications in the human lineage. Several of these genes, discussed here, have known functions that impact brain development and may contribute to the greater size and plasticity of the human brain.

The difference in brain size between humans and closely related non-human primates has been attributed to differences in the proliferative capacity of neural progenitors during prenatal development. A larger pool of progenitor cells can produce greater neuron numbers, resulting in a substantially larger brain (Rakic, 2000). *ARHGAP11B*, which arose through incomplete duplication of the ancestral *ARHGAP11A* approximately 5 million years ago, promotes the production of basal neural progenitors, which are responsible for the production of most cortical neurons (Florio et al., 2016). Similarly, *TBC1D3* has been duplicated in the human lineage, and there are multiple copies of this gene in humans, while there is only one copy in chimpanzees. Overexpression of this gene in mice increases the number of basal neural progenitor cells (Ju et al., 2016). Partial duplication of *NOTCH2* resulted in the human-specific *NOTCH2NLA*, *NOTCH2NLB*, and *NOTCH2NLC* genes, which are all highly expressed in human radial glial cells. Overexpression of human *NOTCH2NL* in mice results in downregulation of genes involved in neuronal differentiation, suggesting a possible delay in the differentiation of neural progenitor cells (Fiddes et al., 2018). Such delay would allow for more rounds of symmetric cell division and thus a larger pool of neural progenitors.

Not every alteration to the genome contributing to changes in brain size has been in protein-coding genes. The non-coding human accelerated *HARE5* gene acts as a regulatory enhancer of *FZD8*. In comparison to chimpanzee *HARE5*, human *HARE5*-enhanced expression of *FZD8* accelerates the neural progenitor cell cycle (Boyd et al., 2015). These genetic changes work together, promoting the production of neural progenitors, allowing them to divide more rapidly and for a longer period of time, producing a substantially larger pool of neural progenitors and therefore greater neuron numbers and a larger brain.

Genes contributing to neuronal and synaptic maturation have been altered over the course of human evolution as well. Of particular interest is the *SRGAP2* gene, which has undergone three human-specific duplications to form *SRGAP2B* (3.4 million years ago), *SRGAP2C* (2.4 million years ago), and *SRGAP2D* (1 million years ago) (Dennis et al., 2012). The ancestral form of *SRGAP2*, *SRGAP2A* is upregulated at the end of cortical migration and promotes synapse maturation. *SRGAP2C* inhibits the functions of *SRGAP2A*, delaying synapse maturation and extending spine production in excitatory and inhibitory cortical neurons (Charrier et al., 2012; Fossati et al., 2016). This prolongs the period of cortical synaptogenesis in humans, and may underlie the extreme plasticity of the human brain during infancy and beyond.

3.4 Causes and Consequences of Brain Plasticity in Infancy

In the last 6–7 million years, since the split from the last common ancestor of humans and the *Pan* genus, brain size has more than tripled over the course of human evolution. This large brain has allowed humans to exploit a unique adaptive niche, becoming highly cultural and intelligent. The evolution of this large brain required developmental shifts, including a smaller relative brain at birth and more postnatal growth and development compared to non-human primates and earlier hominins. While energetically costly, these shifts to accommodate a larger brain resulted in increased neuroplasticity, along with the increased potential for perturbations of development.

Human brain development is characterized by rapid growth prenatally and postnatally, as well as prolonged neuronal maturation and synaptic refinement. This is most extreme in regions of the brain devoted to higher level cognitive processes, such as areas of the prefrontal cortex. These features underlie the extreme plasticity of the human brain in infancy. The brains of human infants have the capacity to be highly responsive to the environment during the development of critical cognitive and social skills, such as joint attention and language, ultimately allowing the emergence of uniquely human cognition and behavior.

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Chapter 4
Childbirth and Infant Care in Early Human Ancestors: What the Bones Tell Us

Jeremy M. DeSilva

Humans are most closely related to chimpanzees and bonobos. Fossil and genetic evidence indicate the common ancestor we share with these African great apes lived ~6 million years ago (Brunet et al., 2002; Chen & Li, 2001). Despite our close relatedness, childbirth and infant rearing strategies are quite different in humans compared with our ape[1] cousins (Trevathan, 2015; Nowell & Kurki, 2020). In chimpanzees, a mother typically gives birth by herself at night after a short labor. The baby's head and shoulders have ample room progressing through a relatively spacious birth canal and the baby is typically born facing forward (occiput posterior). After birth, the mother exclusively carries the infant and does not let another chimpanzee—even a related one—near her infant for months (van Lawick-Goodall, 1967; Goodall, 1986). While juvenile apes can locomote on their own soon after birth, they rely heavily on their mothers for food and are not weaned until they are 4–8 years old.

In stark contrast, birth in humans follows a long labor and involves a corkscrewing motion of the neonatal head and shoulders through a relatively constrained birth canal. A human universal is the presence of helpers during birth, often in the form of experienced female midwives. After birth, alloparents abound and multiple caretakers assist in various ways to help raise the infant (Locke & Bogin, Chap. 6; Hrdy & Burkhart, Chap. 8, this volume). In traditional hunter-gatherer societies, human mothers wean their offspring around the age of 2–3 years old (Konner, 2010), significantly earlier than the weaning age in apes. In the pages that follow, I will

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[1] Humans are hominoids, a clade of tailless, large-bodied, fruit-eating primates that include gorillas, chimpanzees, bonobos, orangutans, gibbons, and siamangs. Hominoid is sometimes shorthanded to "ape." However, it is useful to have a word for us (human) and a word for nonhuman hominoids (ape), so throughout this paper I use the word "ape" as a substitute for nonhuman hominoids.

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investigate how the human fossil record and comparative primate behavior and skeletal anatomy inform our understanding of the timing and circumstances behind our unique childbirth mechanics and infant rearing strategies.

4.1 The Evolution of Human Birth and the Problem with the Obstetrical Dilemma

The evolution of human birth is so often framed around the *obstetrical dilemma* hypothesis (see Dunsworth, 2016, 2018; Dunsworth & Eccleston, 2015) that is necessary to start with this concept. The obstetrical dilemma is frequently pitched as a classic example of an evolutionary trade-off. In short, the human pelvis has altered its shape to maximize efficiency during bipedal travel. But the resulting reduction in the size of the birth canal makes birth more difficult and sometimes dangerous. It has been assumed that a more spacious birth canal would make birth easier and therefore selectively advantageous, but such a wide pelvis would compromise walking. Similarly, it has been assumed that a narrower pelvis would confer walking and running advantages but would make birth untenable. The outcome of this evolutionary trade-off is clear: women have been assumed to be less efficient walkers than men because of their wide pelvises shaped to permit the passage of large-brained, large-bodied infants. As brains increased in size during the Pleistocene, this evolutionary problem became exacerbated. The solution, it was hypothesized, was for humans to give birth more easily to less developed, more helpless infants.

It is an elegant idea, embraced by scholarly and popular (e.g., Harari, 2014) writings alike. But recent experimental and comparative data testing the assumptions of this hypothesis have revealed it to be a deeply flawed idea in need of either complete abandonment (e.g., Dunsworth, 2016, 2018) or significant modification.

Before I dive into the recent literature on this topic, however, it is noteworthy to point out how much the obstetrical dilemma—as originally conceived—was built upon off-hand remarks, rather than on rigorously scrutinized data and empirically derived predictions. The term “obstetrical dilemma” was first used by University of California, Berkeley anthropologist Sherwood Washburn in a *Scientific American* article titled “Tools and Human Evolution.” As the title would imply, Washburn (1960) spent much of the article discussing the relationship between technological advances and anatomical and behavioral changes throughout human evolution. We are, after all, a biocultural primate. On page 74, he wrote,

> In man adaptation to bipedal locomotion decreased the size of the bony birth-canal at the same time that the exigencies of tool use selected for larger brains. This obstetrical dilemma was solved by delivery of the fetus at a much earlier stage of development. But this was possible only because the mother, already bipedal and with hands free of locomotor necessities, could hold the helpless, immature infant….. The slow-moving mother, carrying the baby, could not hunt, and the combination of the woman’s obligation to care for slow-developing babies and the man’s occupation of hunting imposed a fundamental pattern on the social organization of the human species.

Thousands of peer-reviewed pages, written by dozens of scholars, have been devoted to just a part of one of the 25 paragraphs written in a popular science piece by Washburn. I wonder how much thought he actually gave to an idea that would come to be so influential in our field and would even help boost the evolutionary justification for the medicalization of childbirth (see Stone, 2016).

Nine years earlier, University of Pennsylvania anthropologist Wilton Krogman (1951) shared similar sentiments as Washburn's in an article called "Scars of Human Evolution," which also appeared in *Scientific American*. He wrote,

> We have expanded our brain case tremendously, and there can be no doubt that many of the obstetrical problems of Mrs. H. Sapiens are due to the combination of a narrower pelvis and a bigger head in the species. How long it will take to balance that ratio we have no idea. It seems reasonable to assume that the human head will not materially shrink in size, so the adjustment will have to be in the pelvis; *i.e.*, evolution should favor women with a broad, roomy pelvis.

The empirical basis for these observations can be traced to published work by Swiss anthropologist Adolph Schultz (1949) whose comparative study of dimorphism in the primate pelvis led him to conclude that the "widening of the female pelvis represents a vital adaptation to the requirements of parturition…." He noted that this was true in "monkeys as it is in man," though he also pointed out that the reduced anteroposterior dimension of the pelvic inlet was unique to humans.

Let's return to Washburn's original words and unpack the "obstetrical dilemma." Washburn began with the statement that, "In man adaptation to bipedal locomotion decreased the size of the bony birth-canal at the same time that the exigencies of tool use selected for larger brains."

The first part of this sentence—that a reduced bony birth-canal is associated with bipedal locomotion—is supported by fossil and comparative skeletal data. Some of the first changes related to bipedal locomotion happened in the pelvis, as evidenced by the 4.4 Ma *Ardipithecus ramidus* partial skeleton (Kozma et al., 2018; Lovejoy et al., 2009; White et al., 2015). These changes are even more obvious in the fossil pelvises from 2–3.6 Ma *Australopithecus* (Haile-Selassie et al., 2010; Lovejoy, 2005; Robinson, 1972). The second part of this sentence—that bipedal locomotion evolved concurrently with tool use and encephalization, an idea also promoted by Charles Darwin (1871)—is not consistent with the human fossil record. The earliest evidence for at least occasional terrestrial bipedal locomotion in our hominin ancestors goes back 6 million years (Pickford et al., 2002) and perhaps even earlier (Brunet et al., 2002), whereas evidence for habitual terrestrial bipedalism in the form of human-like footprints at Laetoli, Tanzania is 3.6 million years old (Day & Wickens, 1980). The earliest evidence for stone tools is between 2.6 million (Semaw et al. 2003) and 3.3 million years old (Harmand et al., 2015). However, the oldest fossil with a brain size substantially larger than the 450 cc averaged by *Australopithecus* is the 2.03 Ma KNM-ER 1470 *Homo* skull (Holloway et al., 2002; McDougall et al., 2012). Thus, with the evidence we currently have, there is temporal discordance between bipedalism, tool use, and encephalization.

Washburn writes next that, "This obstetrical dilemma was solved by delivery of the fetus at a much earlier stage of development." This is a major crux of the obstetrical dilemma—that humans are born prematurely and that explains their relative helplessness at birth. Portmann (1944) proposed that the early arrival of our infants resulted in an "extrauterine spring" in which development that happened in utero in other primates occurred outside the womb in humans. But is it true that human infants are born earlier than expected? Dunsworth et al. (2012) tested this prediction of the obstetrical dilemma and found that human gestation length is not shorter than expected for a primate of our size; it is slightly longer. Her team hypothesized that energetics, rather than constraints from the bony pelvis, drive the timing of mammalian birth, including humans, an idea termed the *energetic of gestation and fetal growth (EGG) hypothesis*. If human babies are not born prematurely, what explains the relative helplessness of our infants?

Infant mammals have often been dichotomized as *altricial* or *precocial* (terms derived from the avian literature [Portmann, 1939]). Altricial mammals are typically born hairless, eyes closed, and unable to locomote. Newborn bears or mice, for instance, are altricial. Alternatively, some newborns are alert and able to move immediately—or soon after—birth. These so-called precocial infants include seals, most bats, and artiodactyls. Primates fall into this latter category. They are born with a furry covering, eyes open, and with the ability to cling to their mothers soon after birth. The one exception, it has been said, are humans whose infants have been called "secondarily altricial" (Portmann, 1944).

While mammalian development is better treated as a continuum rather than existing within these discrete altricial or precocial categories, relative brain development—or what has been called the "advancement factor" (Sacher & Staffeldt, 1974)—appears to be an anatomical correlate to this developmental spectrum. The advancement factor is the percentage of adult brain volume grown by the time of the infant's birth. At the two extremes are bears and seals, animals in the carnivore family but with divergent strategies of infant development. Brown bear (*Ursus arctos*) infants are helpless at birth and possess only 1.7% of their adult brain volume at the birth, whereas harp seals (*Phoca groenlandia*) already have grown 88% of their adult brain volume and are able to swim alongside their mothers immediately after birth. In fact, mammals categorized as altricial have on average 15% of their adult brain volume present at the time of their birth whereas mammals categorized as precocial have on average 45%. Consistent with their precocial nature at birth, primates have an average advancement factor of 47% (DeSilva, 2016). Humans have an advancement factor of 28%, almost exactly between the altricial and precocial averages (DeSilva & Lesnik, 2006). It follows, then, that they are not easily categorized as precocial or altricial (Trevathan & Rosenberg, 2016).

However, the relationship between brain advancement factor and infant helplessness is complicated by how brains scale during development. There exists a strong linear relationship between the size of the brain at birth and the size of the adult brain in catarrhine primates (DeSilva & Lesnik, 2008). While humans are unusual in possessing large-brained and large-bodied infants compared with the size of the mother's body, human infants are born with a brain sized as one would predict given our average adult brain size. However, the slope of the line describing the relationship between adult and neonatal brain size in catarrhine primates is less than one

($m = 0.77$), meaning that as adult brain size increases in monkeys and apes, infant brain size is *proportionately* less, and necessarily so. The advancement factor of monkeys is around 50%, apes 40%, and modern humans 28% (DeSilva & Lesnik, 2008).

As human brain size increased throughout the Pleistocene, less and less of the adult brain volume would have been completed by birth, meaning that infants would have become more and more helpless even as their absolute brains increased (DeSilva, 2016). Today, while human babies are alert and responsive to facial expressions and various other stimuli in their environment, they remain relatively helpless and immobile and not only require considerable maternal care but benefit from the assistance of others in the group (Hrdy, 2009; Locke & Bogin, Chap. 6; Hrdy & Burkhart, Chap. 8, this volume). But this happens not because they are born early (they are not), but because of the scaling relationship between adult and neonatal brain size in primates and our relatively large brains.

Washburn's final observation about the "slow-moving mother" is similarly problematic. Data collected from modern human hunter-gatherers reveal that women cover an average of 6 miles a day (Marlowe, 2005). But do women cover these miles less efficiently than men? Warrener et al. (2015) tested this hypothesis and found that contrary to the predictions of the obstetrical dilemma, individuals with wider hips do not use more energy than those with narrower hips. In fact, Wall-Scheffler (2012) and Wall-Scheffler & Myers (2007) have repeatedly found that individuals—typically women—with wider hips are more efficient walkers when they are carrying objects. Furthermore, they experience less of an energetic cost when changing speeds. Thus, not only are there *not* costs to having wide hips, there appear to be biomechanical benefits when doing what people do when they travel: carry objects and alter their pace. In general, individuals (typically women) with mediolaterally wide hips also have more transverse plane rotation during walking which functionally increases stride length (Gruss et al., 2017; Wall-Scheffler & Myers, 2017; Whitcome et al., 2017). Thus, while the kinematics of walking differ between the average man and average woman, there is energetic equivalence.

Many of the assumptions generated from the obstetrical dilemma are predicated on the idea that humans have evolved mediolaterally narrow hips for efficient bipedal locomotion. But that assumption may also be in error (Fig. 4.1). Krogman (1951) referred to the "narrower" human pelvis, but only after pointing out that the major difference between our pelvis and that of other mammals was the lowering of the sacrum, such that "the sacrum now encroaches upon the pelvic cavity and narrows the birth canal that must pass the fetus along to life." In other words, Krogman did not emphasize the side-to-side narrowing of the human pelvis, but the front-to-back shortening of it. Similarly, Schultz (1949) remarked on the anteroposteriorly narrow pelvis in humans.

In fact, relative to body mass, humans do not have unusually narrow (side-to-side) pelvises at all. They have, more or less, the expected biiliac breadth, biacetabular breadth, and mediolateral width of the pelvic inlet for a primate of our size. The only side-to-side dimension in which humans have a difference of note from our primate cousins is in the wider bispinous breadth (Fig. 4.2). The limiting dimension

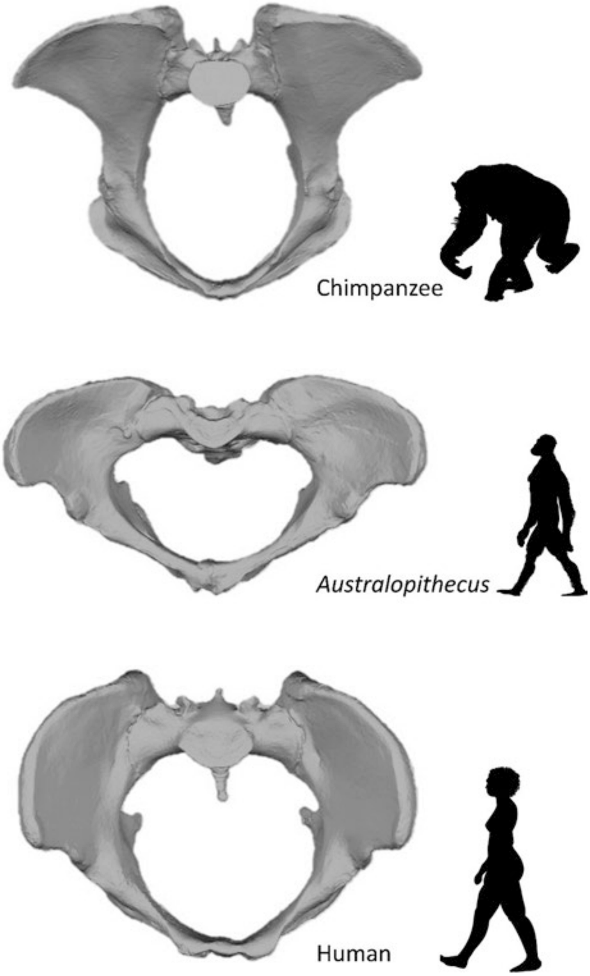

Fig. 4.1 Superior view of the pelvis in a female chimpanzee, Lucy (*Australopithecus afarensis*), and a modern human. These have not been scaled and reflect their relative size. Notice the front-to-back (anteroposteriorly) elongated birth canal in chimpanzees compared with the anteroposteriorly compressed pelvis of *Australopithecus* and modern humans. Also, notice that the side-to-side (mediolateral) width of the ilia is roughly the same in the three taxa

of the birth canal—and thus the narrowest dimension that an infant must pass through during parturition—is here: the mediolateral width of the midplane, or bispinous breadth. However, the bispinous breadth does not correlate in humans with biiliac breadth, meaning that this often-used anatomical correlate with the unfortunate but often used expression "childbearing hips" has little to do with the dimensions that would actually impact the birth process.

Humans, therefore, do not have narrow (side-to-side) hips. Nor have we ever (Rosenberg & DeSilva, 2017). The A.L. 288–1 "Lucy" pelvis from *Australopithecus*

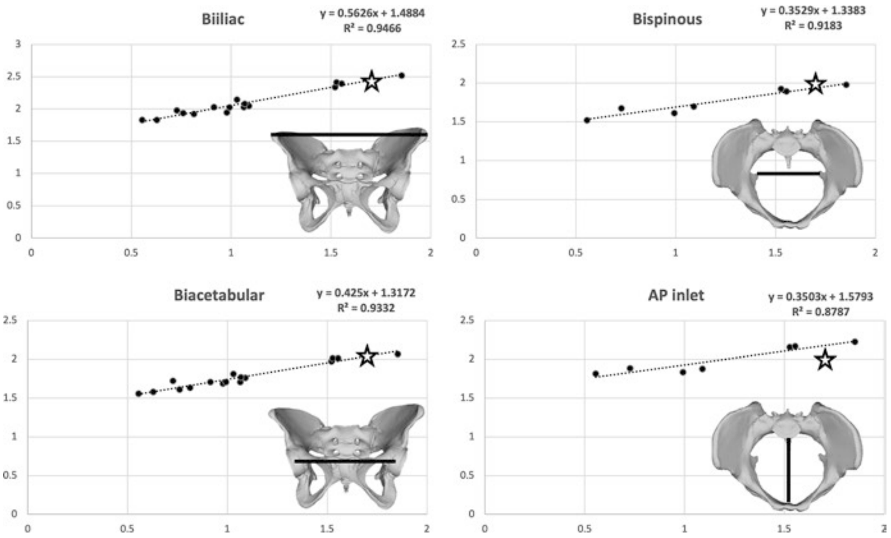

Fig. 4.2 Species averages plotted against average body mass (data from Schultz, 1949; Tague, 1995; Ward et al., 2018). Reduced major axis regression line is drawn through the data and the equation describing the line, along with the coefficient of determination (R^2), is above the graph. Notice that humans (star) have biiliac and biacetabular measurements near to the predict values for a primate of our size whereas the bispinous breadth is slightly larger than expected. Where humans differ, and therefore have a "narrow" pelvis is in the AP (anteroposterior) dimension of the pelvic inlet

afarensis is wide and well-adapted for bipedal locomotion (Fig. 4.1; Lovejoy, 1988). The dimension, then, that needs more consideration is the narrowing of the pelvis in the sagittal plane, where humans (and human ancestors) have evolved a reduced distance between the sacroiliac joint and the acetabulum, a presumed bipedal adaptation that lowers the center of mass and reduces bending forces through the ilium. It is here where future hypotheses testing the "obstetrical dilemma" should be generated (DeSilva et al., 2017).

While female gait kinematics are affected—but not compromised—by differences in pelvic shape, there remains the reality of maternal mortality. Washburn (1960), Krogman (1951), and Schultz (1949) never explicitly discussed the danger of childbirth and maternal mortality rates. However, for many, the "obstetrical dilemma" has come to encompass not just infant helplessness but the relative difficulty and sometimes danger of childbirth. Every woman who gives birth has her own unique experience—a product of many variables from fetal head size, shoulder width, pelvic dimensions, gestation length, and ligament relaxation to cranial molding, stress hormones, birth position, social support, and the advice and approach of the attending midwife or obstetrician. But it remains a fact that 300,000 women and nearly one million babies die annually in childbirth (WHO, 2019). For the mother, hemorrhage or infection are the primary causes. Countries where these death rates are the highest are usually the poorest and ones in which women have the fewest reproductive rights. Systemic institutional racism in the United States makes women of color three times more likely to die in childbirth than white women (Petersen et al., 2019).

Because just a slight increase in linear dimensions of the pelvis would have a marked increase in the area of the birth canal and volume of the fetal cranium deliverable (Epstein, 1973) and because such an increase would not compromise locomotion (Warrener et al., 2015, Warrener, 2017, but see Ruff, 1995, 2017), one may wonder why the pelvis is not more spacious.

This remains an open question. Some have hypothesized that the high rate of maternal mortality is a relatively recent phenomenon, rare in the archaeological record, exacerbated by a simple sugar diet that stunts pelvic growth while simultaneously leading to macrosomatic infants—a combination that could result in a higher frequency of cephalopelvic disproportion and birth complications (Wells, 2017; Wells et al., 2012). In a cross-sectional study of pelvic growth, Huseynov et al. (2016) identified developmental changes to the female pelvis in which the limiting dimensions of the birth canal—the anteroposterior length of the pelvic inlet and the width of the midplane—continue to grow through the age of 20 years. Countries—including ones with child bride practices—in which the average age of marriage is <20 years-old—have an average maternal mortality rate of 1 in every 200 live births, nearly eight times greater than the average maternal mortality in countries where the average marriage age is >20 years (DeSilva, 2021). Others have hypothesized that because a narrow pelvis is more efficient at dispersing body heat and *Homo sapiens* evolved in equatorial Africa, then the real obstetrical dilemma is a trade-off between safely birthing an infant and efficiently regulating body temperature (see Ruff, 1991; Gruss & Schmitt, 2015). Still, others have focused specifically on the bottleneck point of the human birth canal (bispinous breadth) and have hypothesized that widening this region would increase the risk of debilitating pelvic prolapse (Huseynov et al., 2016; Trevathan, 2015). These hypotheses—and others—will require rigorous scientific testing in the coming years.

4.2 What Was Birth Like in Our Ancestors?

Reconstructing birth evolution on the basis of fossil remains relies on our ability to identify osteological female hominins from their pelvic anatomy. This has proven to be difficult, as the standard forensic observations used to distinguish osteological male and female pelvises do not always translate to early hominin fossils. Early hominins, for instance, tend to have a wider sciatic notch than modern humans, making many fossils appear female on the basis of this one trait (Simpson et al., 2014). Taking this into consideration, many of the "female" fossil pelvises used to characterize birth evolution in early hominins have been identified by some scholars as male. "Lucy" (A.L. 288-1) is an osteological female to most scholars (e.g., Tague & Lovejoy, 1986, 1998) but male to another team (Häusler & Schmid, 1995). *Australopithecus africanus* pelves Sts 14 and Sts 65 are identified as female by some researchers (e.g., Berge & Goularas, 2010; Claxton et al., 2016) and osteological males by others (e.g., Gommery & Thackeray, 2006; Robinson, 1972; Häusler & Ruff, 2020). Later *Homo* pelvises are similarly contentious, with some identifying OH 28 and KNM-ER 1808 as osteological females (Walker & Ruff, 1993) and others as osteological males (McHenry, 1991; Simpson et al., 2008; Simpson et al., 2014). The BSN49/P29 pelvis is identified by Simpson et al. (2008, 2014) as a female *Homo erectus* while Ruff (2010) argues that the acetabulum is too small for this specimen to be from the genus *Homo* and instead hypothesized that it belonged to a robust *Australopithecus*. It seems the only pelvis in which researchers unanimously agree on the taxonomy and the osteological sex is the KNM-WT 15000 *Homo erectus* fossil. However, because it belonged to a juvenile male, its utility in reconstructing birth mechanics in early hominins is questionable despite admirable attempts (Walker & Ruff, 1993).

Furthermore, it is important to note that the pelvis is a thin, easily damaged, and distorted bone. Because of its fragility, fossil pelvic remains are rare and often fragmentary, requiring extensive reconstruction (e.g., Lovejoy et al., 2009 for the *Ardipithecus ramidus* pelvis). This fact has naturally led to different researchers reassembling these pelvic remains in slightly different ways, resulting in slightly different reconstructions. For example, despite its relative completeness, two reconstructions of the "Lucy" A.L. 288-1 pelvis (Häusler & Schmid, 1995; Tague & Lovejoy, 1986) differ enough to produce different dimensions of the birth canal. Despite these challenges, paleoanthropologists have pressed on and have been able to use the precious few pelvic remains thus far recovered to generalize birth mechanics throughout human evolution.

4.2.1 Birth in the Last Common Ancestor of Humans and African Great Apes

As our closest living ape relatives, chimpanzees are often used as a substitute for the last common ancestor we shared with them. That is not to say that chimpanzees are time-machines—they, too, have evolved. But it remains instructive to compare birth in humans to the equivalent event in chimpanzees. Chimpanzee gestation averages 32 weeks compared with the average of 39–40 weeks in modern humans (Dunsworth et al., 2012). In the wild, chimpanzees typically give birth at night, in a tree, alone. Human birth, while variable, is typically a social event in which experienced female midwives assist with the delivery (see Trevathan, 1987, 1988, 2010). While wild chimpanzee births are rarely observed, researchers have witnessed and characterized births in captivity. Labor averages 2 h and the baby is usually born facing forward (occiput posterior), though occiput anterior births have also been observed (Elder & Yerkes, 1936; Hirata et al., 2011). *Cephalopelvic indices* (ratio of the fetal head to birth canal dimensions) are low in chimpanzees and there is no evidence for the kind of fetal rotation that characterizes most human births.

Thus, compared with chimpanzees, human birth differs in three important ways: (1) human cephalopelvic indices are much higher than in chimpanzees; (2) human infants typically rotate through the birth canal and are more often born occiput anterior; and (3) human birth is a social event. Biological anthropologists have sought to identify the evolutionary timing and causes of these three distinct aspects of human birth. But that may not be necessary.

Our *other* closest living ape relative, the other member of the genus *Pan*, is the bonobo (*Pan paniscus*). While cephalopelvic indices in the bonobo are similar to that found in chimpanzees and while the birth mechanism appears to be similar between the two ape species, the social nature of these animals differs tremendously. Bonobos are less aggressive than chimpanzees and less territorial. They are curious, cooperative, tolerant, and trusting (see Hare & Woods, 2020). Researchers have observed both captive and wild bonobo females present during the birth of an infant (Demuru et al., 2018; Douglas, 2014). While still unclear, it is possible that the last common ancestor of humans, chimpanzees, and bonobos had social assistance during birth and that chimpanzees are the species that have undergone an evolutionary change in which a once social ancestor became more wary and cautious during delivery, leading eventually to solitary birthing practices. If this proves to be true, then the presence of helpers during birth may have *preceded* the onset of *rotational birth* in humans. Instead of rotational birth leading to the necessity of helpers during delivery, the presence of these helpers made rotational birth a feasible option as the pelvis changed shaped in early bipedal hominins.

The emphasis here is on rotational birth because humans are also not unique in having a high cephalopelvic index. This is also the case for many monkey species (Moffett, 2017; Ponce de León & Zollikofer, 2016; Schultz, 1949; Stoller, 1995; Trevathan, 2015), and it is possible that birth in the last common ancestor of the African apes had a more challenging birth than modern great apes do. There is no fossil pelvis known from the time of the last common ancestor of the African great apes (~6–9 million years ago). However, a recently described pelvis from a ~10 million-year-old ape from Hungary known as *Rudapithecus* has a morphology similar in many ways to that found in hylobatids (gibbons and siamangs) (Ward et al., 2019). If *Rudapithecus* is related to the last common ancestor of the African great apes, then both humans and the African great apes would have experienced divergent pelvic evolution from something more hylobatid-like. Interestingly, hylobatids have a higher cephalopelvic index than other apes (Moffett, 2017; Zollikofer et al., 2017). But whether this means that the last common ancestor of humans and chimpanzees had a high cephalopelvic index or a low one and whether the birth was social or not, only humans experience rotational birth. The question, then, is when did that evolve? And why?

4.2.2 Birth in Early Hominins *(Ardipithecus and Australopithecus)*

While a reconstruction of birth in *Ardipithecus ramidus* has not yet been published, images of the reconstructed pelvis of the ARA-VP-6/500 skeleton (see Fig. 4 in Hogervorst & Vereecke, 2014) indicate that "Ardi" had a more ape-like anteroposteriorly expanded birth canal and would have birthed a small-brained, small-bodied (DeSilva, 2011) infant through the birth canal without any rotation. This scenario changes with the evolution of *Australopithecus*.

In all non-human primates, the long axis of the neonatal head (occipitofrontal) aligns with the widest part of the birth canal (anteroposterior) and birth proceeds without the infant having to rotate. However, this is not the case with humans, whose infants rotate as they descend into the birth canal and meet the pelvic brim to align the occipitofrontal axis of the skull with the mediolateral, or transverse plane. Thus, the reduction of the AP inlet—a consequence of the reduction of the distance between the sacroiliac and hip joints—necessarily changes how a baby enters the birth canal. This shape change in the hominin pelvis is present in fossils of *Australopithecus*, including A.L. 288-1 (Lucy, *A. afarensis*), Sts 14 and Sts 65 (*A. africanus*), and MH2 (*A. sediba*) (Claxton et al., 2016). Thus, a form of rotational birth can be traced back to at least 3.18 million years ago—the age of the Lucy partial skeleton (Fig. 4.3).

Tague and Lovejoy (1986) hypothesized that Lucy's infant would have entered the birth canal with its head transversely oriented and carried on through the birth canal in this manner, its head aligned through the platypelloid inlet and midplane, before it tilted its head under the pubic symphysis in a presentation known as asynclitic birth. Tague and Lovejoy (1986) relied on the geometry of the A.L. 288-1 pelvis and a chimpanzee neonatal cranium as a fill-in for a baby *Australopithecus* to reconstruct this form of birth, which would not have required helpers or midwives. However, Trevathan and Rosenberg (2000) pointed out that Tague and Lovejoy (1986) and others who have attempted birth reconstructions from fossil remains did not consider a key variable that influences, and sometimes impinges on, the birth process: shoulders.

In 2017, we incorporated estimates of neonatal shoulder breadth in an attempt at a new reconstruction of birth in Lucy and found that because the head and shoulders are orthogonal, rotation probably would have to continue beyond the inlet during delivery in *A. afarensis* (Fig. 4.4; DeSilva et al., 2017). In fact, the infant would have to corkscrew through the inlet and the midplane, nearly completing a human-like rotation. On the basis of this reconstruction, we hypothesized that the infant was born close enough to occiput anterior, it would have been selectively advantageous for *A. afarensis* to have helpers. Thus, as Rosenberg and Trevathan have suggested, midwifery is indeed the oldest human profession (Rosenberg, 1992; Rosenberg & Trevathan, 1995, 2001, 2002; Trevathan, 1987).

While birth reconstructions in other hominins have been contentious, other scholars have also hypothesized that *Australopithecus* experienced some form of rotational birth (Berge et al., 1984; Berge & Goularas, 2010; Häusler & Schmid, 1995). Interestingly, using the same approach that we used on the Lucy pelvis on a later *Australopithecus*—*A. sediba*—we found that the geometry of the pelvis and the size of the neonate cranium and shoulders was such that full rotation was not required and that birth may have been more similar to the asynclitic form Tague and Lovejoy (1986) hypothesized for Lucy (Laudicina et al., 2019). While rotational birth was still possible—and perhaps even likely—our findings indicated that there was enough variation in pelvic form in *Australopithecus* that it would be a mistake to assume that

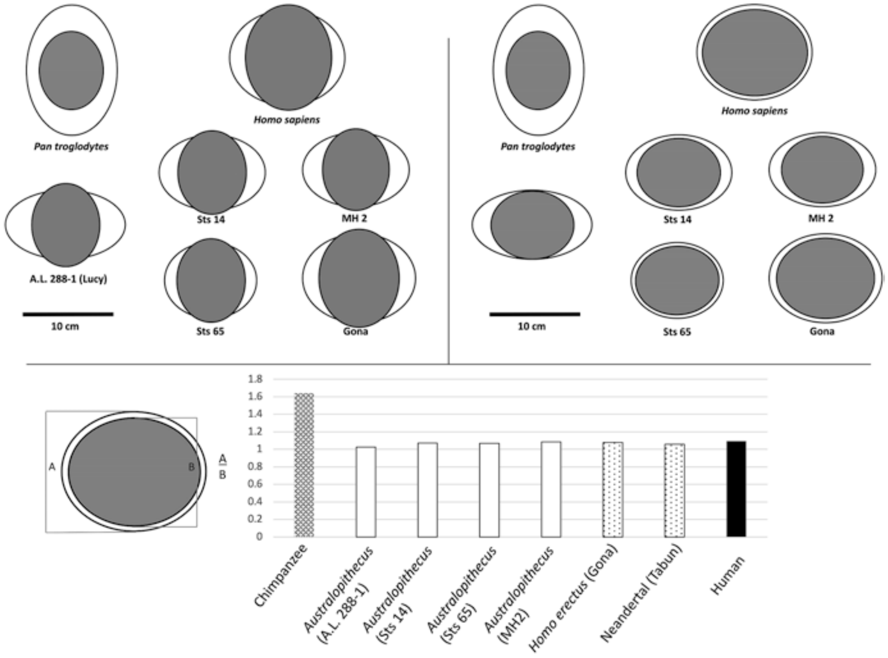

Fig. 4.3 Colored ovals represent the size of the neonatal skull and the black halo represents the size of the average female pelvic inlet in chimpanzees (*Pan troglodytes*), humans (*Homo sapiens*), and fossil hominins (accession numbers listed below each). Notice that the chimpanzee neonatal head fits the pelvic inlet in an anteroposterior orientation. However, a human or ancient hominin neonate could not pass its head into the birth canal in this orientation (left circles). To the right are the same representations; however, the human and ancient hominin neonatal crania have been rotated so that they enter the birth canal transversely. Thus, the beginnings of human rotational birth are at least 3.2 million-years-old. Bottom: cephalopelvic index is reported here as a ratio of the anteroposterior length of the pelvic brim to the biparietal breadth of the neonatal cranium. Notice that this ratio has remained relatively unchanged for the last 3 million years, implying a tight correlation between brain size and this dimension of the female pelvis throughout human evolution

every species in the genus, or every individual in the species, gave birth in the same way (Laudicina et al., 2019). Of course, that is true for humans as well, who exhibit considerable variation in delivery presentations (Walrath et al., 2003).

The only adult pelvis of an early member of our own genus *Homo* complete enough to infer the birth mechanism is from a female *H. erectus* pelvis recovered in the Gona region of Ethiopia (Simpson et al., 2008). It is *platypelloid*, like some pelvises from *Australopithecus*. However, it also is anteroposteriorly expanded relative to earlier hominin pelvises. Interestingly, its anteroposterior expansion is such that it is 8% larger than the biparietal breadth of a hypothetical newborn—the same as what is found in *Australopithecus* (calculated from adult cranial capacity; see DeSilva & Lesnik, 2008). In fact, there is remarkable conservation of female pelvis anteroposterior inlet breadth:neonatal biparietal width proportions from *Australopithecus* through to modern-day humans. These data are consistent with

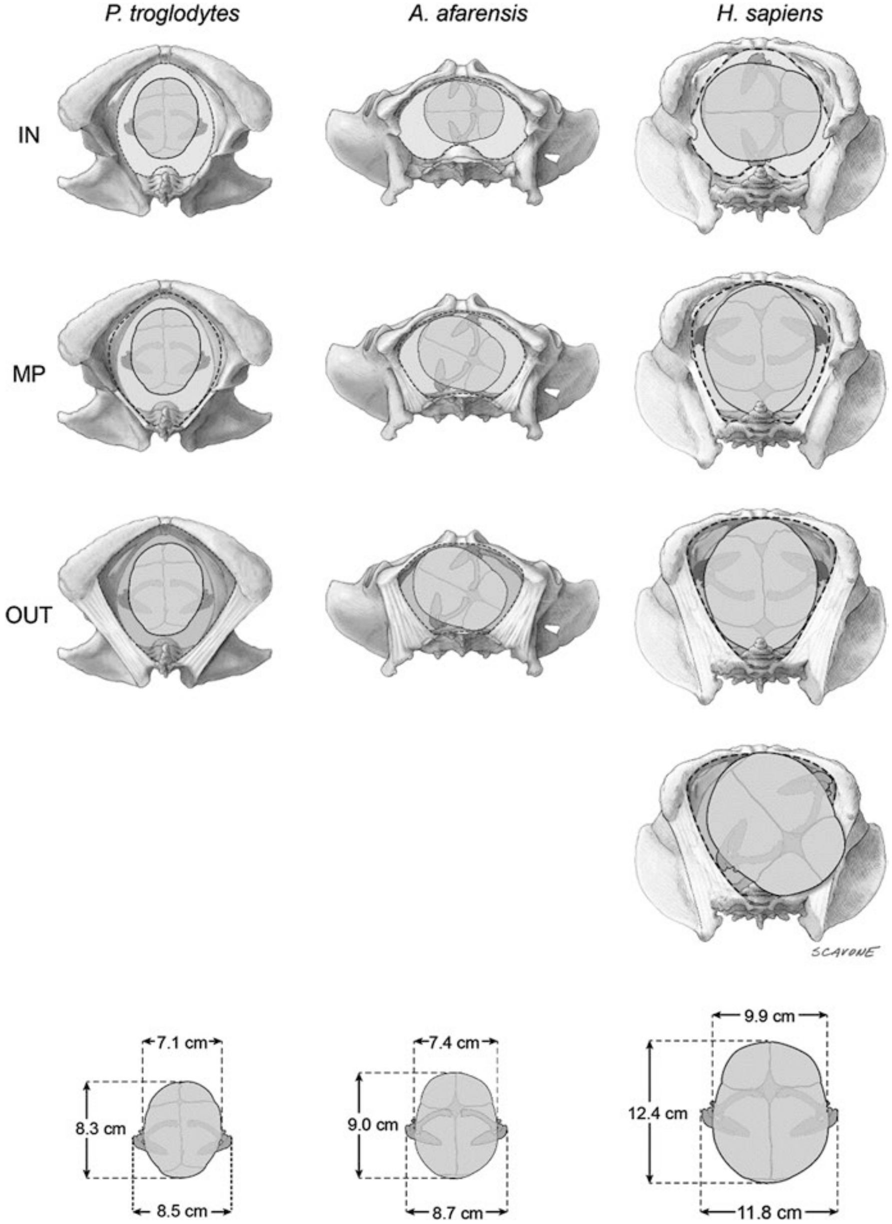

Fig. 4.4 Birth in chimpanzees (far left) is a relatively simple process in which the neonatal cranium passes unobscured through the inlet (IN), midplane (MP), and outlet (OUT) without rotation. In humans (far right), the neonate rotates, and its head enters the birth canal obliquely or transversely (top). At the midplane, the head rotates again to align the narrow biparietal breadth with the narrow bispinous width. The head is in occiput anterior position. A final twist is needed (bottom) to pass the shoulders under the pubis. Middle: In *Australopithecus afarensis*, the neonate must have rotated and entered the birth canal transversely. However, the wide shoulders (biacromial breadth) required additional rotation at the midplane and outlet such that the infant almost presented as occiput anterior and likely required helpers during delivery. Drawing courtesy of William Scavone

recent findings for intraspecific covariation between cranial capacity and pelvic dimensions in modern women (Fischer & Mitteroecker, 2015) and suggest tight selective control over the anteroposterior dimensions of the pelvic inlet. This trend continues through Neandertals, whose birth mechanism has been reconstructed as either human-like (Ponce de León et al., 2008) or non-rotational (Weaver & Hublin, 2009). More complete female Neandertal fossil pelvises are sorely needed to resolve this question.

4.3 Brain Development in Early Hominins

Humans have extraordinarily large brains for a mammal of our size. The human fossil record documents brain enlargement from early hominins with brains no larger than a modern chimpanzee, through *Australopithecus* (20% increase in brain volume), to *Homo* in which brains evolved from an average of 500 cc to around 1400 cc (Fig. 4.5; Wilder & Semendeferi, Chap. 3, this volume). Brain evolution, however, was not linear and progressive, as small-brained hominins *H. floresiensis* and *H. naledi* persisted late into the Pleistocene (Falk et al., 2005; Holloway et al., 2018) and human brains today are, on average, 15% smaller than they were in our late Pleistocene ancestors (Hawks, 2011). Nonetheless, compared with our closest living ape relatives, humans have brains that are over three times larger in volume.

Developmentally, it is known that humans grow their brains for a longer period of time and grow their brains at a faster rate (Leigh, 2004; Wilder & Semendeferi, Chap. 3, this volume). In other words, humans add more brain tissue per year for more years than chimpanzees do. But did this evolutionary change happen in lockstep? The answer appears to be no.

Hominin fossils are rare; even rarer are fossils of juveniles whose thin, fragile bones infrequently preserve. However, four early hominin juvenile crania help piece together brain growth and development in our early ancestors. There are two >3 million-year-old juvenile crania from *Australopithecus afarensis*: A.L. 333–105 and the Dikika Child (Alemseged et al., 2006). Both individuals died at the approximate age of 2 years, 5 months (Gunz et al., 2020). The Taung Child is the first *Australopithecus* fossil ever discovered (Dart, 1925) and represents a roughly 4-year-old of the about 2.5 million-year-old *A. africanus* (Lacruz et al., 2005). Finally, there is a young *Homo erectus* from the ~1.5 million-year-old site of Mojokerto in Java, Indonesia representing a roughly 1-year-old individual (Coqueugniot et al., 2004; Cofran & DeSilva, 2015).

Gunz et al.'s (2020) virtual reconstruction of the Dikika Child's cranium yielded a cranial capacity of 275 ml, while the A.L. 333-105 specimen is a slightly larger 310–317 ml. Compared with the average adult *A. afarensis* brain, Gunz et al. (2020) found that *A. afarensis* juveniles had completed between 62 and 70% of their brain growth by the age of 2 years and 5 months. Chimpanzees of this developmental age already have 90% of their adult brain growth complete. Thus, *A. afarensis* appears to have grown their brains more slowly than modern apes do, more in line with the

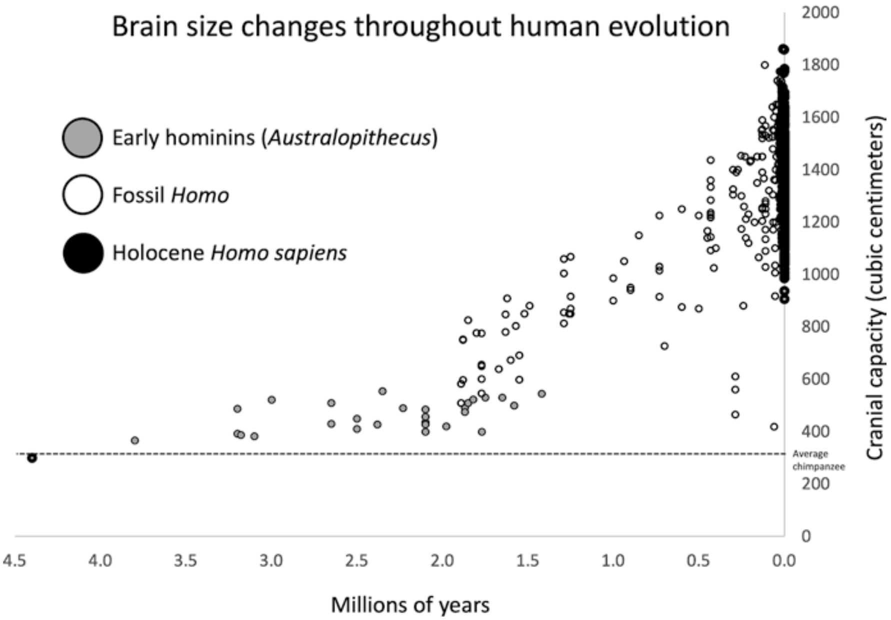

Fig. 4.5 Brain volume changes throughout human evolution. Each dot represents an individual fossil. In gray are fossils belonging to early hominins *Australopithecus* (to the far left is *Ardipithecus*). Notice that *Australopithecus* possessed brains that were ~20% larger than the average chimpanzee (shown as the bottom dotted line). Around 2.0 million years ago, brains began to enlarge in the genus *Homo* (white dots) and continued to enlarge throughout the Pleistocene. However, not all *Homo* taxa were encephalized. The four dots in the bottom right corner represent *H. naledi* and *H. floresiensis*, small-brained, late-occurring members of our genus

developmental pattern of modern humans (Fig. 4.6). In order to achieve the adult brain size of ~450 ml, *A. afarensis* juveniles must have grown their brains for a longer period of time, implying that they were reliant on adult caretakers for longer and may have been buffered against predation at this vulnerable time in their lives by parents and alloparents alike (Gunz et al., 2020).

Interestingly, the South African australopith *A. africanus* appears to have taken a different developmental strategy and was more ape-like, growing its brain more rapidly and achieving adult brain capacity earlier than *A. afarensis* (see Cofran, 2019; McCarthy & Zimel, 2020). Brains are energetically expensive to grow, especially in juveniles (e.g., Kuzawa et al., 2014). *A. afarensis* may have evolved prolonged brain growth not only because it allowed the juveniles to learn for longer, but because it spread the energetic cost of encephalization over a longer period of time. In other words, even though *A. afarensis* had larger brains than modern apes, they added less brain tissue per year and therefore allocated less energy to brain growth annually (Cofran, 2019), because they grew them for longer. This changed with *Homo erectus*. The Mojokerto child had grown ~70% of its adult brain growth by the time of its death (Leigh, 2006; O'Connell & DeSilva, 2013; but see Coqueugniot et al., 2004). But to achieve this size from birth and to continue to grow the brain to

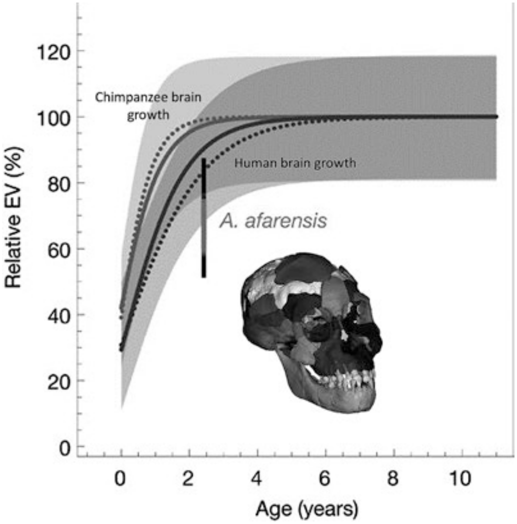

Fig. 4.6 Brain development in humans (bottom labeled), chimpanzees (top labeled), and *Australopithecus afarensis* (vertical line labeled) as represented by the Dikika Child (virtual reconstruction of fossil shown). Notice that the percentage of adult brain size is achieved rapidly in chimpanzees such that the top dotted line is near 100% by the age of ~3 years-old. In human, however, adult brain size is not achieved until ~7 years of age. Even though *Australopithecus* had small brains, they grew them slowly and had only reached ~70% of adult brain size by the age of 2 years and 5 months (the age at death of the Dikika child and another fossil, A.L. 333-105). Such slowed brain development implies the presence of committed caretakers for a longer period of time in *Australopithecus* than in modern apes

the adult volume of *H. erectus*, considerably more energy would be required (Cofran & DeSilva, 2015). This increased energetic burden on female *H. erectus* could be mitigated through food sharing, expansion of dietary breadth, and cooking.

4.4 Weaning Age in Early Hominins

Compared with our ape relatives, humans are characterized by an extended life history. We have a longer gestation, longer childhoods, and longer lifespans. We grow our brains for a longer period of time, take longer to erupt our permanent teeth, and take many more years to grow to our full body size. The exception to this general trend is weaning time. While apes nurse their infants for 4–8 years (Knott, 2001), humans buck the general trend of having an elongated life history by wean *earlier* than other apes. Modern human hunter-gatherers average a weaning age of 2–3 years (Locke & Bogin, Chap. 6; Hrdy & Burkhart, Chap. 8, this volume).

While nursing an infant, an ape mother does not acquire enough energy to simultaneously gestate another baby—a concept known as lactational amenorrhea. However, at the cessation of nursing, ovulation resumes. If humans wean earlier, it means that we can—technically—have more offspring than a non-human ape. But when did this demographic shift happen in our evolutionary history? Some have argued early on, at the origins of the lineage (Lovejoy, 1981, 2009). Furthermore, a weaned 2–3-year-old human is not independent and requires care from multiple members of the group. Thus, understanding the weaning age has implications for reconstructing the social structure of early humans and for identifying the timing and circumstances behind the evolution of humans as cooperative breeders (Hrdy, 2009; Locke & Bogin, Chap. 6; Hrdy & Burkhart, Chap. 8, this volume). But identifying weaning age from fossils has been challenging (see Smith, 2013, 2018).

Aiello et al. (1991) examined tooth wear on hominin fossils in which the first permanent molar had erupted. These included LH 2, a 3.6 million-year-old mandible from *Australopithecus afarensis* and Taung Child, a 2.5 million-year-old fossil from *Australopithecus africanus*. They noticed that the deciduous molars on the LH 2 specimen were relatively unworn, similar to the condition of a nursing great ape of the same developmental age. The Taung Child, however, had very worn deciduous molars, which could be interpreted as evidence that this young hominin had been weaned for some time and had relied on solid foods that eroded its enamel. Similar wear of the deciduous molars can be found on other juvenile *A. africanus* fossils Sts 24 and StW 59 and on the taxonomically ambiguous StW 151. Smith (2018) cautioned, however, that the introduction of solids does not correspond to tooth wear in chimpanzees. Individual variation, differences in diet and environment, and even dental developmental schedules could impact the results and render a simple tooth-wear-to-weaning conversion unreliable. The solution, it turns out, can be found in isotopes.

Smith et al. (2017) demonstrated that the concentration of barium accurately tracks the onset of nursing and the introduction of solids into the diet of infants in both macaques and orangutans. This approach—along with the quantification of calcium and lithium isotopes—has permitted researchers to characterize weaning behavior in early hominins. Thus far, all of the examined hominins introduced solids early, a pattern more similar to what is found in modern humans than the extended nursing practiced by modern apes. Fossils from *Australopithecus africanus* (Joannes-Boyau et al., 2019; Tacail et al., 2019) and *Paranthropus robustus* (Tacail et al., 2019) suggest that these hominins nursed for only their first year of life before being introduced to solids. Barium levels in the teeth of Neanderthal infants (Austin et al., 2013; Smith et al., 2018) demonstrate that solids were introduced by ~2.5 years of age, similar to weaning times in modern human hunter-gatherers. These data are consistent with a shorter, more human-like, interbirth interval in fossil hominins, a reproductive strategy made possible by the presence of alloparents.

4.5 Conclusion

The job of a paleoanthropologist is to squeeze as much information out of rare fossils as reliably possible to help reconstruct the evolutionary history of the human lineage. As this chapter hopefully communicates, fossil pelvises and juvenile skulls are rare, but clever techniques have been employed to infer birth practices, brain development, and even weaning age in our ancestors. The evidence we currently have reveals that pelvic changes associated with bipedal locomotion changed how we give birth early in our evolutionary history making it likely that *Australopithecus* females assisted one another during delivery as far back as 3.2 million years ago.

This assistance continued after delivery (Locke & Bogin, Chap. 6; Hrdy & Burkart, Chap. 8, this volume). Bipedalism changes the orientation of the body in hominins such that an infant cannot simply ride on its mother's back as happens in chimpanzees. An early hominin mother needing to forage or to climb a tree for food or safety would benefit from the help of others in the group, making alloparenting and shared parental care part of the behavioral repertoire of Plio-Pleistocene hominins (see DeSilva, 2011; Stutz, 2014). Changes made possible by the presence of alloparents—detectable in the skulls and teeth of our ancestors—are slowed brain growth and early weaning. Thus, the "it takes a village" adage has deep and ancient roots back to the days of *Australopithecus* and continues through to this day.

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Chapter 5
Infant Mortality

Hannah McDowell and Anthony A. Volk

"No parent should have to bury a child" (Guirgis, 2006, p. 9) is a common refrain of lament and agony upon the loss of a child. Regrettably, the history of infancy is, in fact, a history of parents having to do just this, with alarming frequency (Volk, 2011). Roughly one-quarter of infants born in evolutionary and historical contexts failed to survive their first year of life (Volk & Atkinson, 2013). This staggering reality was a persistent economic and emotional burden to parents (Hanawalt, 1995). Far from being a mundane event, this loss had a tremendous impact on parents, and one can find many examples of the "searing grief" that parents experienced (Heywood, 2018, p. 70). Upon losing his 8-month-old daughter, Martin Luther wrote, "I so lamented her death that I was exquisitely sick, my heart rendered soft and weak; never had I thought that a father's heart could be so broken for their children's sake." (Heywood, 2018, p. 70). Infant mortality was, therefore, a sadly regular event that left an important impact on parents throughout human history.

It also resulted in significant evolutionary pressures on humans, influencing shifts in parenting, pair-bonding, maturation, and intelligence whose impact rival any other evolutionary pressures such as mating or violence (Volk & Atkinson, 2008). The tremendous impact of infant mortality can also be seen in a range of modern responses ranging from mental health to demographic fertility changes (Alburez-Gutierrez et al., 2019). Our chapter aims to review the evidence regarding infant mortality from an evolutionary perspective before turning to modern infant mortality. In both cases, we will discuss the causes and consequences of infant mortality as we review what might well be the most important achievement in our species history: a massive, 50- to 100-fold decrease in the mortality rate of many modern infants.

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5.1 Evolutionary and Historical Mortality Rates

5.1.1 Defining and Measuring Infant Mortality

To begin with, it is important to define infant mortality. While infancy is often extended to refer to development up to the second year of life, infant mortality statistics generally focus on mortality up to the end of the first year of life (Mathews et al., 2015). The infant mortality rate (IMR) is the probability of an infant dying before it is 366 days old. This 365-day period represents the riskiest period of mortality in early life (Lawn et al., 2014). It includes neonatal mortality but excludes prenatal mortality.

Infant and child mortality would be best examined using direct paleodemographic archaeological data (Konigsberg & Frankenberg, 1994; Lewis, 2018; Milner et al., 2000; DeSilva, Chap. 4, this volume). Such data would allow researchers to make definitive claims regarding the intricate patterns of infant and child mortality rates of our Paleolithic hunter-gatherer ancestors. However, unfortunately, there are not enough data in these areas to make such definitive claims, in part, because such archaeological data are generally rare (Milner et al., 2000). More specifically, however, infant archaeological remains are particularly rare due to their fragility and, thus, lack of preservation (Lewis, 2018).

Therefore, in order to discuss and research infant and child mortality rates, we draw upon four separate proxies: twentieth-century hunter-gatherer IMR, historical records of IMR, agriculturalist IMR, and primate IMR. Some concerns exist with each of these populations. However, a general concern is that, as compared to adult deaths, infant deaths tend to attract less general attention and leave less tangible remains or records. Our data are thus, if anything, likely to be skewed toward demonstrating lower mortality rates than existed in the past. With that important caveat in mind, we turn to the study of hunter-gatherer IMR.

5.1.2 Hunter-Gatherer IMR

Striking similarities between hunter-gatherer populations have been highlighted, specifically in population demographics (Blurton-Jones et al., 2002; Foley, 1995; Konner, 1977; Marlowe, 2010). Therefore, data presented will be a combination of modern hunter-gatherer populations and the limited existing Paleolithic data (e.g., Snow, 1948). Estimates of ancestral infant and child mortality rates in hunter-gatherer cultures will be provided through such combination. It should be noted that the modern hunter-gatherer societies from where the data are drawn are highly marginalized, leading the data to represent only one potential environment that was present in the EEA (Lee & Daly, 1999). It is reasonable to have some concern that such marginalization could contribute to increased reports of IMR. Taking such concerns into account, we have applied two solutions: first, our data have been pulled from diverse environments, and second, a hunter-gatherer population that lived in a resource-rich environment has served as a checkpoint (Indian Knoll; Johnston & Snow, 2005).

The average IMR (see Table 5.1) was typically distributed around a mean of 26.8% (*SD* = 6.9%; min = 14%, max = 40.5%; Volk & Atkinson, 2013). These results indicate that levels of infant mortality were consistently high among modern hunter-gatherer populations. This sample most strikingly demonstrates that among modern hunter-gatherers, the average infant had a greater than one in four chance of dying before their first birthday. Surprisingly, these rates hold even for the hunter-gatherer population that lived in an environment rich in resources (Indian Knoll, 30%; Johnston & Snow, 2005, as cited in Volk & Atkinson, 2013). Thus, there is a significant degree of agreement in infant mortality rates in modern hunter-gather populations. But what about in actual historic populations?

5.1.3 Historic IMR

While hunter-gatherer populations are likely to be the best approximations of how humans lived for most of our species' history, it is also worth noting that human evolution did not stop 10,000 years ago. There is some evidence that new

Table 5.1 Hunter–gatherer infant mortality rates (IMR)

Culture	IMR	Source
!Kung	20.2%	Howell (1979) and Hewlett (1991)
Aborigines	28%	Dugdale (1980)
Ache	21%	Hewlett (1991) and Hill and Hurtado (1989)
Agta	34.2%	Headland (1989)
Aka	20%	Hewlett (1991)
Asmat	30%+	Van Arsdale (1978)
Batak	28.5%	Eder (1987) and Hewlett (1991)
Efe	14%	Bailey and Peacock (1988) and Hewlett (1991)
Hadza	21.0%	Blurton-Jones et al. (2002)
Hiwi	24.5%	Hill et al. (2007)
Indian Knoll (~2500 B.C.)	30%	Johnston and Snow (2005) and Snow (1948)
Inuit	20%	Malaurie et al. (1952)
Kutchin	17%	Roth (1981)
Mbuti	33%	Hewlett (1991)
Pumé	34.6%	Kramer and Greaves (2007)
Semang	40.5%	Murdock (1934)
N	15	
Mean	26.8%	

adaptations may have arisen during this time period, such as adults' ability to digest lactose (Cochran & Harpending, 2009; Irons, 1998). Thus, rather than serving simply as proxies for previous populations, relatively recent historical data offer us actual data from the human EEA. As with paleoarchaeological data, death records and written life histories are relatively scant in comparison to their adult counterparts (Konigsberg & Frankenberg, 1994; Rawson, 2003; Walker et al. 1988). This is due to the more rapid decay of children's smaller physical remains and the lower frequency of elaborate infant burials, death records, and written life histories (Lewis, 2007). Therefore, the historical infant and child mortality rates we present should be viewed as conservative estimates that generally err toward underestimating actual historical rates.

The average historical IMR (see Table 5.2) from over 43 historical cultures was normally distributed around a $M = 26.9\%$ ($SD = 4.8\%$; min = 17%, max = 40%; Volk & Atkinson, 2013). This is a remarkably convergent average, not only with respect to the previously discussed hunter-gatherer average IMR (see Table 5.1), but also across the vast swath of historical time periods, cultures, and geographical locations that the historical data represent. From the pre-Columbian Americas to Ancient Rome, to medieval Japan, to the European Renaissance, just over a quarter of infants died before their first birthdays.

It appears that regardless of whether we are using modern proxies (hunter-gatherers) or actual historical data, human infants faced daunting odds of dying in their first year. Obviously, if an individual died during their first year of life their evolutionary contributions would be zero. This makes infancy perhaps the most intensely selected year of human life (Williams, 1957; Jones, 2009). Quite simply, there is no other period in human life that matches the intensity of cost (i.e., life or death) at the same elevated level of ubiquity (25+%) – not adolescence, not mating, not childbirth, not warfare (Volk & Atkinson, 2008). For humans, the first year of life was perhaps the most critical period of life. How do these pressures compare with non-human primate IMR?

5.1.4 Non-human Primate IMR

The third set of data presented (Table 5.3) offers infant mortality rates among non-human primates. As with our modern hunter-gatherer data, it is important to note that the IMR of other primates can be seriously compromised by modern human influences (Köndgen et al., 2008). We therefore focus our primate data in general and for great apes in particular on stable populations that have not been seriously influenced by modern human activities such as poaching, zooanthropic disease transmission, and/or habitat loss.

Within the primate data, infant mortality rates were defined as the risk of mortality from birth to 1 year of age (Volk & Atkinson, 2013). Not surprisingly, there is some variation among different primate species IMR. Neanderthals, who are humans' closest extinct relatives (Green et al., 2006), had a strikingly similar

Table 5.2 Historical civilized infant mortality rates and child mortality rates

Time	Culture	IMR	Source
500–300 B.C.	Greece	25–35%	Golden (1990)
400 B.C.–550 A.D.	Nasca (Peru)	34.7%	Drusini et al. (2001
400–200 B.C.	Spain	25%	Alesan et al. (1999)
200 B.C.–200 A.D.	Rome	30%	Rawson (2003)
0 A.D.	Roman Egypt	33%	Bagnall and Frier (1994)
200–400 A.D.	Rome	30%	Todman (2007)
300–550 A.D.	Teotihuacan	28.8%	Storey (1985)
550–700 A.D.	Teotihuacan	32.4%	Storey (1985)
600–110 A.D.	Wari (Paru)	27.0%	Drusini et al. (2001)
1300–1400 A.D.	Japan	28%	Nagoaka et al. (2006)
1500 A.D.	England	27%	Orme (2001)
1600–1700 A.D.	Sweden	25–40%	Human Mortality Database (2020)
1600–1700 A.D.	Finland	23%	Anderson (1996)
1600–1700 A.D.	France	24.4–28%	Anderson (1996) and Lachiver (1969)
1650-1700 A.D.	England	17%	Anderson (1996)
1650–1800 A.D.	England, Quackers	35%	Landers (1992)
1650–1800 A.D.	Imperial China	26%	Puyi (1964)
1670–1769 A.D.	France	27%	Charbonneau (1970)
1688–1743 A.D.	France	19%	Cohen (1975)
1692–1899 A.D.	Germany	35%	Knodel (1970)
1700–1800 A.D.	Italy	25%	
1700–1800 A.D.	Japan	22–25%	Oris et al. (2004)
1700–1800 A.D.	Germany	22.8%	Knodel and Hermalin (1984)
1700–1800 A.D.	China		Knodel and Hermalin (1984)
1730 A.D.	Quebec	22.5%	Charbonneau et al. (2000)
1749–1773 A.D.	Finland	27.5%	Turpeinen (1978)
1751–1800 A.D.	Finalnd and Sweden	22%	Gille (1949)
1776–1876 A.D.	Japan	28%	Jannetta and Preston (1991)
1786–1865 A.D.	African-American slaves	30–35%	Steckel (1986)
1800–1900 A.D.	Belgium	19%	Oris et al. (2004)
1800–1900 A.D.	Venice	28%	Oris et al. (2004)
1816–1850 A.D.	France	20%	Preston and van de Walle (1978)
1836 A.D.	Ireland	23%	Anderson (1996)
1840–1852 A.D.	Iceland	25–30%	Guttormsson and Garðarsdóttir (2002)
1850 A.D.	United States	21.6%	Haines (2000)
1875 A.D.	Poland	24.0%	Budnik and Liczbińska (2006)
1888–1912 A.D.	Cocos Malay Islands	38%	Smith (1960)
1894–1900 A.D.	Brazil	24%	Sastry (2004)

(continued)

Table 5.2 (continued)

Time	Culture	IMR	Source
1900–1909 A.D.	Mexico	30%	Feliciano (2000)
Late 19th century–early 20th A.D.	Malta	25%	Walz (2006)
1910–1939 A.D.	Manitoba Cree	25%	Moffat and Herring (1999)
1950 A.D.	Afghanistan	28%	United Nations Data (2008)
	N	42	
	Mean	26.9%	

Table 5.3 Primate infant mortality rates and juvenile mortality rates

Culture	IMR	Source
Neanderthal	~28%	Trinkhaus (1995)
Chimpanzee	28.2%	Goodall (1986), Wrangham et al. (1992), and Sugiyama (1994, 2004)
Bonoboo	16–32%	Furuichi et al. (1998) and De Lathouwers and Van Elsacker (2005)
Gorilla	23.5%	Harcourt et al. (1981), Schaller (1963), Watts (1989), and Yamagiwa and Kahekwa (2001)
Orangutan	11%	Debyser (1995), Van Noordwijk and van Schaik (2005), and Wich et al. (2004)
Boboons (*Papio cynocephalus*, *Papio hamadrayas*, *Papio ursinus*)	36%	Altmann et al. (1977), Jolly (1973), Sigg et al. (1982), and Cheney et al. (2004)
Macaques (*Macaca sylvanus*, *Macca fuscata*, *Mcacaca mulatta*)	37.3%	Ménard and Valet (1996), Takahata et al. (1998), Melnick (1981), and Dittus (1977, 1981)
Colobus monkey (*Colobus guereza*)	38%	Dunbar and Dunbar (1974)
Smaller New World monkeys (*C. faccus*, *L. rosalia*, *S. fuscicollis illigeri*, *S. fuscicollis* hybrids, *S. oedipus*)	58%	Dyke et al. (1993)
Lemurs (*Lemur catta*, *Propithecus verreauxi*, *Propithecus diadema edwardsi*)	49%	Gould et al. (2003), Richard et al. (2002), and Wright (1995)

average IMR of 28% (see Table 5.3; Volk & Atkinson, 2013) comparable to hunter-gatherer (Table 5.1) and historical (Table 5.2) averages. Chimpanzees, our closest living relatives (Britten, 2002), have a similar average IMR of 28.2% (see Table 5.3). This suggests that infant mortality has been a consistent pressure within the human family tree for several million years.

Intriguingly, gorilla IMR have a slightly lower average of 23.5%, while orangutan IMR is much lower at 11%. This suggests that not all great apes/hominids faced equal IMR pressures. In particular, orangutans have much lower levels of infant mortality, perhaps due to their solitary existence (i.e., fewer social stresses) and intensive maternal investment, as witnessed by relatively long interbirth intervals of approximately 8 years (Wich et al., 2004). This is of great significance for evolutionary theorists, as it suggests that there are different adaptive responses to IMR among great apes. This in turn implies that there are adaptive reasons or trade-offs associated with the maintenance of chimpanzee, Neanderthal, and human IMR over the last few million years.

When we turn to look at more distantly related primates, we find much higher average IMR, ranging from 36% in large-bodied primates like baboons to 58% IMR in smaller primates (see Table 5.3). While these data are likely to be skewed at least in part by the shorter lifespans of non-ape primates, they are nevertheless instructive in illustrating that IMR appears to have a degree of phylogenetic stability and is thus, at least in part, a function of different evolutionary pressures. Why does this matter? It matters because it suggests that IMR is not a fixed or constrained feature of primate development, but rather primate IMR are a reflection of different responses to differing environmental pressures. Among humans, this is perhaps best illustrated by looking at agriculturalist IMR.

5.1.5 Agriculturalist IMR

Agriculturalists are indigenous cultures who get the majority of their calories from farming, even if they engage in some levels of hunting and gathering. Agriculturalists are different from hunter-gatherers not only in their diet, but also in their typically greater exposure to Western medicine, education, food, and laws. We know that exposure to these factors leads to a demographic transition that results in lower infant mortality (Coale & Watkins, 1986; Kramer & Greaves, 2007; Roth, 1981). We therefore caution the interpretation of these data as directly resembling even previous agriculturalist societies. That said, their inclusion can offer a perspective on how environmental factors can and do influence human IMR. The average agriculturalist IMR (see Table 5.4) was $M = 20.6\%$ ($SD = 4.8\%$; min = 11%, max = 53%). While there is a variation among these groups' IMR relative to their degree of Western contact, perhaps the more salient point is that IMR can be influenced by behavioral, cultural, and/or technological changes. To understand what these causes and changes are, it is instructive to first understand the causes of infant mortality in the EEA.

5.2 EEA Causes of Infant Mortality

There are a relatively diverse range of causes of mortality among hunter-gatherer infants. When considering a broad range of groups such as !Kung, settled Ache, forest Ache, Machi-guenga, Agta, !Kung, Tsimane, and Aborigines, Gurven and Kaplan (2007) found that 65% of total child mortality was due to disease, mainly gastrointestinal and respiratory, 9.5% due to congenital problems, 8% due to

Table 5.4 Agriculturalist infant mortality rates and child mortality rates

Culture	IMR	Source
Ayoreo	26.2%+	Diez and Salzano (1978)
Bambara	23.8%	Hewlett (1991)
Bari	11%	Hewlett (1991)
Datoga	20.8%	Borgerhoff Mulder (1992)
Dusun	17.1%	Salzano et al. (1967)
Fulani	21.1%	Hewlett (1991)
Gainj	16.5%	Wood (1987)
Kipsigis	25.4%	Borgerhoff Mulder (1988)
Lese	17.9%	Hewlett (1991)
Masai	53%	De Vries (1987)
Ngbaka	24%	Hewlett (1991)
Nyimba	21.6%	Levine (1988)
Plateau Tonga	16%	Colson (1958)
Pumé	13.2%	Kramer and Greaves (2007)
Semai	23.4%	Hewlett (1991)
Tamang	20.4%	Fricke (1984)
Tikopia	28.6%	Firth (1983) and Hewlett (1991)
Twareg	22.8%	Hewlett (1991)
Yanomamö	21.8%	Early and Peters (1990), Hewlett (1991), and Neel and Weiss (1975)
N	19	
Mean	20.6%	

accidents, and 17% due to violence. The forest Ache and the Hiwi hunter-gatherer groups were the most aggressive groups of the sample, and if they were removed, child mortality due to violence fell to 5%. It is important to note that violent deaths were due to intraspecific violence rather than predation. The actual predation of hunter-gatherer children was virtually absent, although it is known to have occurred in the past (Wrangham et al. 2000). This contrasts with other primate populations that face significant, population-altering levels of mortality (Hart & Sussman, 2005; Hill & Dunbar, 1998). Predation rates are as high as 40% in baboons (Bulger & Hamilton 1987) and 65% in chimpanzees (Boesch & Boesch-Acherman, 2000). Thus, while disease, genetics, accidents, and intraspecific violence were important concerns for human children of all ages, predation was a weak threat compared to other primates.

With respect to disease, barring major mortality events such as the plague (McEvedy, 1988), pneumonia was the single biggest killer of infants in the EEA (Gurven & Kaplan, 2007). While EEA data are missing, in modern times, malnutrition is the single greatest risk factor for pneumonia (Troeger et al., 2018). It may therefore be reasonable to presume that malnutrition played a similarly important role in leaving ancestral infants vulnerable to pneumonia. Given the relative frequency of historical famines, as well as the slow population growth of hunter-gatherers, it is reasonable to infer that malnutrition was relatively common in the EEA. The risk of malnutrition on developing pneumonia is magnified if infants are not receiving adequate amounts of breastmilk (Lamberti et al., 2013), either due to a lack of maternal supply or reliance on other infant foods.

Exclusive breastfeeding also helps protect against the second primary pathogenic killer – infant diarrhea (Lamberti et al., 2011). Diarrhea is associated with a lack of sanitation and/or clean drinking water (United Nations Children's Fund, 2010). There is some evidence that the risks of diarrhea are greater in the warmer summer months due to the proliferation of bacteria and other pathogens (Cheney, 1984). In contrast, close proximity to others and the presence of fire smoke are found in colder months and both contribute to pneumonia (Dherani et al., 2008). Infants, therefore, faced a potentially year-round threat from pathogen-based mortality.

Among historical settings, disease (and to a much lower extent, accidents such as home fires) were the primary causes of infant mortality (Hanawalt, 1995). Further, in some historical settings, abandonment or infanticide were primary causes of infant and child mortality, with up to 50% of infants being abandoned in times of severe economic hardship (Budnik & Liczbińska, 2006; Cunningham, 2005; Rawson, 2003). In the fifteenth to eighteenth centuries, European infants were placed in institutionalized or private care where mortality rates could exceed 90% (Cunningham, 2005). That this was a method of last resort can be witnessed by parents' attempts to pay for the return of their infants should they regain their economic standing (Cunningham, 2005). Infants thus faced a broad area of both recurring and novel causes of mortality. An interesting question then arises: did these mortality risks lead to any adaptive changes in human behavior and diminish these levels of IMR?

5.3 Evolutionary Consequences of EEA Infant Mortality

As noted above, infant mortality is not a biologically fixed outcome. A number of factors can increase or decrease the rate of infant mortality. Not surprisingly, parental care is perhaps the most important factor in ancestral environments. Absence of parental care (especially maternal care) can lead to near-certain infant mortality in both historical (Cunningham, 2005) and hunter-gatherer (Hrdy, 1999; Sear & Mace, 2008) populations. The general availability of parental resources is a good predictor of infant mortality both between (Preston & van de Walle, 1978) and within populations (Houweling & Kunst, 2010). More specifically, an increase in food quality and quantity decreases mortality (Gage, 1994; Houweling & Kunst, 2010). An increase in alloparental support can also decrease mortality levels (Hawkes et al., 1989; Sear & Mace, 2008; Sear et al., 2002), with some researchers suggesting that the importance of alloparental and paternal care can be seen in the evolution of human social structures (Chapais, 2009; Hrdy, 2009; Locke & Bogin, Chap. 6; Hrdy & Burkart, Chap. 8, this volume). Parenting does seem to be a learned skill, with first-borns suffering from higher infant mortality rates (Cohen, 1975), perhaps due to the inexperience of their parents (Smith, 2005). Interestingly, being a first-time mother does not appear to affect child mortality rates (Cohen, 1975), perhaps because older children are less susceptible to first-time parents' mistakes. In a related fashion, in stressed populations, mothers with higher IQs may have higher child survival rates (Čvorović et al., 2008).

Family size is also positively related to mortality rates, presumably because (all else being equal) in larger families, each child has access to fewer resources (Cohen, 1975). Hygienic practices surrounding newborns can also profoundly impact mortality rates by regulating the amount and type of pathogens that infants are exposed to (Wood, 1983). Other behavioral factors that affect IMR include breastfeeding (e.g., Golding et al., 1997; Volk, 2009), reduced inter-birth-intervals (Alam, 1995, Bøhler, & Bergström, 1995; Hobcraft et al., 1983, Palloni & Millman, 1986), and polygyny (e.g., Omariba & Boyle 2007). Mothers in polygynous families may compete with each other over the capacity to provide for their infants as a means of intrasexual competition (Hrdy, 1999, Volk & Franklin, 2020). There are almost certainly other factors that relate to infant mortality rates, leaving plenty of room for the evolutionary pressures of infant mortality to influence the development of human behavior and infant development.

This volume is replete with examples of how infants are designed to not only learn about their environment but to survive them. At the most basic level, one of the oldest evolutionary theories on behavior is that infants form attachment bonds with caregivers that promote their survival (Bowlby, 2008). Hart (Chap. 7, this volume) discusses how critical this was with regard to breastfeeding. As noted in this chapter, breastfeeding is an important element of infant survival. But mothers are not the only adults who provide care to infants. Infants have evolved neotenous cues that evoke feelings of parental care from adults in general (Bjorklund, Chap. 2, this volume). Intriguingly, there is some evidence that these cues are weaker at birth than they are later in life, suggesting that it may be parents who evolved to prefer "safer" neotenous cues (Franklin et al., 2018). This could be an example of mother-infant conflict (Salmon & Jaeger, Chap. 11, this volume), where the needs of an individual infant are weighed against a mother's commitment to providing for her entire family. The fact that these two energy expenditures do not always align highlights how important infant mortality was as a selective evolutionary pressure for both infants and mothers.

That said, it is clear that adults beyond the mother (and often father) are important for infants' wellbeing and development (Locke & Bogin, Chap. 6; Hrdy & Burkart; Chap. 8; Henry & Morelli, Chap. 10, this volume). Infants appear to be adapted to understanding and interacting with other minds in their environment, perhaps as a way of deepening bonds and soliciting care while they simultaneously use those external minds to learn about their environment (Buttelmann, Chap. 13, this volume). At the same time as they are learning from others, infants also possess predispositions that help them safely navigate their physical environment, such as the development of appropriate fears to manage risks (Rakison, Chap. 14, this volume). These examples are but a small sample of the wide range of infant and adult adaptations that appear to have evolved, at least in part, to offset the risks of infant mortality. There are likely many more that remain to be discovered as elevated IMR of 26%+ were truly a significant evolutionary selection pressure that humans, and their close relatives, had to deal with. With that said, we now turn to an examination of modern IMR and what they tell us about both successes and remaining challenges for infants.

5.4 Modern Changes to IMR

Modernity has clearly reinforced the idea that IMR is influenced by external factors. In what is perhaps the most significant event in human history, infant mortality decreased significantly between prehistoric times and the twenty-first century (Stearns, 2006), with modern infant mortality rates falling to lows below 0.28% in some developed countries (United Nations, 2019). This represents a shocking 100-fold increase in the survival of infants as compared to infants in hunter-gatherer or historical times! As impressive as this achievement is, IMR today continues to fall. Between 1990 and 2017, the global annual infant mortality rates decreased by 51% (Hug et al., 2019). Reductions in rates of infant and child mortality can be attributed to a variety of global trends.

The *demographic transition theory* discusses how infant birth and death rates change as a result of economic development, with high birth rates and high infant death rates being present in societies with little to no technology, education, or industrial development, and low birth rates and low death rates being found in nations with more advanced technology, higher levels of education, and significantly better economic development (Thompson, 1929). This pattern follows two general trends: (1) a drastic population increase due to decreases in death rates (specifically in infants and children) is brought on by industrialization, followed by (2) a decline in population growth due to decreased fertility levels (Herzer et al. 2012; United Nations, 2019). Over the past several decades, a decline in fertility and infant mortality has been seen in nearly all countries (United Nations, 2019). As IMR fall, parents tend to implement fertility control as the infants they have are expected to survive and they can, therefore, risk having fewer offspring (Amin & Basu, 2004).

Increased infant and child survival can also be attributed to medical research and advancements. Today, when infants are born premature, or when children become ill, there are resources and protocols to save them. In the last two decades, leaps and bounds have been made in the medical field to preserve infants' lives (Stoll et al., 2015). Ironically, the improved ability to successfully cope with earlier preterm infants has led to a somewhat artificial stagnation of infant mortality rates in developed countries (Tomashek et al., 2007). This is a result of infants being born at preterm ages that would not have been viable in the past (Larroque et al., 2004; Malloy, 2015). The fact that these infants are viable today is unequivocally a continued improvement worth celebrating, even if they depress the average IMR, as these preterm infants represent a previously impossible expansion of infancy. That caveat aside, there are a number of factors that account for the drop in modern IMR.

Vaccines are one of the more visible means of reducing infant mortality (McGovern & Canning, 2015). For example, in rural Bangladesh, the measles vaccine was administered to infants and children between the ages of 9 and 60 months (Koenig et al., 1990). Mortality rates among vaccinated infants and children were as much as 46% less than those for nonvaccinated children. Evidence like this is a strong testimony to the need to counteract conspiracy-based antivaccination theories that have the potential to imperil the lives of infants (Kata, 2012), either directly or indirectly, through the loss of herd immunity (May & Silverman, 2003).

In order for infants and children to reap the benefits of such resources as vaccines, they must have access to them. This first required the development of a scientific approach to medicine that allowed for unprecedented progress in both knowledge and practice (Porter, 1999). The incorporation of science-based health care allows access to medical resources without financial strain, leading people to decrease delays in seeking treatment (Dykes, 1950). This is exemplified in Luhrmann and Wilson's (2018) finding that within one year of the introduction of universal health care in the UK, there was a 17% reduction in infant mortality due to more timely access to treatment. Another government-sponsored initiative that benefitted children was the development of formalized sanitation systems. The significance of sanitation in decreasing rates of infants' and children's mortality cannot be ignored and is exemplified in numerous studies (e.g., Mara et al. 2010; Satterthwaite et al. 1996). In 2010, UNICEF highlighted that sanitation interventions were the most cost-effective intervention for decreasing infant and child mortality (UNICEF, 2010). Such implementations are standard due to the fact that diarrhea and parasite infections are the most common causes of death in many developing countries (e.g., Black et al., 2010). But not all interventions require government or medical-based systems. Investing in individuals can also yield significant results for IMR, especially if those individuals are mothers.

In every culture that has ever existed, mothers are, on average, the primary caregivers of infants (Hrdy, 1999). It is therefore not surprising that by giving mothers the tools and power that education affords results in significant benefits to their infants' survival. The strong negative association between maternal education and infant and child mortality has been well documented (e.g., Bicego & Boerma 1990; Cleland et al. 1992; Nakamura et al., 2011) and is considered to be a critical factor in reducing rates of mortality (Andriano & Monden, 2019). The negative association between women's empowerment and infant mortality has been studied extensively (e.g., Boehmer & Williamson 1996; Smith et al. 2003; Scanlan 2010). Women's empowerment can create such extensive and positive changes in children's lives, in that women are much most likely to use the resources available to them to help their children and ensure the family needs have been satisfied (Hoddinott & Haddad, 1995) and tend to favor spending resources on things that aid in infant and child survival, such as vaccinations, education, and nutrition (Quisumbing, 2003).

5.5 Future Directions

It is appropriate to end a discussion of infant mortality rates following a discussion of empowering women, who have been and remain today, the primary caregivers of children (Hrdy, 1999). Given infants' obvious inability to lobby for systemic changes and improvements to IMR, it rests on the shoulders of motivated adults to do so for them. Ironically though, the near-total success of this endeavor has hidden the horrifying history of infant mortality from many scholars. It is our hope that the true significance of this human achievement (i.e., lowering IMR) does not come at the price of ignorance of our past and the tremendous risks that infants faced in surviving their first year of life. This would be particularly ironic given the potential role that infant and child death played in Darwin's decision to write and publish *The Origin of Species* (Keynes, 2002). We would thus like to end our chapter by calling for continued research into the evolution of infancy, infant caregiving, and the role of IMR in shaping human evolution.

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Part III
Social Context of Infant Development

Chapter 6

An Unusually Human Time: Effects of the Most Social Stage on the Most Social Species

John L. Locke and Barry Bogin

More than a century ago, the US Supreme Court issued a ruling that speaks to a basic feature of human nature and, indirectly, the role of infancy in human development. The decision referred to some horrific events that had taken place in penitentiaries. "A considerable number of prisoners fell … into a semi-fatuous condition, from which it was next to impossible to arouse them," Court records indicate, "and others … became violently insane; others still, committed suicide." Most of the survivors failed to "recover sufficient mental activity to be of any subsequent service to the community" (Haney & Lynch, 1997, p. 484).

What was done to the prisoners? We might guess that they were fed rancid food or physically tortured, or perhaps used as guinea pigs in a medical experiment. But the cause of the prisoners' condition was neither physically cruel nor invasive. They were simply left alone – literally *alone* – denied the opportunity to see and interact with other prisoners.

This material was included in the Court's ruling because concerns were growing over the use of solitary confinement. When they prepared a rough summary of America's experience with this punishment, it was to rule on a case involving a man who had been found guilty of murder and was being held in isolation while waiting to be hanged. The Court concluded that solitude *was worse than hanging*, based on the experiences recounted above, and ordered the prisoner's immediate release.

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What this suggests, of course, is that humans need to be around others. If we go too long without relating, many of us will become lonely or depressed, and if we have too few friends, we may become physically ill or even die (Caccioppo & Patrick, 2008; Hawkley & Cacioppo, 2010).

We even need images of people. One indication is anthropomorphism, a "man-in-the-moon" sort of phenomenon in which normally adjusted people naturally imbue nonhuman entities with human qualities (Eddy et al., 1993; Heider & Simmel, 1944), or infer their characteristics from human artifacts, including art, literature, and tools (Donoghue, 1983; Stephen, 1874, p. 252; Tylor, 1974).

More directly relevant to claims we will make here are findings on institutionalized infants who are given basic care but denied normal levels of social contact. Even with food and opportunities to exercise, many of these neglected infants fail to develop physically and mentally, and some die (Spitz, 1945; Sonuga-Barke et al., 2017). Significantly, as we will see later, there is also a specific relationship between social deprivation in infancy and brain volume in adulthood (Mackes et al., 2020).

6.1 How Did We Get to Be So Social?

The other primates are extremely social (Humphrey, 1976; Jolly, 1966), more gregarious than most other animal species (Bogin et al., 2014; Boyd & Richerson, 2009; Burkart et al., 2014; Hrdy, 2016), and ours is undoubtedly the most social species of all. This raises questions as to what events made us humans so gregarious. When, in evolution, did our need for social stimulation and interaction become so intense?

For some theorists, an early beginning point was the out-migration from Africa more than 100,000 years ago, which may have reduced the morbid effects of certain parasites and diseases (McNeill, 1976), increasing the number of humans on earth. Others point to reductions in megafauna and the onset of agriculture within the past 15–20,000 years, which increased the size of residential groups (van der Kaars et al., 2017). But it has been claimed that even before then, group living decreased the threat of predation (Port et al., 2020). When it did so, residential groups increased competition for needed resources, shifting vigilance from group-external events to the behavior of group members (Locke, 2008). If groups were to be kept together, their members would have to become socially tolerant, restrained, and, if they were to maximize their productivity, cooperative (Hare et al., 2007). Cooperation would have enabled many things, including "social capital," the exchange of assistance, knowledge, tools, and other resources that presuppose the existence of relationships based on trust (Coleman, 1988). Since exchanges are based on assumptions regarding repayment, social capital required that individuals keep track of who was owed and who was owing.

It is also assumed that living in close proximity to individuals who were capable of competition *and* cooperation, and at any given time might be intending either, required the ability to "read" people, that is, to evaluate their personal qualities and anticipate their actions; to know when people were attempting to mislead; to infer what people were planning, given what they were likely to know; and to remember which information had been shared with which others or had been withheld.

At some time in human evolution, “mental ledgers” of things to be shared or withheld, and people with whom to cooperate or compete, were formalized into social kinship systems that define obligations and expectations between the members of a social group (Mauss, 1925/2002). In traditional societies, which include foraging groups (hunter-gatherers), pastoralists, and horticulturalists, the central organizing principle for determining obligations is kinship, the “glue” that binds human societies together. Kinship applies most strongly in traditional preindustrial societies, but includes modern nation-states with economies based on intensive agricultural or industry, as well as contemporary postindustrial states (Carsten, 2000; Höllinger & Haller, 1990; Schneider, 1984). As we discuss in the following section, human kinship plays a significant role in the care of pregnant women and their infants and is learned by infants from birth.

For many theorists, the most significant evolution in the area of social cognition was theory of mind, that is, the awareness that others know things that one might not, and the ability to infer the nature of that knowledge; and intentionality, that is, the ability to anticipate what one or more other people know, or are thinking, that *others* know or are thinking (Cole, 2014; Lewis et al., 2017; Povinelli & Preuss, 1995; Povinelli & Vonk, 2003).

Where nonhuman primates are said to have “Napoleonic” brains that evolved the potential for complex cognitive processes in response to behavior pressures exerted by heterospecific animals (Ashton et al., 2020), we humans are said to have brains that are “Machiavellian,” after the sixteenth-century Italian diplomat who advised young politicians on ways to use deception to negotiate their way through complex social situations (Byrne & Whiten, 1988). Five centuries later, it is clear that even if we choose to follow a straight and narrow path in our own lives, we are still Machiavellian in our capacity to deal with various kinds of human entanglements, even if doing so requires that we be able to implement or detect various acts of deception (Locke, 2008). That’s why we are said to have Machiavellian brains, ones that enable us to prosper in complex social situations.

Of particular importance here is the *Social Brain Hypothesis*, the claim, associated primarily with anthropologist Robin Dunbar, which holds that increases in the size of hominin groups added to the complexity of social relations, ultimately enhancing the size of the brain, especially the neocortex (Dunbar, 1992, 1998, 2003, 2009). It is assumed that the enlargement of groups increased the ability of hominins to handle social complexity, enabling them to maintain the social cohesion required to keep groups together. With a brain equipped for so many different social operations, it is safe to assume that our ancestors found new ways to relate to, connect with, and interpret the behavior of others (Burkart et al., 2009, 2014), imbuing us – their descendants – with cognitive resources and strategies that facilitate socialization and cooperation.

While accepting the need for an hypothesis such as Dunbar’s, we will offer a complementary hypothesis of our own, one that altered important properties of infancy, extending and intensifying socially formative experiences associated with care.

6.2 The Evolution of Development

No account of human evolution can be complete, wrote zoologist Walter Garstang a century ago, if it fails to identify the environmental changes that produced relevant traits *in development*, and the reasons why the new traits would have conferred contemporaneous reproductive advantages (Garstang, 1922). He said it was absurd to suppose that a new trait could evolve in mature members of a species, a judgment that has been repeatedly confirmed in recent years (Gould, 1977; Hall, 2002; Northcutt, 1990; West-Eberhard, 2003). This is why, if our questions relate to the evolution of behavior, we must consider any role that may have been played by evolutionary changes in infancy (see Bjorklund, Chap. 2, this volume).

Although a great deal of evolutionary thinking is associated with behavioral traits that develop, we will, in the spirit of Garstang, focus on the evolution of development itself, with particular attention to infancy. If this stage was transformed by the advent of new social practices or pressures, infancy itself may have become a variable in the evolution of human sociality. Taking the infancy of other primates as a starting point, we will ask how our own infancy evolved, then offer an *Infant Care Hypothesis* which holds that this stage in life history contributed to the evolution of sociality in our species, perhaps in tandem with operations identified under the *Social Brain Hypothesis*.

6.2.1 A Brief Note on Primate Infancies

Nonhuman primates provide a clear starting point in that they have an infancy with different properties than ours. This enables us to ask what changed the ancestral infancy to the modern one, and what the modern infancy, as changed, may have contributed to our species that the ancestral one could not.

A primate infant, whether it is human or nonhuman, is usually in intimate contact with its mother, or in a few species, the father or an individual that is genetically related to the mother. The infant cannot survive without near-constant care and protection, usually from its mother, who provides some or all of its nourishment by way of lactation. Depending on the primate species, lactation lasts from months to years. One reason is biological: infants lack teeth and jaw strength to process the adult diet. Another reason is emotional: the physical bond with the mother provides the physical touch, social support, and cognitive stimulation that all primate infants require to survive and grow into healthy adults.

Here, we provide a brief overview of infancy, followed, in a later section, by a more detailed look into the several phases and intervals within a human infancy in which specific developmental operations occur.

6.2.2 An Overview of Human Life History

Before proceeding further, let's take a brief glance at the stages of *human* postnatal development in relation to physical growth in length or height. Note, in Fig. 6.1, that it is the velocity curve that best pinpoints the transition between stages.

Among the changes in life history that we discuss here are ones that left the human infant unusually helpless – unable to survive without an intensification and extension of care (Bogin, 1997, 2021; Hrdy, 2009, 2016; Locke & Bogin, 2006a; see Hrdy & Burkart, Chap. 8, this volume). An important change occurred when

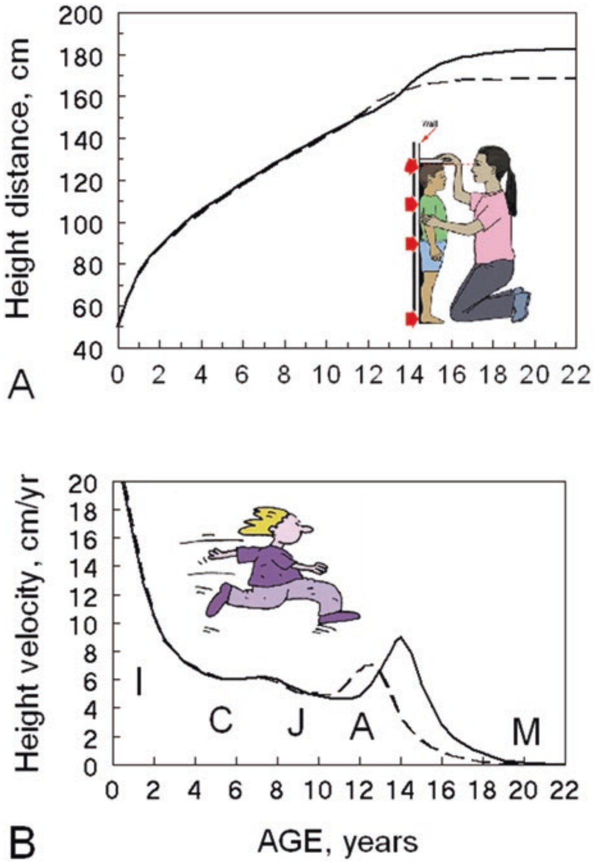

Fig. 6.1 Average distance (**a**) and velocity (**b**) curves of growth in height for healthy girls (dashed lines) and boys (solid lines). Distance is the amount of height achieved at a given age. In part A, the image shows a child's height being measured. Velocity is the rate of growth at a given time, in this case shown as centimeters per year. In part B, the running figure represents "velocity." The velocity curves show the postnatal stages of the pattern of human growth. Note the spurts in growth rate at mid-childhood and adolescence for both girls and boys. The postnatal stages: *I* infancy, *C* childhood, *J* juvenile, *A* adolescence, *M* mature adult. Original figure B Bogin

weaning, which marks the end of infancy, was reduced from five years – the age of chimpanzee weaning – to three. This truncated the period of maternal lactation, allowing the mother to invest energy and other resources into a new pregnancy. We assume that reduction of the interbirth interval was selected, as it would have increased the reproductive success of our premodern ancestors, at least if previous infants were kept alive.

6.2.2.1 Caring for Many Infants

Human ancestors solved the problem of postweaning care by enlisting the assistance of other people in their social group. None of the nonhuman apes practices this kind of cooperative breeding (some South American monkeys and nonprimate mammals do) (see Hrdy & Burkart, Chap. 8, this volume). We discuss the human type of cooperative breeding later in this chapter. Our point here is that the resulting increase in other dependent siblings would have stiffened competition for care, pressuring infants to find new ways to attract attention and assistance.

Feeding by lactation defines the infancy of humans and all other mammalian species (see Hart, Chap. 7, this volume). The evolution of lactation required behavioral changes in mothers and their offspring. One change, as we will discuss, is bonding, which maintains the infant in contact and communication with the mother so that it can be suckled when hungry. The mother-offspring contact ensuing from this feeding method establishes a period of dependency in the young and a reciprocal period of investment by the mother.

6.2.2.2 The Neonatal Stage

Birth involves a critical and stressful transition from intra- to extra-uterine environments. Neonates must quickly adjust their own metabolism to the extra-uterine environment, and this involves temperature regulation, breathing, sleeping, eating, digestion, elimination, and other autoregulatory processes (Ward Platt & Deshpande, 2005). The neonate, of course, cannot do all of these on its own and receives much care, especially for feeding, and we focus here on a few important aspects of human lactation. In the following discussion, we consider only full-term (37–42 weeks' gestation) human neonates of normal birth weight (2.5–4.3 kg) because preterm, low-birth-weight, or high-birth-weight neonates are at elevated risk of mortality. (The medical technology needed to sustain such neonates has been available for only 50 years or less.) Thus, during all but a sliver of evolutionary history, there was strong selection against neonates born outside the range of full-term and normal birth weight.

The human neonate is born with a large body mass relative to other apes. This is due, in part, to the fact that human infants are born with a greater reserve of fat than any other mammal (Kuzawa, 1998). This reserve not only allows for survival during the first few days after birth but also fuels the rapid brain growth shown in Fig. 6.2.

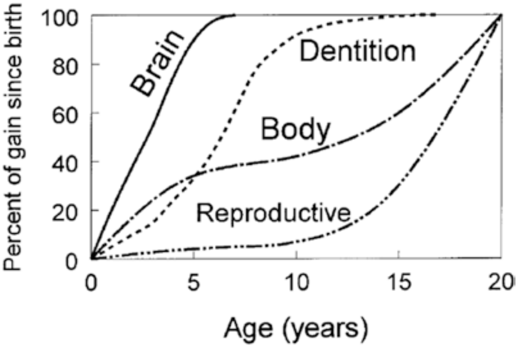

Fig. 6.2 Growth curves for different body tissues. The "Brain" curve is for total weight of the brain. The "Dentition" curve is the median maturity score for girls based on the seven left mandibular teeth (I_1, I_2, C, PM_1, PM_2, M_1, M_2). The "Body" curve represents growth in stature or total body weight, and the "Reproductive" curve represents the weight of the gonads and primary reproductive organs. (From Bogin (2021) which provides citations to the data sources)

By the fifth postnatal day, human milk composition begins to mature in terms of energy and other nutrient content and is fully mature by 4–6 weeks postpartum (Ballard & Morrow, 2013). That it matures no sooner than 28 days after birth is, in our view, the single most compelling reason to consider that duration as the neonatal period. Biologically, this duration also makes sense in that both the neonate and the mother make physiological adjustments during this time from pregnancy to extrauterine life. Even with these adjustments in place at the transition from neonate to one-month-old infant, that infant remains motorically altricial and depends on its mother and others for care and feeding.

Lactation and infancy prolong this period of dependency but allow for rapid and high-quality growth and greater physical and behavioral adaptability (Pond, 1977). Infancy may also increase the latter by giving young mammals the time required to practice and improve innate behaviors, such as the stalking of prey in carnivores. Bonds between mothers and infants also increase opportunities for young mammals to acquire learned behaviors by observing and imitating their mother or other adult animals with whom she interacts.

In neurologically more advanced mammals, especially the primates generally, mothers and infants remain in virtually constant contact for several weeks or months after birth, but most primate females give birth to one infant per pregnancy. (Rare exceptions include South American marmosets and tamarins that regularly give birth to twins and, not coincidentally, practice cooperative breeding.) These singleton births facilitate intimate physical contact in that there is no competition between siblings for the mother. Suckling is done "on demand," 24 hours per day. Primates grow slowly relative to most other mammals, and the concentration of energy in the milk of primates is lower than that of the faster-growing "primitive" mammals. But the efficiency, constancy, and quality of physical contact and nutrient supply in the primates are superior (Widdowson, 1976).

Newborn primates are highly active, traveling with the mother, clinging to her body, and experiencing many of the same things that she experiences while developing their own motor and sensory skills. The relatively slow growth rate of primate infants intensifies their dependency on and intimacy with the mother. Infant dependency extends the period of growth, development, protection, and opportunity for infants to learn survival skills by observing successful maternal behaviors (Jolly, 1985). These benefits of infant dependency increase the probability that the newborn will reach reproductive age, increasing their own and their mother's fitness.

In some ways, dependency seems disadvantageous to the primate mother. Competition for nesting space and breeding territories, aggressive encounters with conspecifics for mates, and mating itself are often impossible for mothers with dependent young. Infant dependency is also incompatible with some features of adult behavior, particularly further reproduction. The reason is that the energy demands of lactation, along with the care and carrying of the infant, suppress fecundity. Even if the mother could conceive while caring for her current infant, her delicate energy balance and the total physical stress of pregnancy and infant care would increase the risk of mortality to the mother, her infant, and her fetus.

6.3 Infancy from a Physical Perspective

We begin by discussing physical features of infancy, then ask how these and other features evolved. In doing so, we will review some changes that occur in development, for example, in teeth and bones. At first glance, these measures may seem trivial – we might wonder what they could possibly say about our highly social and intelligent species – but they may have contributed to much larger changes in our nature. The analogy in archaeology might be a partial footprint or fragment of bone that means nothing by itself but, when dated, suggests when human-like bipedalism evolved or migration to a new land took place in prehistory.[1]

By the start of the second trimester of human pregnancy, the differentiation of cells into tissues and organs is complete and the embryo is now a fetus. Physical growth is extraordinarily rapid. The fertilized egg cell, which is no larger than the period at the end of this sentence, divides and its daughter cells enlarge so that by the sixth month the fetus is recognizably human and between 36 and 38 cm long (14–15 inches), which is about 74% of average birth length of 50 cm. Increases in weight during this same period are also rapid, with the greatest gains during the third trimester of pregnancy. During this last trimester, the development and maturation of several physiological systems, such as the circulatory, respiratory, and digestive systems, also occur, preparing the fetus for the transition to extra-uterine life following birth.

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[1] Detailed description of fertilization, embryonic development, and fetal growth are beyond the scope of this chapter but are available online and in print (see review in Bogin, 2021).

Infancy, including the neonatal first month after birth, spans the first three years of postnatal life. It is characterized by the most rapid growth velocity of any stage in the life history of our species. During the first year, infants grow an average of about 28 centimeters in length, an increase of more than 50% of birth length (about 50 cm), and seven kilograms in weight, which more than doubles birth weight (about 3.4 kg).

The rate of decrease in velocity is also very steep, which makes infancy the life stage with the most rapidly *changing* rate of growth. The infant's curve of growth, with rapid and decelerating velocity, is a continuation of the fetal pattern, in which the rate of growth in length reaches its peak in the second trimester and then begins a deceleration that lasts until childhood (Fig. 6.1).

One surprising feature of human growth during infancy is the similarity that most infants show both in the amount and rate of growth during the first six months of life. One might expect that variation in hereditary and environmental factors between individual infants and populations leads to marked differences in amounts and rates of growth. But several investigative teams (Habicht et al., 1974; Van Loon et al., 1986) have shown that in the first six months of life, the growth of healthy infants of normal birth weight is remarkably similar across a wide variety of ethnic and socioeconomic classes in developed and developing nations. This is one of the shared characteristics that makes human infancy a species-specific period of growth and development.

As indicated, the other primates are considered less social than humans, which may be related, indirectly, to the fact that their brains develop relatively sooner than ours. By birth, the rhesus monkey has already achieved 68% of its ultimate brain weight, whereas the human newborn's brain is only about 26% of what it will weigh in maturity (Harvey & Clutton-Brock, 1985; Lindburg, 1982; see Bjorklund, Chap. 2; DeSilva, Chap. 3, this volume). Growth curves of the body tissues shown in Fig. 6.2 place the priority of human postnatal brain growth in context.

The brain of a human newborn is about 341 cm^3 in volume, more than double the size of a chimpanzee brain at birth (c. 155 cm^3; Holland et al., 2014). By the age of seven years, the chimp brain has grown to about 350 cm^3, but the human brain surpasses a median size of 1300 cm^3, meaning that the chimpanzee brain has expanded by 2.3 times and the human brain by 3.8 times (Fig. 6.3).

Although the motor skills of human infants are relatively delayed, as we will discuss, they develop rapidly as infancy progresses. At birth, states of wakefulness and sleep are not sharply differentiated, and motor coordination is variable and transient, but a month later the typical infant can lift its chin when prone and by two months lift its chest by doing a "push-up." By 4 months, infants can sit with support, and by 7 months, they can do so without it; by 8 months, they can crawl, and by 10 months, infants can walk with support (Fig. 6.4).

Early infancy ends at about 12 months as the first unsupported bipedal steps are taken. With the transition to the middle-to-late infancy period, walking, running, object manipulation, and other motor skills continue to appear in a mostly gradual manner for many years. By two years, infants can walk without assistance and leaf through a book one page at a time. There is a similar gradual progression in problem

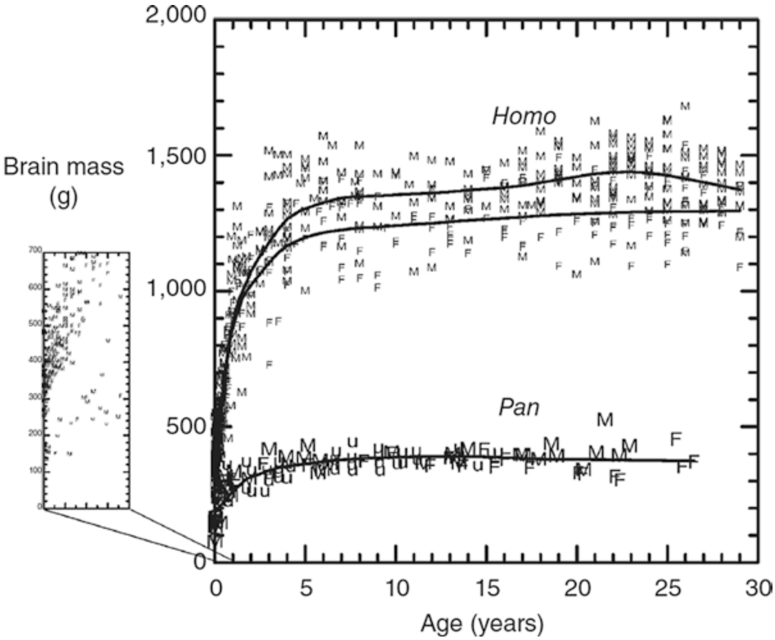

Fig. 6.3 Brain-mass growth data for humans (Homo sapiens) and chimpanzees (Pan troglodytes). Brain mass increases during the postnatal period in both species. Lines represent best-fit Lowess regressions through the data points. "M," males; "F," females; "U," sex unidentified (Vrba, 1998). The human regressions separate into male (upper) and female (lower) curves. The inset shows brain-mass growth for each species during the first postnatal year. Vrba proposed that the human difference in brain mass growth was due to hypermorphosis, that is, the heterochronic process of prolongation of the rapid fetal growth seen in the chimpanzee. Vrba described the chimpanzee pattern as ancestral to the human pattern. Leigh (2004) re-analyzed the data with more appropriate mathematical and statistical models and found no evidence for prolongation or heterochrony. Rather, humans evolved new patterns of rapid growth before and after birth. See the text for more details. (Reproduced from Leigh, 2004, with kind permission of the author)

solving and general cognitive abilities of infants. In contrast, some specific motor-cognitive skills, especially spoken language, develop more rapidly. Typically, the rudiments of a linguistic system are operative by the end of infancy (Locke, 1997; Locke & Bogin, 2006a).

The development of the skeleton, musculature, and nervous system are responsible for the infant's motor and cognitive advancements. Especially important is the rapid growth of the brain, which grows more rapidly during infancy than almost any other tissue or organ of the body (Figs. 6.2 and 6.3; see Bjorklund, Chap. 2; DeSilva, Chap. 3, this volume). In general, the various regions of the brain develop quickly, whether they control physical growth and the reproductive system or behavioral and cognitive development, especially the latter.

From a physical perspective, the emergence of the last deciduous tooth is important, for this is one of the events that signals the end of infancy in humans. Emergence

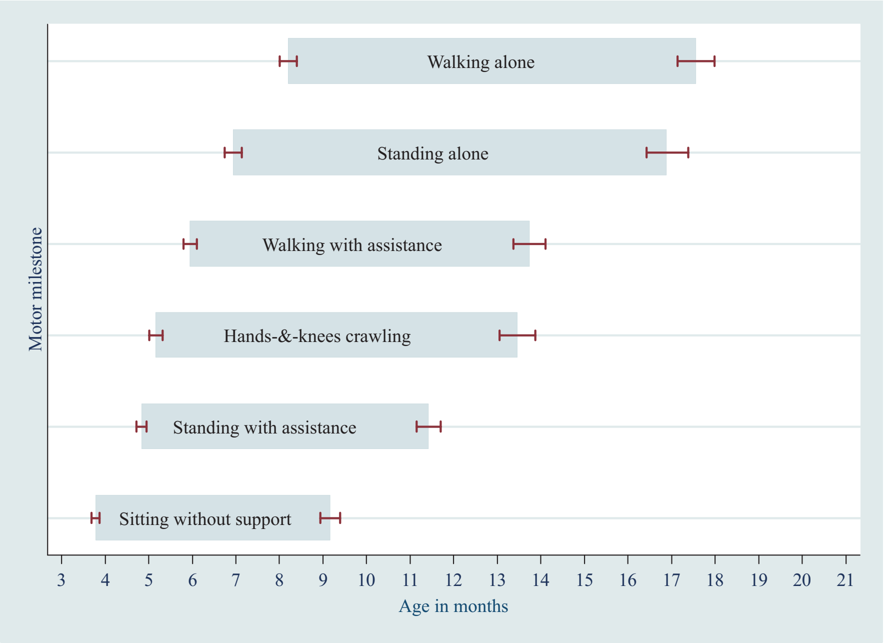

Fig. 6.4 Windows of achievement for six gross motor milestones. Source: World Health Organization Multicentre Growth Reference Study Group (WHO Multicentre Growth Reference Study Group 2006, https://www.who.int/childgrowth/standards/mm_windows_graph.pdf?ua=1, public domain)

of all the deciduous teeth allows the infant to switch from dependence on breastfeeding to eating appropriate weaning foods. In traditional hunter-gatherer, horticulture, pastoral, or agricultural societies, weaning occurs between 24 and 36 months of age. By this age, all the deciduous teeth have erupted, even for very late maturing infants. Thus, by 36 months of age, both biological developments (motor development, tooth emergence) and behavioral changes in the mother-infant relationship (weaning) occur, as well as the cognitive and linguistic achievements mentioned above, signaling the end of infancy.

6.4 Infancy from a Behavioral Perspective

The human neonate has a large body relative to other apes, a small brain size relative to the human adult, and, as we will discuss, a prolonged period of extreme motor immaturity relative to other ape neonates (Trevathan & Rosenberg, 2016). These traits – an unusual combination for a primate newborn – make the human infant a costly creature to carry around, protect, and feed – burdens usually falling on the mother.

Trevathan and Rosenberg emphasize that human *altriciality* – an underdeveloped and helpless state – requires maternal commitment to the neonate, which has important behavioral implications for the social group. Humans have been called "super cooperators" in that they display cooperative assistance, support, and mutual aid in relation to reproduction, care of pregnant women, and the rearing of offspring (Nowak & Highfield, 2011; see Hary & Burhart, Chap. 8, this volume). But humans take super-cooperation much further than any other cooperatively breeding species, adding language, especially kinship names for carers with well-defined responsibilities, and marriage, which unites groups of kinfolk and creates networks for the exchange of care of pregnant women, infants, and children.

The human pattern of reproduction results in decreased fertility (number of births), but this is offset by greater survival of offspring, and the net result is that human mothers can have more offspring in their reproductive lifetime than nonhuman primate mothers. More offspring, of course, means more intense social stimulation and interaction, and the greater the advantage of infants with unusually well-developed brains and social skills.

The human style of super cooperation in offspring production and care is best conceptualized as *biocultural reproduction* (BCR), which includes the set of marriage- and kinship-based rules for extra-maternal cooperation in the production, feeding, and care of offspring (Bogin et al., 2014; Bogin et al., 2018). With the assistance of other group members, women not only have more births than other apes but also keep alive more of their offspring until they reach adulthood.

BCR allows humans to create social networks to share the energy and labor costs for producing food, preparing meals, and feeding, caring for, and protecting offspring and their mothers. Reiches and colleagues conceptualized the human style of care and feeding for offspring and their mothers in the form of a "pooled energy budget," which they defined as the combined energetic allocations of all members of a reproductive community that might result in direct or indirect reproductive effort (Reiches et al., 2009; Fig. 6.5). According to Reiches et al., the pooled energy budget allows women to sustain a higher fertility and greater offspring survival than would be possible for energetically isolated individuals. If so, the biobehavioral characteristics of human infancy, childhood, and BCR may have coevolved as derived characteristics of our species, for no living ape species practices these types of behaviors or has a childhood, the ensuing stage of human life history.

BCR is in sharp contrast to the cooperative breeding practiced by some nonhuman species, which is based primarily, if not entirely, on a strict biological kin selection, that is, the degree of genetic relatedness between mothers and their assistants (called alloparents; Lukas & Clutton-Brock, 2012; see Hrdy & Burkart, Chap. 8; Henry & Morelli, Chap. 10, this volume). Human BCR is maintained through socially defined kinship and friendship networks, which operate independently of the degree of genetic relationship (Bogin et al., 2014).

BCR and cooperative breeding have something in common: in both cases, infants receive care from a number of different individuals, which surely contributes to the sociality of that stage in life history. But we think that BCR may contribute something to the social nature of infancy that cooperative breeding does not, at least not

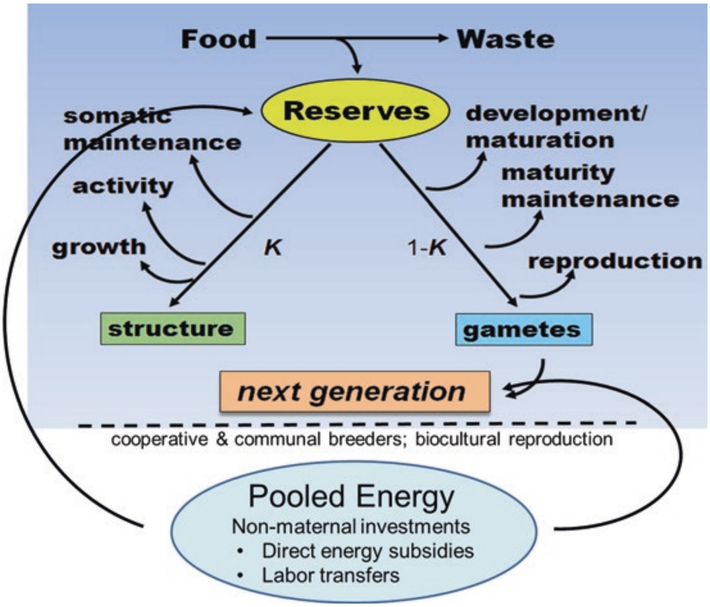

Fig. 6.5 Energy trade-offs in life history. For all animals, energy is extracted from food consumed, digested, absorbed, and metabolized. Otherwise, the energy is lost in waste (feces, metabolic heat loss, etc.). Available energy may be used to build biological reserves, which may be either used by the individual's body for maintenance (including basal metabolic activity and immune activity), physical activity, or growth. These energy uses are labeled "K." The remaining energy, labeled "1-K" (with 1 = 100%), may be used for developing and maintaining the reproductive system and for all aspects of reproduction (gamete production, mate acquisition, gestation, parental investment, etc.). For animal species practicing cooperative and communal breeding (Lukas & Clutton-Brock, 2012), and for human biocultural reproduction (below the broken line), there is an additional input of energy from social group members who directly contribute food or provide labor to breeding females and to their offspring that reduces the energy expenditure of the breeding female (reduces her "K"). The helpers contribute to a "pool" of energy that is shared to enhance reproductive success. Nonhuman animals share the pooled energy with close genetic relatives. Humans share the pooled energy with both genetic kin and socially defined kin. Original figure, B Bogin

to the same degree; it's the breadth and flexibility of social interaction, since in BCR there may be more variation in the carers themselves, including their motivation to participate.

Nearly 40 years ago, Robert Trivers (1974) pointed out that carers have competing responsibilities, including the management of other children, and thus look for opportunities to withdraw care, which infants attempt to forestall by mounting increasingly clever bids for attention, and by monitoring parental responses to these behaviors. When there is competition for care, infants are inclined to invent ways to attract it (Locke, 2006; see Hart, Chap. 15 this volume).

How and when in human evolution biocultural reproduction appeared is unknown, although there are several speculative hypotheses, including greater reliance on stone tools, the use of fire and other extractive technologies (Wells &

Stock, 2007), the evolution of language (Locke & Bogin, 2006a, b), and the increasing size and complexity of social groups leading to brain and cognitive expansion (Burkart et al., 2009; Dunbar, 1998, 2009). Whatever the causes, and it is likely that all these and others were involved, the transition to biocultural reproduction probably coevolved with the biological, behavioral, cognitive, and linguistic characteristics that coalesced with the appearance of Homo sapiens about 300,000 years ago, if not more recently, enabling humans to "stack" offspring into overlapping stages of development. By "stack" we mean that a mother may become pregnant when her current infant is nearing the end of lactation (around 30 months after birth) and may also have one or more other offspring.

It is important to note here that we are not discussing mating practices that take place within and outside of stable pair bonds and marriage. Rather, our focus is on cultural rules for the care and provisioning of offspring, regardless of their genetic relationship to the caregivers. Marriage and kinship-based rules include delegating responsibilities for feeding, clothing, housing, and educating the infants, children, and youth of the society, and often similar rules for the care of women of reproductive age.

The evolved nature of human pregnancy, birth, infancy, and the biocultural reproduction required to care for pregnant women and their offspring likely evolved synergistically with the foundations for human language and culture.

6.5 Infancy as the Most Social Stage

Earlier, we said that humans are more social than other species. Our claim here is that infancy is more social than other stages in life history, making it an unusually human time in our unusually social species. If we were approaching infancy from a purely experiential perspective, it would be easy to see why. Their first exposure to other humans begins *prenatally,* continues *neonatally,* and intensifies during *infancy* proper, when social stimulation is intimate and nearly continuous over a period of several years.

6.5.1 An Odd Asynchrony

One might suppose that everything that develops in infancy does so at the same rate, but this stage in human development is characterized by an oddly productive asynchrony. It appears as an acceleration in the growth of one set of faculties twinned with a slower rate of development in another (i.e., heterochrony, see Bjorklund, Chap. 2, this volume). Infancy and human sociality are shaped by this combination of physical strengths and weaknesses, the proportions of which are unique to our species. Our young, we will suggest, are physically helpless at a time when it is advantageous for them, and our species, to be so.

The odd juxtaposition of strengths and weaknesses that we will address here – the developmental equivalent of footprints and bones – involves motor abilities that emerge altricially, that is, perhaps a third or half of the way into infancy, and cognitive abilities that appear much earlier, or precocially.

6.5.1.1 Motorically Altricial

Human infants are motorically altricial; they cannot walk, hunt, or forage, as many other animals are perfectly equipped to do. The range of variation in the age of achievement for six gross motor milestones is shown in Fig. 6.4. Some infants are more than 1-year-old before able to crawl or stand with assistance. In anything but a protective family environment, altriciality would pose considerable risk, but there are huge advantages to this state.

It seems paradoxical that we humans, so successful among living species, would be born *unable* to do many basic things, and to remain so, from grasping and crawling to climbing and walking. But this "design flaw" is one of our greatest strengths, for it produces a dependency that brings infants into near-constant contact with others – even negotiations with others – at a time when their brain is receiving information about others through the eyes, ears, nose, and skin. If a human is ever to be helpless, infancy seems to be the perfect time, for it sets in motion a reliance on others that, in succeeding stages, is likely to prove more beneficial than strict self-reliance.

In human evolution, a considerable portion of brain development was shifted into the postnatal period (see Bjorklund, Chap. 2; DeSilva, Chap. 3, this volume). Nevertheless, the human newborn's head is relatively large, as the neonatal brain is bigger than that of any other primate (Leutenegger, 1974; Sacher, 1975). It is also large in relation to the maternal birth canal, meaning that birth must occur at a time in gestation when the head is small enough for safe passage. Why? Skeletal evidence suggests that when early hominins began to stand erect and to walk – 4 to 7 million years ago (mya) – pressures on the hip and pelvis were altered (LeBarre, 1954, 1973). Since body weight is transmitted downward through the sacroiliac joint, and ground reaction is transmitted upward through the hip joint, torques are produced at these pressure points. Having the entire weight of the body on the hind limbs caused a ventral tilt of the pelvis and eventually shortened the distance between sacroiliac and hip joints (Leutenegger, 1974, 1980; Ward, 2002). While this made for more efficient bipedal locomotion, it created an "obstetrical dilemma" (Washburn, 1960; see Bjorklund, Chap. 2 and DeSilva, Chap. 3, this volume), inasmuch as it narrowed the birth canal, not an immediately adaptive change given expansions in the human brain and the newborn's head (Dunbar 1992; also see Harvey & Clutton-Brock, 1985; Mithen, 1996).

Another problem for the mother is that the fetal brain is metabolically expensive, therefore a drain on her resources (Dunsworth et al., 2012). It is easier for the mother to meet the costs of infant brain growth via lactation, so long as the mother's diet is enhanced, and her activity expenses reduced, which is exactly the scenario of the human type of hyper-cooperation of mother-infant care derived from BCR with its "pooled energy budget" to support mothers and feed infants, as described earlier.

The evolutionary solution to problems posed by these obstetrical and metabolic dilemmas was an earlier birth, one that occurs, according to Ashley Montagu (1961) and Stephen Jay Gould (1977), nine months too soon. It was a momentous solution, for if less of the infant's brain growth occurred before birth, when infants were in a relatively asocial environment, and more of it would take place later, when they were in direct sensory contact with various individuals. Because of this, the modern infant's brain *does most of its forming during a protracted interval of intense social stimulation* (see Bjorklund, Chap. 2, this volume).

Normally, helplessness would not seem to be a positive trait, but consider the alternative. The central nervous system of altricial animals is in a highly malleable and absorptive state during exposure to a variety of experiences. If newborns were able to wander off shortly after their birth, fully able to feed and protect themselves, they wouldn't receive constant stimulation from others during a time when their brain is developing at a rapid rate, clearly a condition that favors social development. One can hardly think of a developmental circumstance that would more favorably affect the disposition to solve environmental problems socially.

Earlier, we referred to the fact that in a human infancy, there is an odd asynchrony between the rate of motor development, which, as we have seen, occurs fairly slowly, and the rate of cognitive development, which occurs far more rapidly.

6.5.1.2 Cognitively Precocial

If the infant's cognitive abilities were also immature, physical limitations would not be so socially advantageous, but they're not delayed. In fact, they're precocial. Within seconds of their birth, neonates begin – if they haven't already begun – to take in indexical cues, that is, information about the sight, sound, smell, and feel of their mother, in effect, her sensory signature.

Newborns display a preference for the face of their mother within the first day or two days of postnatal life (Field et al., 1984; Bushnell, 2001), a reflection of the fact they are, at the moment of birth, drawn by visual patterns that look remotely like a face. In a study reported by Goren et al. (1975), *nine-minute*-old neonates, who had never seen an unmasked face, looked longer at a somewhat normal facial arrangement than faces with inverted or scrambled features.

Breastfeeding neonates are very sensitive to their mother's odor within two days of birth and can discriminate her from other women using olfactory cues alone (Balogh & Porter, 1986; Cernoch & Porter, 1985; MacFarlane, 1975; Porter et al., 1992).

In the first few days of extrauterine life, neonates display a preference for their mother's voice to the voice of another mother (DeCasper & Fifer, 1980), a preference that continues for at least 20–30 days (Mehler et al., 1978).

6.6 Prenatal Learning

6.6.1 The Ambient Life of a Fetus

The womb is a “sensational” place, one in which the fetus is exposed to stimulation in most if not all sensory modes, from auditory, thermal, and tactile to gustatory, olfactory, and vestibular (Andre et al., 2017). It also affords opportunities for movement at a developmental stage in which much of the infant’s processing machinery is already turned on.

When it comes to physical activity, the fetus does not wait to be born. By 15 weeks, ultrasonographers have been able to record as many as 16 fetal movement patterns that resemble those observed in newborns (de Vries et al., 1982). In one study, somersaults and lateral rotations, which require organized limb and body control, were observed during this period (Suzuki & Yamamuro, 1985).

Since humans are considered the most social species in the world, it is not surprising that the human fetus seems ready to interact with others *at* birth, and it may even be ready to do so *before* birth. Using ultrasound, Umberto Castiello and his colleagues looked for evidence of social interactions in five twin pregnancies (Castiello et al., 2010). They observed a number of movements that appeared to be specifically aimed at the co-twin. In other twin research, it was found that between the 15th and 22nd weeks, prenatally, self-touching decreased and other-touching increased. This contact appeared to be intentional rather than accidental.

6.6.2 Very Early Experience

There is no shortage of books on human development with a subtitle such as *Birth to Three* or some other age. That’s understandable. At some point, certain behaviors have mostly developed and there is little left to say. Specifying a terminal age is understandable, but why begin *as late as* birth? One assumes that it has something to do with the possibility of observation. Certainly, it should not be that birth is the beginning of development, which obviously has occurred since fertilization, and it should not be the onset of postnatal experience, including learning, for studies over the past several decades have established that the intrauterine environment is *sensational* during periods of development in which sensors are operative and the brain is receptive. There is something there to be learned.

The embryologist Gilbert Gottlieb was among the first to show that behaviors appearing early in life are not necessarily – and certainly not entirely – determined by genetic factors. Although his research was on ducks, not humans, his work is instructive. Gottlieb was aware that newly hatched chicks approached conspecific calls more often than heterospecific ones, and that this suggests an innate preference for conspecific vocalization. But Gottlieb noted that duck embryos are capable of hearing and vocalizing three days *before* hatching, while still in the shell. This could enable chicks to hear their own voice in the shell, then, after hatching, to approach the source of maternal vocalization simply because it sounded like their own.

To test this, Gottlieb used surgical glue to "devoice" some embryos but not others. At hatching, control chicks showed the usual conspecific effect, but the vocally deprived chicks, as expected, approached conspecific and heterospecific sources equally often (Gottlieb, 1978). In the research to be reviewed below, we'll encounter studies that were similarly empirical in their approach, equally open to innate and experiential effects.

Although there is little to see in the womb, it now appears that the human fetus has sensory access to maternal vocalization. But, how well can the fetus hear it? Can the fetus hear noises that originate within its mother? They can if she's talking. The fetus can hear sounds across a frequency range that includes the more intense vocal sounds in the adult female voice (see an early review in Locke, 1993). That's partly a function of the auditory sensitivity of the fetus in the final trimester of gestation and the fact that maternal vocalization radiates downward through soft tissues in the mother's body.

6.6.3 Prenatal Learning of Maternal Vocalization

At various times, one of us has wondered why all national languages are spoken when it is clear that signed languages are learned just as readily and work nearly as well (Locke, 1998). One possibility, purely speculative, is that infants are born with a bias for the voice of its mother, therefore, vocalization itself. But how could such a bias be acquired *before birth*?

DeCasper and Fifer (1980) measured the nonnutritive sucking rate of day-old infants; during the same day, the mothers were tape-recorded while reading a children's story. Then, a computer was programmed to play the mother's voice every time a neonate sucked with a longer (or shorter) than normal inter-burst interval, and another mother's voice when the inter-suck interval was shorter (or longer) than the basal measurement. These newborn infants were, thus, in complete control of their listening material. DeCasper and Fifer found that they electively sucked at rates that exposed them to their own mother's voice significantly more often than they sucked to the voice of another mother.

How did the infants acquire this bias in the first day? They didn't. They already had it, but it didn't arrive genetically; it was learned in utero. This was possible because infants, during the final trimester of gestation, are sensitive to indexical and prosodic cues in the maternal voice (DeCasper & Fifer, 1980; DeCasper & Spence, 1986; DeCasper et al., 1994).

Prenatal exposure to maternal prosody may explain a postnatal listening preference for the language spoken by the mother during pregnancy. In a study by Moon, Cooper, and Fifer (1993), it was found that newborns whose mothers had spoken Spanish or English during their pregnancies were presented with recordings of a different woman – a stranger – speaking one of these languages. Using a sucking paradigm in which infants controlled the duration of spoken passages, infants maintained the passage read in their prenatal language longer than the other language, which implies prenatal learning. The mother's tongue was on its way to becoming the infant's mother tongue.

6.6.4 Neonatal Learning

Learning of maternal vocalization continues as learning of the native language. Mehler and his colleagues (1988; Bertoncini et al., 1989) found that at four days of age, babies born in Paris of French-speaking women preferred the sound of French to Russian. Babies whose mothers spoke a different language during pregnancy lacked this preference for French over Russian; indeed, they gave little evidence that they were even able to discriminate these languages.

As infants take in information about vocal characteristics of the ambient language, they also store utterances. There is evidence of this as early as five months, when infants react unusually to their name (Mandel et al., 1995). Here, students of child language find something to explain, something relevant to the learning of words (Locke, 1997).

6.7 A Mind for Care

Earlier, we discussed the Social Brain Hypothesis, which attributes the size of the human brain to the number and complexity of cognitive operations associated with expanded and complex patterns of group living in adults. Here, we consider a second hypothesis, the *Infant Care Hypothesis*, which attributes expansions in the brain and social cognition to intense socialization associated with evolutionary changes in human infancy. Unlike the Social Brain Hypothesis, the Infant Care Hypothesis is concerned with sociality itself, including issues addressed at the beginning of the chapter: the need to be around and to interact with others, and to enjoy the feeling of belonging (Baumeister & Leary, 1995).

6.7.1 Alloparents

In the first postnatal year, infants get a great deal of exposure to the mother, but when normal levels of maternal contact are unavailable or disrupted, neonates naturally expand their focus to include other adults (Hittelman & Dickes, 1979). This, we suggest, augments the social stimulation that they need (Hrdy, 2016).

Anthropologist Sarah Hrdy once wrote that "new modes of child-rearing meant changing our minds" (Hrdy, 2016). Hrdy was referring to the fact that in evolutionary history (and in many places today), infant and child care was spread across multiple *alloparents*, not offered by the mother alone. To be successful, alloparental care required that infants' and children's, "…minds grow within the context of their relationships with family … [and required] … revising our ideas about exactly who constituted 'family'" (Hrdy, 2016, p. 23; see Hrdy & Burkart, Chap. 8, this volume). Hrdy's claim was that the intense care and social bonding provided by multiple carers changed our species' cognitive biases, emotional preferences, attachments to parental figures, and neuroendocrine profiles and networks (Burkart et al., 2009). These changes created new mental phenotypes that promote the ability and desire to adopt the perspective of others (i.e., shared intentionality, pretense, social kinship, and storytelling). Hrdy also suggested a "Mothers-Plus-Others" hypothesis for the new emotional capacities of our hominin ancestors, which promoted human cognitive accomplishments distinguishing our species from the other primates (Hrdy, 2016).

Did intense parenting build our brains? For some reason, Hrdy left her hypothesis as a thought experiment, though, like Dunbar, she did emphasize that social stimulation played a role in evolution of the size and complexity of the primate and human brain. Our Infant Care Hypothesis formally proposes that human infancy is a critical period of development for building the size and neurological complexity of the brain as well as the specifically human behavioral, cognitive, and emotional capacities required for biocultural reproduction, language, kinship, marriage, and related unique human cultural capabilities. It has long been known that infants reared in social isolation experience less brain growth, and are born with smaller heads, than those who are socially reared (Rutter et al., 2012; Sonuga-Barke et al., 2017). There is an extensive literature dating as far back as 1701 that documents the evidence for the relationship between the psychosocial environment and human development (Peiper, 1955). Research in the twentieth century demonstrated the contribution of physical touch, intense social interaction, and love to physical and mental development (Spitz, 1945; Field, 1988, 2007; Goldschmidt, 2006; Rogol, 2020).

Here, we describe one recent natural experimental study by Mackes et al. (2020) showing the critical nature of social interaction during infancy to build a healthy human brain in both size and function. Mackes et al. imaged the brains of 67 young adults (mean age 25.3 years) who were exposed to severe deprivation as infants when confined to Romanian orphanages during the *Ceaușescu* era and then adopted by UK families. The Romanian adoptees suffered between 3 and 41 months of deprivation due mostly to being isolated in their cots, sometimes restrained so that they could lie in only one position. The infants' only interactions with other people were confined to feeding, diaper changing, and bathing, which took place on a fixed schedule. The infants were not held, spoken or sung to, or consoled if crying.

Later, as young adults, these adoptees were compared with 21 nondeprived UK adoptees. The researchers reported that as adults, "Romanian adoptees had substantially smaller total brain volumes than nondeprived adoptees (8.6% reduction), and total brain volume was strongly negatively associated with deprivation duration. This effect persisted after covarying for potential environmental and genetic confounds" (p. 641). The lower right inferior frontal surface area and volume of adoptees were especially smaller and decreased in direct measure with deprivation duration. The adoptees had, "…both lower intelligence quotient (IQ) and higher levels of attention deficit/hyperactivity disorder symptoms" (p. 641). These brain-structure deficits and cognitive-behavioral pathologies were incurred during a socially deprived infancy and could not be overcome despite the enrichment and treatment provided by adoptive families for at least two decades.

Human care of infants via biocultural reproduction optimizes infant brain growth and development and later social-cognitive behavior. We contend that the intense and socially diverse nature of human infant care not only prevents pathology but also stimulates greater brain growth of neurons, neuronal connections, neuroendocrine system, and the development of motor-social-cognitive-emotional capacities. While the Social Brain Hypothesis attributes a number of social-cognitive operations to the size of human groups, the advent of alloparenting – which increased the number of carers from one to many – was undoubtedly responsible for increases in the breadth of social stimulation received by human infants.

To us, the Social Brain Hypothesis makes more sense if it is linked to the Infant Care Hypothesis by way of biocultural reproduction. At all stages of development, brain size enlarged with increases in social group size, especially when there was a greater number of alloparents assisting with infants (as shown in a meta-analysis by Isler & van Shaik, 2012). In a classic feedback relationship, increases in the size of the fetal head contributed to earlier birth, increased infant helplessness, and more diverse alloparental care, intensifying social activity over a period of months and years at precisely the time when brain size increases at its fastest rate. This diversification of social stimulation by multiple alloparental carers undoubtedly broadened and intensified expectations of social stimulation and increased the motivation to solve problems by cooperating with others (Burkart et al., 2009).

6.8 Closing Thoughts

Members of our species are social before they are born – aware of and responsive to the presence and some activities of their mothers – and for reasons that we have discussed, the levels of social stimulation and interaction mightily increase in the months after birth, and continue, unabated, for several years thereafter. There can be little mystery that ours is considered the most social of all animal species.

We began this chapter by quoting zoologist Walter Garstang, who said that to be complete, accounts of human evolution must identify the environmental changes responsible for new traits *in development*, and the reasons why these traits would have conferred contemporaneous reproductive advantages. We took his words to mean that our task was both to discuss the evolution of infancy and the contribution of infancy, once evolved, to characteristics of our species, whenever they might appear. Toward that end, we discussed events, for example, bipedalism and pelvic realignment, that led to altered conditions of birth and care that may have contributed to enhanced sociality.

We emphasized especially the nature of human biocultural reproduction. BCR describes a suite of biological and sociocultural adaptations, including (1) cognitive capacities for nongenetically based marriage and kinship behavior that provide demographically and ecologically flexible, but culturally universal, alloparental care for infants; (2) early weaning, leading to an increased rate of reproduction for mothers; and (3) a life history phase of childhood, characterized by the absence of nursing but considerable ongoing nutritional dependence, creating extended needs for the provision of care by individuals other than the parents and opportunities for intense social interaction and an extended period for brain growth and development. Sometime in human evolution, possibly with the appearance of the first members of the genus *Homo*, there occurred a shift from the typical ape pattern of a unique attachment dependence between the infant and the biological mother to the human pattern, in which attachment is expanded outward to other members of the social group in a locally and culturally defined fashion via language and rules of kinship and marriage. It is this decoupling of allocare from genetic relatedness, more than anything, which sets humans apart from other cooperative breeding species. Biocultural reproduction with its intense and diverse infant care establishes the basis for all of human culture.

Within the more general BCR model, we developed a new understanding of connections between the Social Brain and Infant Care Hypotheses. Where the Social Brain Hypothesis holds that social pressures related to group living enlarged the neocortex – brain space needed to support *cognitive operations* that occur in the adult mind – the Infant Care Hypothesis places a value on social stimulation emerging from infants' receipt, even their own negotiation, of care, contributing to our species' need to relate. In their study of allomaternal care across primate species, Burkart and her colleagues found "the extent of allomaternal care provides the best explanation for the distribution of proactive prosociality among primate species, including humans" (Burkart et al., 2014, p. 3).

In conclusion, our Infant Care Hypothesis, like the Social Brain Hypothesis, is based on changes in the socialization of our species. But ours has less to do with the evolution of *minds*, and more to do with the evolution of *sociality itself* – specifically, the motivation to socialize and to coordinate one's own physical and mental activities with others. We suggest that our disposition to develop and apply our social, and social-cognitive, abilities is best developed during a human infancy, an unusually human time, the most social stage of the most social species.

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Chapter 7
Attachment and Caregiving in the Mother–Infant Dyad: Evolutionary Developmental Psychology Models of their Origins in the Environment of Evolutionary Adaptedness

Sybil L. Hart

Maternal caregiving of infants and infant–maternal bond formation are species-wide features of women and infants. This chapter addresses the origins of these two phenomena, and we begin by addressing maternal caregiving and by asking whether it has a particular form that is known for being presented universally, since this would offer clues as to the nature of a genetic mechanism that may be involved (Durant & Ellis, 2013; Geary, 2000). The outline of an answer emerges upon recognizing that although styles of parenting differ across and within generations and cultures (Bornstein, 2002; Harkness & Super, 2002), breastfeeding has served as the primary source of infant nutrition throughout most of evolutionary history, which allows for conceptualizing it as a hard-wired feature of maternal caregiving. This interpretation of breastfeeding speaks to the possibility that beyond its contribution to caregiving, lactation may have been responsible for the inherited component of another species-wide phenomenon that involves mothers and infants, namely the psychological bond that links mothers and infants to each other. This possibility inspired us to approach the genetic basis of maternal caregiving and infant–maternal bond formation through inquiry into inherited features of lactation.

The chapter begins by focusing on aspects of lactation that are known to be inherited. These are physiological characteristics that are evident in contemporary nurslings and their mothers. This material is followed by sections on psychological features of lactation and the ecological conditions under which they arose. These conditions are believed to have been those that were inhabited by modern humans hundreds of thousands of years ago during the Pleistocene epoch, in settings known as the *environment of evolutionary adaptedness* (*EEA*). We then theorize on physiological, psychological, and ecological features of lactation in the EEA, and the

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way in which these could have coalesced so as to have underpinned universality in maternal caregiving of infants, the bond that links infants to their mothers, and that which links mothers to their infants. We follow with material on maternal caregiving and bond formation as features of the mother–weanling relationship, and conclude with suggestions for future research.

7.1 Nurslings as Proximate Influences on Maternal Caregiving

Insight into breastfeeding as a universal form of maternal caregiving can be gleaned by considering particular features that are responsible for its onset in present-day settings during the perinatal period. Breastfeeding does not happen immediately upon parturition. Even in the current era, it is not uncommon for neonates to lose weight during the first week of life. During this interval, maternal hormones, primarily oxytocin and prolactin, already elevated prior to childbirth, increase further. Yet, the reflexive response, known as the *let-down reflex*, that is responsible for milk ejection does not take place without stimulation by an infant's presentation of a behavioral repertoire that constitutes suckling. The repertoire involves an infant's state of mental arousal that enables at least a low level of wakefulness, as well as reflexive movements of the head and mouth, including rooting, latching-on, sucking, and swallowing (Lawrence & Lawrence, 2015; Riordan & Wambach, 2010). At times, the suckling repertoire is accompanied by bodily activity that has been described as a hunger reflex (Sugar, 1976), in which an infant will extend her arms and hands as she reaches for, touches, and strokes or grabs onto a woman's body (Uvnas-Moberg, 2013). Suckling that is required for stimulating the mother's release of prolactin leads to milk synthesis and the release of oxytocin, which causes contractions in breast tissue that force milk to be ejected.

In instances where there are long intervals between feeding sessions, milk synthesis begins to decline. Therefore, frequent bouts of breastfeeding are important, not only for initiating lactation, but also for minimizing risk of *insufficient milk syndrome*. With prolonged interruption, milk synthesis comes to a complete halt that is usually irreversible. Without appropriate substitutes for breast milk, infants are placed at risk of faltering growth (Lawrence & Lawrence, 2015; Riordan & Wambach, 2010). Unlike other newborn reflexes that wither or are replaced within a few months of parturition, and unlike neonatal behaviors, such as imitation, that are present, but unreliable (Keven & Akins, 2016), behaviors responsible for suckling are exceptionally robust. In fact, these reflexes are so robust that infants are routinely provided with commercially available pacifiers that are often in constant use, sometimes throughout the entire duration of infancy.

Breastfeeding has been linked with newborn and premature infants' superior neurobehavioral functioning (Feldman & Eidelman, 2003; Hart et al., 2003, 2011). To some degree, these positive outcomes are attributable to their consumption of a suite of nutrients, growth factors, and hormones in breast milk that play a role in brain development (Belfort, 2017; Horta et al., 2018; Purdy & Melwak, 2013;

Reynolds, 2001). Essential fatty acids (EFAs), especially docosahexaenoic acid (DHA) and arachidonic acid (ARA), are of importance to neurodevelopment by supporting myelination as well as synaptic and membrane function (Guesnet & Alessandri, 2011; Guxens et al., 2011; Innis, 2008). Greater concentrations of DHA in breast milk have been found associated with neonates' superior ability to maintain optimal arousal (Hart et al., 2006), and with infants' and toddlers' heightened visual attention and reduced distractibility (Colombo et al., 2004). In low- and middle-income countries, where breastfeeding is less likely to be confounded by self-selection, longer durations of breastfeeding have been associated with children's greater academic attainment and higher IQ. In part, these dose–response relationships have been attributed to children's prior consumption of DHA in breast milk (Prado & Dewey, 2014).

Cortisol is a hormone that is found in breast milk (Jonas et al., 2018; Neelon et al., 2015). Consistent with evidence that umbilical cord-blood levels of cortisol are associated with alertness in neonates (Bell et al., 2012), greater concentrations of cortisol in breast milk have been associated with superior behavioral regulation in neonates (Hart et al., 2004) and with amplified emotional reactivity in infants (Grey et al., 2013; Nolvi et al., 2018). Secretory immunoglobulin A (SIgA) is an immunoprotein found in breast milk that has been linked with neonates' superior ability to orient to social stimuli (Hart et al., 2004). Breast milk has also been linked with analgesic effects (Gray et al., 2002; Upadhyay et al., 2004), calming effects during infant exposure to painful procedures (Baudesson de Chanville et al., 2017; Nishitani et al., 2009), and more robust recovery during treatment for opioid exposure (Bogen & Whalen, 2019; Welle-Strand et al., 2013).

These characteristics of breastfed infants translate into decreases in fussiness along with increases in eye contact and attentiveness, features that facilitate the infant's capacity to orient to social stimuli and elicit adult attention in return (Beebe et al., 2005). Features that prompt caregiver attentiveness are especially effective when they include presentations of positive affect, which is a feature that amplifies the extent to which infants are found appealing by caregivers. Adults are receptive toward smiling by infants (Messenger, 2008; Strathearn et al., 2008), especially if the adults are lactating mothers (Krol et al., 2014). Reciprocally, infants with greater experience of breastfeeding are particularly receptive toward adult figures' expressions of happiness (Krol et al., 2015). With these capacities for social engagement, nurslings are able to communicate in a manner that prompts and reinforces caregiving, which is a notable achievement given that it takes place early in development, when infants are ill-equipped to do so in any other way.

In sum, the infant's suckling repertoire is pivotal, not only to initiating breastfeeding, but toward maintaining it as well. Some evidence suggests that the benefits of breast milk to infant health and general sense of well-being are augmented by constituents, including DHA, cortisol, and SIgA, that support infants' cognitive functioning, and by features that boost pain tolerance, calmness, and resilience. These attributes enhance the infant's capacity for sociality so as to heighten the ability to entice caregiver attention. Equipped in this manner, nurslings are active agents in the care that they enlist from their mothers, which establishes them as proximate influences on maternal caregiving.

7.2 Lactation-Based Cohesion

Milk production that is precipitated by infant suckling is notable in that it too is behavior that rests on physiological influences. Because the let-down reflex is an involuntary form of maternal parenting behavior, breastfeeding can be practiced even if a nursing mother is not fully cognizant of whether her infant is in need of care, nor the precise nature of care that is needed. For example, a lactating mother, even an inexperienced primipara, will breastfeed her infant even if she is not fully recovered from childbirth, nor fully awake. She would find that breastfeeding usually attenuates infant distress, and this would be the case even if she had failed to correctly identify whether her infant was distressed by hunger or by any number of other possible sources of distress that are often alleviated by breastfeeding.

What is more, lactation does not depend on maternal affect. Feelings of tenderness and affection are regular features of nursing mothers, but they are not necessary preconditions for a mother to decide to breastfeed. A mother can even feel disinclined to breastfeed, yet find that an untimely eruption of breast milk cannot be ignored for long. Once the let-down reflex triggers contractions, a mother's breasts become swollen with milk and she has little choice but to suckle her infant. Unless she has access to a breast pump, failure to do so can result in engorgement and eventually to mastitis, an infection of breast tissue that causes fever and pain. Spontaneity in the milk ejection reflex is vividly illustrated once breastfeeding has been fully established, usually within a few weeks of parturition. From this point onward, the mere sound of an infant crying—that is, even without stimulation of suckling—is enough to trigger the let-down reflex (Lawrence & Lawrence, 2015; Riordan & Wambach, 2010).

Because milk removal by the infant precipitates milk synthesis by the mother, the ensuing relationship is characterized as bidirectional (Ventura & Terndrup, 2016). In literature on lactation, it is described as a "biological dialog" (Raju, 2011) that involves "cue-based co-regulated feeding" (Shaker, 2013; Thoyre et al., 2013). These depictions speak to recognizing the nursling–mother relationship as a biobehavioral bond marked by cycles of bidirectional involvement that connect nurslings to their mothers much as they connect mothers to their nurslings. The reciprocal nature of the relationship denotes connectedness that we refer to as *lactation-based cohesion*.

7.3 Mothers' Milk and Infant Survival in the EEA

Due to its biological underpinnings, lactation-based cohesion that arose in the EEA is likely to resemble the bonds that occur among contemporary breastfeeding dyads (Jonas & Woodside, 2016) and to operate in a manner that is similar to that seen in contemporary harsh environments where the rate of mortality in children is as high as it is understood to have been in the EEA, almost 50% (Volk & Atkinson, 2008, 2013; see McDowell & Volk, Chap. 5, this volume). In countries marked by extreme poverty, mortality in children is greatest among those up to the age of 5 years, and the major cause of death is infectious disease, specifically, respiratory tract infections, followed by diarrheal diseases, HIV, and tuberculosis (Christian, 2008; Naghavi et al., 2017; see McDowell & Volk, Chap. 5). Due to the increased metabolic demands that are imposed by disease, undernutrition independently worsens the outcomes of illness, which is why death rates among malnourished children are twice as high as those of well-nourished children. Among those who are severely malnourished, death rates are seven times greater (Alberda et al., 2006; Bhutta et al., 2017; Worthman, 2010). Acutely malnourished children are also vulnerable to diseases, such as marasmus and kwashiorkor, that have etiologies that are specific to various types of severe nutritional deficiencies (de Onis, 2008; Prentice, 1991).

A major contributor to malnutrition in young children is premature weaning, that is, weaning of infants under the age of 4 years. Due to scarcity of energy- and nutrient-rich, easily digestible sources of nutrition, infants in this age range depend on breast milk for macronutrients (carbohydrates, proteins, and fats) and micronutrients (vitamins, minerals, and trace elements). Furthermore, vulnerability to disease, which is typical of infants due to their immature immune systems, compels reliance on breast milk for its immunomodulatory, antimicrobial, and anti-inflammatory properties that provide passive resistance to disease. In environments marked by both nutritional deprivation and poorly functioning health systems, 2- and 3-year-old weanlings are exceptionally vulnerable to cognitive deficits associated with impaired brain structure and function, growth faltering, morbidity, and mortality (Black et al., 2015; Prado & Dewey, 2014).

Appreciation of conditions in present-day harsh environments leads to understanding the EEA as a setting where morbidity and mortality were especially prevalent among infants and children up to 5 years of age. The leading causes of death are likely to have been infectious diseases and malnutrition-related diseases. Due to food scarcity and the absence of health systems, it seems likely that the infants and young children who were able to survive did so with the benefit of nutrients and immunoprotective properties that they derived from consuming breast milk. Because dependence on breast milk lasted throughout the first 3 years of life, lactation-based cohesion must have been a species-wide feature of ancestral infant–maternal dyads that lasted approximately 3 years.

7.4 Ancestral Women and Infants

Physiological data for hunter-gatherer populations indicate that the metabolic costs involved in energy expenditure by ancestral hunter-gatherers resemble those of present-day Westerners (Pontzer et al., 2012), and so it seems likely that the metabolic costs of lactation are also largely unchanged. In contemporary settings, these surpass those that are already elevated during pregnancy in that they involve further increases by 25% for energy needs, 54% for protein needs, and 0–93% for various vitamins and minerals (Dewey & Cohen, 2007). These costs are met by mothers increasing energy intake, by decreasing physical activity, and by utilizing existing stores of fat tissue that can jeopardize maternal nutritional status (Dufour & Sauther, 2002; Quinn, 2016).

For ancestral mothers, the energy costs of breastfeeding are believed to have been so steep as to have placed them at increased risk of malnutrition. It is also notable that these women are believed to have breastfed throughout most of an interbirth interval (IBI) that was soon followed by a subsequent pregnancy that would again lead to breastfeeding during most of the next IBI that was similar in duration (Davis, 1986; Konner & Worthman, 1980; White, 2014). Consequently, breastfeeding resulted in increased risk of malnutrition that lasted throughout the majority of time when a 16- to 40-year-old ancestral woman was not pregnant, which amounted to almost the entire reproductive lifespan. These risks would have been exacerbated in cases where breastfeeding coincided with pregnancy, which requires energetic support for overlapping nutritionally dependent offspring, one a nursling the other a fetus (Conde-Agudelo et al., 2000; Ronsmans, et al., 2006).

In harsh present-day settings, women who give birth following an IBI of only 9–14 months are 2.5 times less likely to survive childbirth than women who give birth following an IBI of 27–32 months (USAID, 2002). To some degree, these risks are offset by the effect of lactation on birth spacing (Berhan & Berhan, 2014; Kassebaum et al., 2014). In the EEA, where effective methods of contraception were nonexistent, lactation served as the only mechanism that played a role in regulating fecundity, which it did by interfering with the release of hormones necessary for triggering ovulation, especially in undernourished women. By causing delay in a subsequent pregnancy, breastfeeding helped extend IBIs so that in most cases these could last as long as 4 years (Bocquet-Appel, 2011; Davis, 1986). In light of the magnitude of the costs to ancestral women as well as the time and energy that they allocated to breastfeeding, it can be argued that, much as it is recognized as a defining feature of ancestral infants (Geary & Bjorklund, 2000), breastfeeding deserves to be recognized as a defining feature of ancestral women.

Unlike the biology of lactation, which is largely unchanged, ecological factors that help sustain it have undergone changes over time. The most significant one took place during the Neolithic age, approximately 9000 BCE, with the emergence of agrarian villages where the adoption of plant and animal husbandry yielded alternatives to breast milk. The domestication of certain mammals meant that animal milks, such as sheep's and goats' milk, were available to use as substitutes for breast milk. At the same time, the advent of agriculture yielded complementary foods, particularly grains, such as maize, that were soft enough to be consumed by infants lacking full dentition (Bocquet-Appel, 2011; Howcroft et al., 2012). Since breastfeeding is likely to have entailed energy expenditure that placed ancestral mothers at increased risk of malnutrition, it is not surprising that they turned to substituting breast milk with animal milks and grains as soon as these options became available during the Neolithic age (Davis, 1986; Dettwyler, 1995; Ellison, 1995).

This had unfortunate implications for Neolithic-age toddlers. The availability of breast milk substitutes made it possible for mothers to lower the metabolic cost of lactation through the early introduction of complementary foods and by shortening the duration of breastfeeding to intervals that were less than 3 years. However, without any alternative method of birth control, the IBI was not as well preserved, and so a subsequent pregnancy quickly ensued, along with heightened probability of depleted milk production, producing supplies of breast milk that were deficient in nutrient content, and premature weaning (Spielmann, 1989; Stuart-Macadam, 1995). These outcomes of short IBIs contributed to the rise in rates of mortality in young children during the Neolithic era (Bocquet-Appel, 2011; Howcroft et al., 2012), and they continue to do so in contemporary harsh environments (Bøhler et al., 1995; Dyson, 1977; Fotso et al., 2013; Khoshed et al., 2000). The detrimental impact of short subsequent IBIs, that is, the period of time from birth until a sibling's arrival, on toddler mortality has been well documented in public health and epidemiology reports. These frequently attribute it to undernutrition as a consequence of premature weaning (Bøhler & Bergström, 1995; Jakobsen et al., 2003; Nath et al., 1994; Thapa et al., 1988). Tragically, this scenario is so prevalent that *kwashiorkor* is a word in the Ga language that literally means, "the disease the deposed baby gets when the next one is born" (Williams et al., 1935, p. 1151).

Until 9000 BCE, and throughout human and pre-human evolutionary history, our ancestors lived in pre-agrarian societies, made up of nomadic tribes of hunters and gatherers. They were still living in this way when the EEA arose, 200,000 to 300,000 years ago (Galway-Witham & Stringer, 2018), with the appearance of modern *Homo sapiens*. In these societies, food sharing is thought to have been commonplace (Kaplan et al., 2005), except when it came to sharing breast milk. Allomaternal breastfeeding could not have been customary since these thinly populated clans consisted of only approximately 50 persons including children (Eibl-Eibesfeldt, 1989; Narvaez et al., 2014), and so lactating mothers could not have been numerous. Moreover, the few who may have been present would have been reluctant to share a resource as precious and depleted as their breast milk because doing so would have come at a cost to their own infants' viability (Hart, 2016a), which was a sacrifice that most women were unwilling to offer (Hrdy, 2007).

Grandmothers may have been willing to invest in their grandchildren (Hawkes et al., 1997; Sear et al., 2002) by breastfeeding (Williams, 1933). Although this may have provided infants with comfort, it is difficult to see how a possibly undernourished ancestral grandmother who had reached reproductive senescence could have had much to offer in the way of nutrition. Younger, premenopausal grandmothers were more likely to produce breast milk, but they would have reserved it for infants of their own. Lactating women who were childless, usually as a consequence of infant mortality, were the most likely candidates for providing dedicated service as wet nurses, in that doing so would not have imperiled any biological offspring. However, these women would have been scarce (Dettwyler, 1995; Stuart-Macadam, 1995). Even in contemporary traditional societies, allomaternal breastfeeding is not normative (Hewlett & Winn, 2014) and is usually limited to cases where it has been compelled by perinatal morbidity and mortality (Terashima, 2014). In a similar vein, reports on behavior of primates include observations that langur mothers rarely suckled infants other than their own offspring (Hrdy, 1977). Consequently, it seems likely that an ancestral infant's *own* mother was his sole source of breast milk (Hart, 2016a).

Taken together, lactation was costly for ancestral women, but it also helped delay a subsequent pregnancy. Doing so benefited ancestral toddlers' chances of survival by helping preserve the IBI. This interval was crucial to toddlers' survival since threat posed by a newborn sibling (Bjorklund, Chap. 2, this volume; Bjorklund & Ellis, 2014; Myers & Bjorklund, 2018; Hart, Chap. 15, this volume; Salmon & Hehman Chap. 9, this volume; Trivers, 1974) was forestalled during the IBI, which gave toddlers protection against competition with a newborn sibling while they were at an age when being deprived of breast milk placed them at increased risk of malnutrition, morbidity, and mortality. For ancestral toddlers, this nature of risk would have been inevitable in that the ever-present risks of hunger and disease were exacerbated by having to give up mothers' milk to another child, and in most cases, the other child was a newborn sibling. Given the energetic cost of milk synthesis and the limited availability of healthy breast milk substitutes and allomaternal breastfeeding, a closely spaced subsequent pregnancy presented undernourished ancestral mothers with the dilemma of having to sustain two offspring with a supply of breast milk that was adequate for only one. To avoid placing both at risk, they would have chosen to suckle only one, and the one they usually chose was the more vulnerable newborn infant rather than the toddler.

Finally, it is conceivable that by causing delay in a subsequent pregnancy, breastfeeding benefited ancestral toddlers' chances of survival by preserving the IBI as a period of time during which they retained some protection against the lethal ramifications of fast reproductive pace. In the absence of protection against short interpregnancy intervals (IPIs), toddlers were placed at increased risk of morbidity and mortality by finding themselves, not only malnourished and vulnerable to disease, but also motherless.

7.5 Lactation-Based Caregiving

The benefits of breastfeeding to ancestral infants' survival that stemmed from consuming breast milk and extending the IBI are likely to have been augmented by benefits that relate to the quality of maternal caregiving. Recall that the let-down reflex can be triggered in a lactating mother simply upon hearing her infant cry. In fact, her infant's scent or the mere thought that her infant might be hungry are enough to trigger the reflex. Amazingly, the stimulus infant does not even have to be her own child (Gallup Jr et al., 2010). Given that medical complications of malnutrition and malnutrition-related disease were the leading causes of death, it is difficult to overstate the significance of this manner of maternal responsivity.

Involuntary responsivity of this nature corresponds with findings on voluntary forms. Studies that have included controls for confounds that stem from self-selection, such as maternal age, education, income, and marital status, have consistently observed breastfeeding mothers' heightened responsivity to their infants' cues (Britton & Gronwaldt, 2006; Edwards et al., 2015; Else-Quest et al., 2003). The problem of self-selection has also been addressed in research that examined dose–response effects. Greater breastfeeding has been associated with greater maternal sensitivity (Smith & Ellwood, 2011; Tharner et al., 2012; Weaver et al., 2018). In a different line of work, several studies reported lower incidences of child maltreatment in cases where the perpetrators were or had been breastfeeding mothers (Kelly et al., 2017; Kremer & Kremer, 2018; Strathearn et al., 2009). These studies followed earlier reports that linked breastfeeding with lower incidence of infant abandonment (Buranasin, 1991; Lvoff et al., 2000).

The basis of such protectiveness is poorly understood (Ventura, 2017), though several possible mechanisms have been entertained. Lactation has been associated with greater attentional bias to infant distress (Pearson et al., 2011). The neurological underpinnings of such responsivity were illuminated in work by Kim and associates (Kim et al., 2011) who found that when exposed to the sound of their infants crying, mothers who breastfed differed from formula-feeding mothers by showing greater activation in regions of the brain that are linked with sensitivity during mother–infant interactions. Breastfeeding has also been associated with feelings of greater calmness, reduced symptoms of anxiety, and depression (Groër, 2005**;** Mezzacappa et al., 2005**;** Mezzacappa & Katkin, 2002), and heightened resilience following mistreatment (Kendall-Tackett et al., 2013; Miller-Graff & Scheid, 2019). Breastfeeding mothers who suffer from depression are less inclined to exhibit intrusive parenting behavior and to perceive their nurslings unfavorably (Field et al., 2002, 2010). Such indices of emotional well-being have been found to correspond with physiological underpinnings that include superior cardiac vagal tone modulation, lower blood pressure, and reduced heart rate reactivity (Hahn-Holbrook et al., 2011; Mezzacappa et al., 2005; Quigley et al., 2017). In a similar vein, atypical EEG patterns that can characterize depressed mothers have been absent in depressed mothers who breastfeed (Hambali et al., 2015; Jones et al., 2016). Breastfeeding is also associated with the neuropeptide oxytocin. Elevated levels of this hormone have been associated with maternal responsivity to infant distress (Kim et al., 2014), and with lactating women's lower symptoms of depression and anxiety (Stuebe et al., 2013). More generally, oxytocin has been associated with the proclivity toward the formation of social bonds (Dozier, 2000; Feldman et al., 2007; Swain et al., 2014).

Breastfeeding has also been associated with heightened maternal responsivity to infants' positively valenced cues, specifically smiling (Krol et al., 2014). Infants' full cheeks are thought to act as a stimulus that prompts adults to provide caregiving (Eibl-Eibesfeldt, 1989; Glocker et al., 2009). It seems likely that in cases where the adult happened to be an ancestral infant's lactating mother, she would have provided caregiving by breastfeeding. In addition, she may have interpreted her nursling's full cheeks as a sign that it had been because of *her* milk that her infant was thriving. Sentiment of this nature has been identified as a factor that motivates mothers of infants with compromised health status to continue to breastfeed despite the obstacles involved in doing so (Rossman et al., 2013). This possibility resonates with the construct of breastfeeding self-efficacy—the breastfeeding mother's confidence in her ability to nurture her infant. In contemporary settings, it is a predictor of prolonged lactation (Blyth et al., 2002; Thomas-Jackson et al., 2016), and so it may have operated comparably in ancestral settings.

In sum, the breastfeeding mother's manner of caregiving of nurslings is notable for being characterized by greater responsivity to infant hunger, distress, and positive emotionality, as well as by lower risk of child maltreatment and abandonment. These patterns highlight lactation as a protective influence on the quality of maternal caregiving. Efforts to explain such protectiveness have pointed to higher vagal tone and neuroendocrine substrates of lactation that are associated with activation in regions of the brain that are linked with sensitivity during mother–infant interactions, and with the breastfeeding mother's more positive mood, feelings of calmness, resilience, and attentional bias to infant distress. Increases in the breastfeeding mother's release of oxytocin have been associated with maternal responsivity to infant distress, lower symptoms of depression and anxiety, and may enhance the proclivity toward the formation of social bonds with her infant.

Associations of this nature lead to conjecture that the neuroendocrine profile of lactation is a mechanism that is responsible not only for breast milk synthesis and built-in forms of maternal responsivity, as in the let-down reflex, but also for supporting voluntary behavior characterized by receptiveness to nurslings as proximate stimuli of caregiving. Thus, we posit the construct of *lactation-based caregiving* to capture maternal caregiving of nurslings that is delineated by presentations of voluntary and involuntary responsivity to infant cues that are underpinned by physiological features of lactation. Furthermore, we submit that lactation-based caregiving must have been a salient feature of mothers of infants in the EEA. Given the steep costs of breastfeeding, its neuroendocrine underpinnings are likely to have operated as protective influences that factored into an ancestral woman's decision to breastfeed, rather than abandon, her infant.

7.6 Lactation-Based Caregiving and Cohesion Come to Conclusion

Unlike infants, for whom breastfeeding came with few, if any, costs, lactation was costly for ancestral mothers, and so it is not surprising that in most cases it was terminated, not by infants, but by their mothers upon deciding that it was time for weaning to come to conclusion. As we have shown, that decision would have had serious implications for ancestral infants' chances of survival. Therefore, it is thought that unless weaning was compelled by a subsequent pregnancy, an ancestral mother was likely to concede to her nursling's demand for prolonged breastfeeding. However, she would do so only until the appearance of a sign of her infant's readiness for being fully weaned (Dettwyler, 1995; Stuart-Macadam, 1995).

By nurslings' third year, maturation of their digestive and immune systems would have reduced their dependence on breast milk for nutrition and passive immunity to disease. Of course, ancestral mothers would not have been aware of such maturation. However, they would have been aware of the eruption of their nurslings' permanent molar teeth. Since nursing mothers must teach their infants how to suckle without biting, ancestral mothers would have been keenly aware of maturation in their infants' dentition. It has been suggested that the appearance of full dentition was interpreted by ancestral mothers as a sign that their infants were now able to consume the available solid foods, such as meat, roots, and nuts, that were difficult to chew without molar teeth. At this point, it would have been apparent that their infants' metabolic requirements could be satisfied without breast milk, which allowed mothers to bring weaning to conclusion (Dettwyler, 1995; Humphrey, 2010; Locke & Bogin, Chap. 6, this volume).

Remarkably, an observable sign of readiness for weaning, molar teeth, happened to appear just as ancestral infants' physiological dependence on breast milk subsided. The overlap in timing may not have been purely by chance (Bjorklund, 2015; Bjorklund & Yunger, 2001; see Bjorklund, Chap. 2, this volume). Rather, it may have been a reflection of an evolved sequence of developments that arose so as to promote infant survival by influencing the timing of weaning so that it would not come to conclusion until infants' digestive and immune systems had matured to the point when breast milk was no longer essential to their survival.

7.7 The Cradle of Attachment

So far in this chapter we have shown that in ancestral times all mothers breastfed their infants, and all infants depended on their mothers' milk for at least 3 years. While promoting infant survival by providing nutrition, passive resistance to disease, and extended IBIs, breastfeeding generated a biobehavioral bond, lactation-based cohesion, arising as a species-wide feature of infant–maternal dyads. We now turn to asking whether 3 years of lactation-based cohesion could have been responsible for the ontogenesis of a type of bond that could withstand being untethered to lactation.

Insight into this issue can be gleaned by considering how ancestral nurslings could have derived psychological benefits from ecological factors associated with breastfeeding. Skin-to-skin body contact and heat transfer are inherent features of lactation that would have engendered feelings of comfort and positive hedonic sensations. These sensations would have been especially salient when experienced within the context of bed-sharing, a practice that was universal among ancestral nursing dyads and one that would translate into extended periods of time during which infants experienced feelings of intimacy (Field & Hernandez-Reif, 2012; Thoman, 2006; Uvnas-Moberg, 2013). Bed-sharing is also believed to have encouraged feelings of safety. Given the degree to which ancestral individuals were at risk of predation, the need for relief from fearfulness would have been especially acute during nighttime, when darkness and cold would have amplified feelings of vulnerability. Indeed, work has shown that when infants were exposed to an eliciting condition where they were separated from their mothers, which is a situation that is thought to elicit fear, those with history of breastfeeding and co-sleeping exhibited lower cortisol reactivity, suggesting superior ability to regulate fearfulness (Beijers et al., 2013).

Since ancestral mothers suckled only one infant at a time (Hart, 2016a), nurslings would have experienced contact with their mothers within contexts that were characterized by exclusivity, or at least a degree of contact that was unparalleled by other children. For nurslings, such priority could have engendered expectations of privileged status in the infant–maternal relationship (Hart, 2016b, 2018; Chap. 15, this volume). Perhaps by signifying promise of fidelity, privileged status allayed deep-seated fears of abandonment that have been noted in young children (Mahler et al., 1975; Winnicott, 1964, 1977). It is also possible that such status infused infants with feelings of "specialness," a sense that is thought to characterize the breastfeeding relationship (Bottorf, 1990, p. 208), while also constituting a core feature of the construct of attachment (Cohen, 1974, p. 207).

Consequently, breastfeeding exposed ancestral nurslings to a constellation of pleasurable sensations. In addition to satiety, physical well-being, and enjoyment of breast milk's sweet taste that stemmed from ingesting breast *milk*, ecological features of breastfeeding endowed infants with psychological experiences of intimacy, exclusivity, safety, and comfort. The salience of such exposure can be appreciated further by recognizing that an overarching feature of lactation relates to the simple fact that breastfeeding commands close physical contact between mothers and infants. In ancestral times, where technologically advanced options, such as tube feeding, were nonexistent, the only way of delivering breast milk to infants was by breastfeeding, and so close physical contact with mother was compulsory. Recall too that until the Neolithic age, lactation was conducted intensively, in that it was practiced without supplementation by breast milk substitutes, such as formula or animal milks, without the assistance of allomaternal nursing, and absent separations between mother and infant that were long enough to either interfere with the mother's ability to maintain her supply of breast milk or cause her discomfort of engorgement. Therefore, ancestral nurslings would have had proximal contact with their mothers that is stunning, not only for the extent to which it entailed profoundly satisfying physical and psychological sensations, but also for the sheer magnitude of its regularity and enduringness throughout periods that lasted several years.

7.8 Transition from Lactation-Based Cohesion to Child-to-Mother Attachment

Proximal contact with a caregiver is widely recognized as the basis of a psychological bond, known as *attachment* (Simpson & Jaeger, Chap. 11, this volume). Notably, this feature of infants is not evident at birth. Rather, it unfolds through a developmental process that takes place during the first three years of life (Bowlby, 1973).

The importance of proximal contact during this time frame has been amply demonstrated in contemporary settings in situations where infants have been separated from their mothers. Such circumstances have been met by infants demonstrating separation protest, followed by despair. The most serious consequences occur in cases involving, “very prolonged or repeated separation during the first three years of life” (Bowlby, 1973, p. 12), whereupon infants demonstrate detachment, a state in which any feelings of connectedness have been relinquished. These observations echoed earlier reports (Heinicke & Westheimer, 1966; Robertson & Robertson, 1971) that for “the normal 2-year-old, being placed in a residential nursery, even if only temporarily, is very likely to be experienced as a traumatic event” (Heinicke & Westheimer, 1966, p. 4). An evolved basis of infants’ vulnerability to trauma of separation from attachment figures was addressed in cross-cultural research (Kagan et al., 1978). This work revealed that separation protest is a universal phenomenon, which points to the involvement of an inherited mechanism in the process through which infant–caregiver attachment unfolds.

Insight into this mechanism can be gleaned by considering that, as discussed earlier in this chapter, the zero-to-three age range was also the time frame during which ancestral infants were vulnerable to the leading causes of mortality: malnutrition and morbidity. The overlap in timing raises the possibility that the infant’s psychological vulnerability to trauma of separation and the physiological vulnerability to starvation and disease arose in tandem, not by chance, but rather as coevolved mechanisms due to their adaptive function during this time frame (Bjorklund, 2015; Bjorklund & Yunger, 2001; see Bjorklund, Chap. 2, this volume). Importantly, each type of vulnerability would have been adaptive by eliciting caregiving, yet the manners of caregiving were distinctive of each other. Whereas psychological vulnerability to trauma of separation compelled dependence on caregivers who were able and willing to provide proximal contact and emotional support (Ainsworth et al., 1978; Bowlby, 1969/84), physiological vulnerability to malnutrition and morbidity compelled dependence on caregivers who were able and willing to provide breast milk.

Most likely, these disparate manners of caregiving came to be paired with each other via a cascade of events in which 3 years of proximal contact with a caregiver that infants required in order to form bonds of attachment were mandated by the 3-year period during which they required breast milk in order to survive. In turn, the 3-year period during which infants required breast milk was assured by the timing of the eruption of molar teeth. Because molar teeth were necessary in order for infants to be able to chew the available foods, and because molar teeth did not appear until infants approached their third year, an ancestral mother’s only way to address her infant’s nutritional needs was by breastfeeding for 3 years. Because contact with an ancestral breastfeeding mother entailed steady and enduring exposure to a constellation of profoundly satisfying sensations, mental representations of mothers as emotionally available caregivers are likely to have ensued. Plausibly, these representations permeated infants’ experiences of the biobehavioral bond that we refer to as lactation-based cohesion so as to have spawned child-to-mother attachment.

As a relationship born of proximal contact, child-to-mother attachment would have resembled attachment relationships with caregivers other than mothers (Ainsworth et al., 1978; Bowlby, 1969/84). However, it would have also been distinguished by at least two features. Crying is known to serve as an elicitor of caregiving (Bowlby, 1969/84) that is easily prompted by sensations of hunger. However, unlike threatening stimuli, such as environmental danger, that can also trigger crying, hunger is perceived endogenously, and so infants are aware of it from the moment of birth. Furthermore, unlike other kinds of endogenously experienced aversive stimuli, such as coldness or fatigue, hunger is encountered inevitably, frequently, and at regular intervals. The earliness and inevitability of regularly perceiving hunger coincides with infants' innate ability to act on hunger cues. Of course, hunger cues that trigger crying also trigger sucking, and both behaviors are among a number of responses, such as clinging and following, that are recognized as proximity-promoting behaviors through which infants initiate contact with a caregiver and invite engagement in a manner that precedes attachment (Ainsworth et al., 1978; Bowlby, 1969/84). However, whereas clinging and following are behaviors that become operative only after several months of development, crying and sucking are within the repertoire of neonates. In most cases, it is demonstrated immediately upon parturition.

Thus, hunger prompted earlier and steadier effort to elicit caregiving from mothers than from other caregivers. In fact, using olfactory cues, breastfed neonates recognize their mothers within the first 48 hours of life (Locke & Bogin, Chap. 6, this volume; Porter et al., 1992). The head start and greater activity along the pathway toward attachment to mother versus the pathways toward attachments to various alloparents would have lent the mother-directed pathway prominence during the period responsible for the onset of hallmarks of attachment, separation protest and jealousy protest, becoming evident by as early as an infant's ninth month (Ainsworth et al., 1978; Bowlby, 1969/84; Hart, 2016a, 2018; see Hart, Chap. 15, this volume). Also, regardless of whether it was cued by hunger, crying must have been an especially effective stimulus of caregiving when it was directed toward an infant's mother. Unlike most alloparents, who could opt to ignore crying without inflicting pain upon themselves, mothers of infants could ignore crying only until the let-down reflex was triggered. At that point, the biology of lactation would have been responsible for increasingly severe discomfort of engorgement that was difficult to alleviate without breastfeeding (Lawrence & Lawrence, 2015; Riordan & Wambach, 2010).

In sum, we propose that child-to-mother attachment originated as an outgrowth of lactation-based cohesion via a pathway that was unique by being embedded within the context of lactation as practiced in the EEA. In this context, ancestral nurslings were guaranteed of steady exposure to a constellation of profoundly satisfying psychological and physiological sensations throughout periods that lasted approximately 3 years, starting from the very moment of birth. Because such experience was specific to contexts that included infants' mothers and because it is likely to have engendered mental representations of mothers as emotionally available caregivers, we theorize that over deep time it accounted for a psychological bond, child-to-mother attachment, arising as the only child–caregiver relationship that is recognized as a species-wide phenomenon.

7.9 Caregiving of Weanlings and Mother-to-Child Attachment

The point at which weaning came to conclusion marked a transition that was pivotal, not only for ancestral weanlings, but for their mothers as well. In the EEA, the juncture would have happened after 3 or more years of breastfeeding at substantial energetic costs for undernourished ancestral women. Earlier in this chapter, we argued that these costs were of such magnitude that it seems unlikely that these women could have borne them without support that they derived from the neuroendocrine profile of lactation. As the foundation of lactation-based caregiving, the profile would have served for years as a protective influence not only on involuntary forms of caregiving, but on voluntary forms as well. Hence, it is conceivable that the loss of such support upon the conclusion of weaning was problematic.

Even in contemporary settings, mothers have been known to be perturbed at this juncture. For some, perturbations stem from hormonal changes involved in postlactational mammary gland involution, the physiological process during which the breast changes from a milk-producing organ to one that is largely quiescent (Gallup Jr et al., 2010). Others have been known to worry that without a dependable parenting strategy that they had relied on for attenuating infant distress, future efforts to provide responsive care would falter. Mothers have also been troubled by the possibility of experiencing sense of loss resulting in symptoms akin to postpartum depression. Some have expressed concerns over lesser feelings of calmness that had coincided with the release of oxytocin (Bottorf, 1990; Parsons, 1978; Susman & Katz, 1988), and diminished experiences of skin-to-skin contact and related sensations, such as infant odor (Fleming et al., 1993; Lundström et al., 2013; Okamoto et al., 2016), that had been sources of pleasure. Concerns of this nature amount to fears that weanlings differ from nurslings in terms of their ability to function as proximate stimuli on maternal caregiving.

These issues point to the possibility that the transition to caring for weanlings would have been especially problematic in environments as harsh as the EEA. Granted, caregiving of weanlings was less costly than lactation-based caregiving of nurslings, but it was still demanding and impactful. Rates of mortality in children are thought to have remained high until children's fifth year, and so child survival was still at stake (Eshed et al., 2004; McDowell & Volk, Chap. 5, this volume). Thus, in order to see to their children's survival and ultimately their own reproductive success and inclusive fitness (Salmon & Hehman, Chap. 9, this volume), it is not unreasonable to postulate that ancestral mothers required some source of support to help sustain behavior as demanding as caring for weanlings. We submit that source of support was mother-to-child attachment, a construct that we define as a psychological mechanism that bound ancestral mothers to their former nurslings. In most cases, this would have been an affectional bond, and although it operated outside the context of lactation, it is construed as a mechanism that was forged during several years of lactation-based cohesion.

Mother-to-child attachment would have underpinned attachment-based caregiving, a psychological foundation that replaced biological underpinnings for upholding caregiving at the juncture when an ancestral mother transitioned from caring for a nursling to caring for a weanling. Notably, in non-contracepting premodern societies where mothers breastfed throughout most of an IBI, the interval between weaning one infant and giving birth to another would not have been lengthy (White, 2014). As is the case at times in contemporary societies (Konner & Worthman, 1980), a woman could have been breastfeeding one infant and gestating another at the very same time. This scenario leads to conjecture that the transition to attachment-based caregiving could have posed challenges for ancestral mothers. Like contemporary mothers, they may have feared that the quality of care would be impaired by hormonal changes, feelings of loss of connectedness that had been ensured during 9 months of pregnancy and several years of breastfeeding, and anxiety over the prospect of having to parent absent support they had derived from various biological and ecological features of lactation. However, the substantiveness of these troubles would have been offset by occurring only during intervals when they were *not* breastfeeding—and these intervals were years apart and relatively brief, possibly as brief as 9 months, or even less.

During these intervals, attachment-based caregiving that was provided to weanlings would have been distributed among weanlings' older siblings. In such cases, ancestral mothers must have realized that it was impossible to satisfy every child's needs. Nevertheless, such concerns are likely to have been allayed upon realizing that children would not be harmed by the dilution of maternal resources since the children's needs could be met by alloparents (Apicella & Crittenden, 2015; Hrdy, 2005; Hrdy & Burkhart, Chap. 8, this volume; Henry & Morelli, Chap. 10, this volume). Overall, these conditions speak to conceptualizing mother-to-child attachment as a mechanism that was important toward upholding maternal caregiving. However, it would have been an infrequently tapped mechanism that could have taken as long as 3 years to unfold. Once in effect, it would have underpinned caregiving that was distributed among any number of weanlings and older offspring who, having access to alternative sources of care, were likely to have been able to survive even if the quality of maternal care was compromised by maternal vulnerability to symptoms of anxiety, depression, and perturbation stemming from hormonal changes. Depending on the quality and availability of allomaternal caregivers, some of these children may have been able to survive without the benefit of maternal caregiving altogether (Sear et al., 2002).

As a form of caregiving that could have been infrequently adopted, slow to unfold, diluted among several offspring, at times unreliable, and advantageous but not imperative to child survival, attachment-based caregiving departed substantially from its roots in lactation. Recall that there were no substitutes for lactation-based caregiving. It would have commenced with minimal delay upon parturition and, being reserved for a single nursling, it was not diluted among several offspring. Furthermore, the ancestral mother's supply of breast milk could not be maintained without suckling at regular intervals, which rendered lactation-based caregiving so reliable that it was essentially guaranteed. Arguably, it was as robust as any form of behavior that is known to have been evident in ancestry. At the very least, it was more reliable than attachment-based caregiving.

To be clear, breastfeeding was integral to maternal parenting of infants—but only after a mother had arrived at the decision to breastfeed, which was *not* guaranteed. Disinvestment, as in maternally perpetrated infanticide, was not unknown (Bjorklund & Jordan, 2013; Hausfater & Hrdy, 2017), which has led to thought that "there is no maternal instinct of a kind that ensures a new mother will provide appropriate care for her infant" (Bjorklund & Jordan, 2013, p. 69). In line with this formulation, we are suggesting that conditions in the EEA were such that a mother had no choice but to breastfeed if she wanted her infant to survive, and that desire could have been motivated neither by instinct nor by love, but rather by a practical reckoning of cost–benefit trade-offs concerning her health, her opportunities for reproduction, her ability to provision, and to retain the resources of her male partner (Salmon & Hehman, Chap. 9, this volume). However, once the decision to breastfeed was made, it is our position that it would have commanded lactation-based caregiving and cohesion which foretold a pathway toward mother-to-child attachment.

7.10 Conclusions and Suggestions for Future Research

In this chapter, we have shown that the life stage of infancy can be defined as the 3-year period of ancestral infants' dependence on caregiving that was provided specifically by their mothers. It would have been bracketed by a newborn's cries of hunger at the moment of birth, and approximately 3 years later by the eruption of full dentition that signaled readiness for weaning. At that juncture, physical maturity in infants' digestive and immune systems, which released them from dependence on their mothers for breast milk, coincided with psychological maturity, which released them from reliance on their mothers for proximal contact. The convergence of physical and psychological maturation would have represented a turning point marked by the conclusion of breastfeeding along with its fitness payoffs for infants: protection against starvation and disease, preservation of the IBI as a haven against usurpation by a newborn sibling, and the psychological benefits of exposure to the constellation of profoundly satisfying experiences that were inherent features of lactation-based caregiving and cohesion.

We also recognize this time frame as the basis of infant–caregiver attachment formation. The infant's need for proximal contact with a caregiver has been established in mainstream psychology as a mechanism that facilitated access to caregivers that altricial infants depended on for survival. In the process of having that need met by a caregiver over the course of 3 years, a bond of attachment was formed with that caregiver (Bowlby, 1969/84). Advancing on that premise, we contend that in most cases that caregiver would have been the infant's mother since infants' 3-year-long need for close contact with a caregiver coincided with the period during which they required breast milk, and the most likely source of breast milk was an infant's mother. Since propinquity is an inherent feature of breastfeeding, steady and enduring experiences of close contact were inevitable features of infant–maternal dyads that would have been responsible for attachment bonds arising as a species-wide feature of humans.

In contemporary Western settings, nutritionally adequate substitutes for breast milk are widely available, and so it is no longer the case that infants' needs for breast milk overlap with those for proximal contact with a caregiver. Hence, maternal caregiving of infants is not synonymous with breastfeeding, and breastfeeding is not a defining feature of present-day Western mothers of infants. Even so, it is a manner of parenting that is known to have been practiced in the EEA that is still in practice today. Moreover, it features psychophysiological underpinnings in both mothers and infants, and these are largely unchanged. These underpinnings highlight features of lactation that were adaptive in the EEA and they appear to continue to exert influence in contemporary settings. Yet, the nature of such influence and the possibility of its continued protectiveness are poorly understood. Therefore, lactation is a relevant and researchable topic of investigative attention that deserves increased attention for its potential to shed light on mothers, infants, and the infant–maternal relationship.

Thus, we conclude by calling for investigative attention to the constructs of lactation-based caregiving and cohesion. Insight into lactation-based caregiving is likely to emerge through attention to constituents of breast milk that help infants set the biological dialog (Raju, 2011) in motion and help sustain their functionality as proximate influences on maternal caregiving over the course of infancy. We also call for efforts to unpack the basis of the breastfeeding mother's responsivity to those cues. Such efforts hold potential to yield fresh insight into maternal caregiving of infants as it originated—under conditions where it was supported, not only by exogenous influences that mothers derived from alloparental caregivers (Hrdy & Burkhart, Chap. 8, this volume; Henry & Morelli, Chap. 10, this volume), but also from endogenously organized influences that mothers derived from various biobehavioral and ecological features of lactation.

Finally, productive efforts to address lactation-based cohesion will require openness to the relevance of questions that pertain to the breastfeeding relationship which is a topic that has been marginalized since the publication of Harlow's (1958) work, *The Nature of Love*. Yet, as rates of breastfeeding rise, and familiarity with it grows, the breastfeeding relationship is increasingly being recognized for entailing "particular unity" (Leckman et al., 2006, p. 120). The basis of such "unity" can be approached through attention to biobehavioral synchrony in the nursling–mother dyad, particularly features that support it in mothers and those that are responsible for the way in which it is experienced by infants. For infants, these physical and psychological experiences derive from sensations of satiety, sweetness, and physical well-being that come from consuming breast milk, as well as ecological features that have been found to engender feelings of intimacy, exclusivity, safety, and comfort. Fruitful treatments would address continuity and change in these experiences over the course of prolonged breastfeeding. Ideally, longitudinal approaches would illuminate ancestral infants' trajectory along a pathway from lactation-based cohesion to bonds of attachment able to withstand being untethered to lactation by the time the life stage of infancy came to conclusion.

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Chapter 8

How Reliance on Allomaternal Care Shapes Primate Development with Special Reference to the Genus *Homo*

Sarah Blaffer Hrdy and Judith M. Burkart

8.1 Setting the Plio-Pleistocene Stage

Apes with the life history attributes of *Homo sapiens* could not have evolved unless male and female allomothers had helped mothers care for and provision their exceedingly costly, slow-maturing offspring born after relatively short inter-birth intervals. We refer to this as the *Cooperative Breeding Hypothesis* (Hrdy, 2009, 2016a). Across the animal world, breeding systems characterized by female or male group members other than parents (alloparents) helping parents to care for and provision offspring have evolved many times in social insects, in 9% of 10,000 species of birds (Cockburn, 2006), and in perhaps 3% of 4500 species of mammals. The prevalence of allomaternal care tends to be higher among social carnivores (Clutton-Brock, 2016). The prevalence of shared care is higher still among primates where females or males other than the mother care for and *at least minimally provision* offspring in more than 30% of species in the Order Primates (Isler & van Schaik, 2012a; Perry, 2020). However, the only primates with *extensive* alloparental provisioning involving group members definitely known not to be the genetic parents as well as parents, occur among humans and in a distantly related subfamily of New World monkeys, the Callitrichidae, containing marmosets and tamarins.

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Various circumstances conducive to the evolution of cooperative breeding pertained among hominins in Plio-Pleistocene Africa (Meindl et al., 2018). These included cohesive social groups containing close relatives; production of increasingly costly, slower maturing young; increasing reliance on hunting and extractive foraging such that immatures began to depend on adults to acquire or process food for them and to facilitate their learning appropriate skills (Clutton-Brock, 2016; Emlen, 1991; Hawkes, 2020; Hrdy, 2009; Jaeggi & van Schaik, 2011; Langen, 2000; O'Connell et al., 2002), and importantly, ecological instability (Burkart et al., 2017; Jetz & Rubenstein, 2011).

Unpredictable rainfall against a background of increasing aridity rendered the emergence of shared provisioning more and more critical for the survival of dependent hominin offspring (Anton et al., 2014; Magill et al., 2013; Morgan et al., 2020; O'Connell et al., 2002; Richerson & Boyd, 2020). In spite of recurring periods of food shortage accompanied by high child mortality, hominin mothers in the line of bipedal apes leading to *Homo sapiens* were producing slower maturing, increasingly large-brained, energetically more costly offspring, yet also beginning to produce infants after shorter intervals. How? Along with others, we have hypothesized that by 2 million years ago with *Homo erectus*, hominin mothers increasingly relied on assistance from other group members to supplement offspring who even after weaning still remained years from nutritional independence (Burkart et al., 2009; Hawkes, 2020; Hawkes et al., 1998; Hrdy, 1999; Konner, 2010; Meehan & Crittenden, 2016). (Fig. 8.1).

It's not easy to date gradual, often subtle, life history changes from the fossil record. This unusual combination of prolonged nutritional dependence accompanied by earlier weaning permitting mothers to resume cycling, conceive again, and reproduce faster, would almost certainly have required some type of allomaternal assistance. In our previous work, we have tentatively tied these life history changes to the early Pleistocence with the emergence of somewhat larger brained *Homo erectus*. However, some paleontologists hypothesize that slower development, and with it, longer dependence and allomaternal assistance, were already getting underway with *Australopithecus* by 3 million or so years ago (De Silva, 2011; Gunz et al., 2020). A few researchers push allomaternal assistance (involving fathers) back even earlier to *Ardipithecus* (Raghanti et al., 2018).

Over time, stacking of closely spaced dependent offspring would further intensify reliance on allomaternal provisioning. By the Pleistocene, we suspect that hominins were adopting even more flexible residence patterns than those found in the other Great Apes (Koenig & Borries, 2012), with "multilocal" residence patterns beginning to resemble those typical of twentieth-century hunter-gatherers (Hill et al., 2011; Marlowe, 2010). Greater female autonomy of movement and the emergence of pair-bonds (why they emerged being a topic still debated) would increase chances that probable fathers and matrilineal kin resided nearby (Behar et al., 2008).

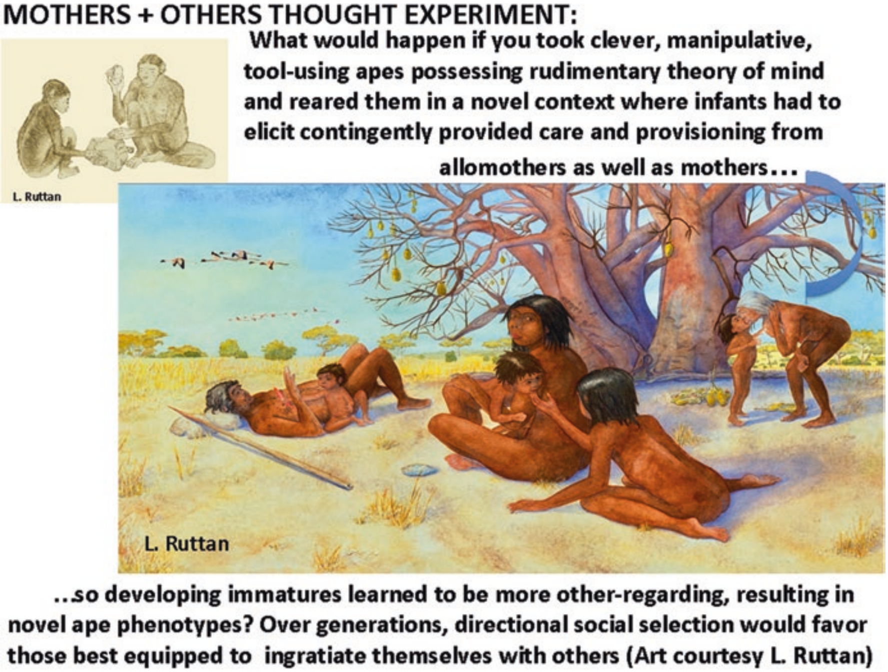
Greater postpartum tolerance on the part of ordinarily possessive ape mothers coevolved with increasing, albeit still facultative, neurophysiological responsiveness on the part of fathers and other allomothers increasingly motivated to care for immatures (Abraham et al., 2014; Numan, 2014; Raghanti et al., 2018). The more

Fig. 8.1 We hypothesize that by two million years ago, with the emergence of *Homo erectus*, mothers were already beginning to wean infants somewhat earlier than among other apes. Earlier weaning and shorter inter-birth intervals were only feasible because alloparents (group members other than genetic parents) as well as parents helped to care for and provision nutritionally dependent, slow-maturing hominin young. ("The real Pleistocene family" as reconstructed by artist Viktor Deak, copyright SbhLit)

dependent upon allomaternal assistance primate mothers are, the more sensitive they become to cues of social support, especially postpartum (Hrdy, 1999, 2016b). Compared with the reflexive protectiveness and possessiveness typical of all but the most stressed or inexperienced Great Ape mothers, postpartum commitment of these hominins would likely have been more conditional. Across traditional societies, mothers are known to abandon at birth infants considered defective as well as adjust parental investment in line with social and ecological circumstances (Hrdy, 1999, chapters 12 and 13; Konner, 1972; Scrimshaw, 1984; see Salmon & Hehman, Chap. 4, this volume).

Infants who could no longer count on being the sole priority of a single-mindedly dedicated mother had to elicit and maintain maternal commitment while also attracting and ingratiating themselves with others. Rewarded when they succeeded, over the course of development, infants learned to express otherwise latent sociocognitive potentials. As we use the term, "ingratiating behaviors" refer to anything an infant does to increase his or her chances of being chosen as the object of beneficent attention (including provisioning) where offspring best at ingratiating themselves with others would be most likely to survive. Over the course of development, these youngsters learned to monitor and be interested in the intentions, thoughts, and feelings of others, even internalizing their preferences. Over generations, youngsters best at doing so would be more likely to survive, resulting in populations of apes emotionally very different from their ancestors (Fig. 8.2).

In this contribution, we reconstruct how growing up in such a social environment may have impacted dependent immatures along with the cascading consequences this would have had on uniquely human forms of learning and language. We start by asking: How would dependent immatures respond to the challenges of eliciting vital, but facultatively proffered, maternal and allomaternal attentions? What would this little ape need to do? Because none of us can go back in time to observe how early hominin infants would have behaved, we draw on evidence for how nonhuman ape and modern human babies responded in "virtual" experiments with and without allomaternal care to test assumptions made here about how hominin infants would have behaved with allomaternal care (Hrdy, 2016a), as well as on evidence from



MOTHERS + OTHERS THOUGHT EXPERIMENT:

What would happen if you took clever, manipulative, tool-using apes possessing rudimentary theory of mind and reared them in a novel context where infants had to elicit contingently provided care and provisioning from allomothers as well as mothers...

..so developing immatures learned to be more other-regarding, resulting in novel ape phenotypes? Over generations, directional social selection would favor those best equipped to ingratiate themselves with others (Art courtesy L. Ruttan)

Fig. 8.2 This thought experiment traces dual ontogenetic and evolutionary processes set in motion when mothers in the line leading to the genus *Homo* began to rely on alloparental care and provisioning to rear increasingly costly, sometimes more closely spaced, offspring. Intermittent behavioral conditioning would encourage youngsters to repeat and refine facial expressions, attitudes, and vocalizations most likely to appeal to potential caretakers. This would lead to the expression of otherwise latent potentials and the formation of novel neural networks. Over generations, these quite novel ape phenotypes would be exposed to directional social selection favoring youngsters best at ingratiating themselves with others, setting in motion a causal chain of adaptive evolution that began with development (West-Eberhard, 2003) other primate infants reared in contexts where they had to rely on allomaternal care and provisioning. Although inevitably speculative, this reconstruction is informed by both comparative evidence and a growing understanding of the survival challenges hominin infants must have confronted.

8.2 Growing Up as a Cooperative Breeder – Callitrichid-Hominin Parallels

As our point of departure, we begin with callitrichid monkeys (comprising marmosets and tamarins), the only extant primates besides humans with *extensive* alloparental in addition to parental care and provisioning of infants. Even though not all elements of human cooperative childcare are also present in callitrichids, they nevertheless face many similar challenges and thus share some critical proximate mechanisms of helping, including hormonal regulators and psychological predispositions (Burkart et al., 2017).

Callitrichids face similar challenges to those hominin infants would have faced, although they do so endowed with far smaller brains. Callitrichid mothers customarily give birth to twins, and due to post-partum oestrus are immediately pregnant again (Erb & Porter, 2017; Garber, 1997). They are thus lactating and gestating at the same time, and the new set of offspring is born before the previous one is fully independent. This costly reproduction is only possible because other group members help by carrying infants, protecting them, and substantially provisioning them (Guerreiro Martins et al., 2019). Like human mothers, callitrichid mothers are highly tolerant toward other group members interested in carrying their babies, and they adjust their maternal investment relative to how much help is available (Bardi et al., 2001; Fite et al., 2005; Hrdy, 1999). Helpers provisioning immatures exhibit highly prosocial motivations (Brügger et al., 2018; Guerreiro Martins et al., 2019). Callitrichid twins are thus confronted with challenges similar to youngsters born to hominin mothers who, when conditions permitted, similarly produced more closely spaced young (in "as-if" litters).

A system reliant on allomaternal care is only feasible if mothers are willing to allow access to their infants and if other group members are interested in caring for offspring that are not their own (Burkart et al., 2009; Burkart et al., 2018b). Among cooperatively breeding primates such as callitrichids, caretaking includes carrying, feeding, and protecting the infants. Infant carrying requires not only high tolerance by mothers but also among all other group members because vulnerable neonates are handed over from one caregiver to the next in coordinated joint actions. Since only mothers lactate, others feed immatures by sharing and actually proffering palatable foods, unusual behaviors among primates. Since immatures are not always close to adults who find food, adults even offer it proactively with food-offering calls. This requires a high level of donative intent. Finally, group members have to coordinate and take turns in activities such as infant transport, vigilance, and protection.

To fulfill these tasks, high levels of social tolerance among adults during everyday life are mandatory. Moreover, a predisposition to not only care about one's own well-being but also about that of others and to be willing to help them is essential for proactive provisioning and the coordination of cooperative activities (Fig. 8.3).

So, is it the case that primate species exhibiting extensive levels of shared care tend to be more cooperative and prosocial than other species? Group Service experiments estimating cooperation in 24 groups belonging to 15 different primate species, including humans, suggests that both social tolerance and proactive prosociality are indeed correlated with the amount of allomaternal care (Burkart et al., 2014, Fig. 8.4).

The coordination of these cooperative activities, and figuring out who is willing to take over an infant to carry it, is smoother if individuals are constantly monitoring the whereabouts, activities, and intentions of their group members. This attentional predisposition toward monitoring others in a relaxed way is evident in the lack of gaze aversion in callitrichid monkeys and has recently been documented with gaze-tracking studies comparing active vision in the cooperatively breeding marmoset and the independently breeding macaque monkeys. The marmosets had longer inspection times for faces, and looked at them directly more frequently compared to the macaques (Nummela et al., 2019). Together, these predispositions per se can already facilitate performance in sociocognitive tasks such as social learning or

Fig. 8.3 Cotton-top tamarins in a group service experiment. The individual on the right-hand side pulls the food reward to within reach of its group members, without being able to get anything for itself. To assess group-level proactive prosociality, the percentage of food items made available to the group is measured

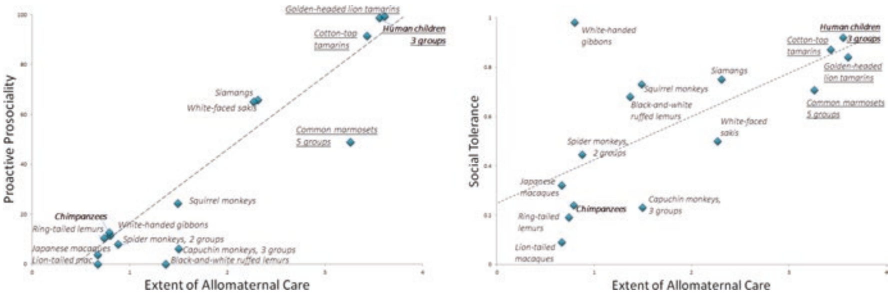


Fig. 8.4 Results from group service experiments described in Burkart et al. (2014). The amount of allomaternal care directly predicts proactive prosociality (left-hand side; % of food items made available to group members) and social tolerance (right-hand side; 1 = high, 0 = low) across primate species, including humans. Great apes are highlighted in bold, cooperatively breeding primates are underlined

cooperative problem-solving (Burkart & van Schaik, 2010), and impact the development of youngsters born into such groups.

In addition, however, immatures face an additional set of specific challenges in such a social environment, and those best at mastering them have increased fitness. Most importantly, immatures have to appeal to and solicit succor from allomothers as well as mothers. Human infants and infants in the distantly related callitrichids appear to have converged on some similar modes of doing so. So how might such solutions be extended and transformed if dependent immatures were endowed with much more powerful ape cognitive systems to begin with? And what might have been the cascading consequences for uniquely human forms of learning and language? It is time to look at little apes reared under the novel circumstances pertaining among Pleistocene hominins.

8.3 The Hominin Infant's to-Do List

8.3.1 *First Order of Business: Appeal to Mother*

Although born with open eyes, able to blurrily seek the eyes of someone else, all newborn apes are otherwise altricial, utterly dependent on others for warmth, protection, locomotion, and food (Bard, 2012; Tomonaga et al., 2004). Fortunately, apes enjoy the built-in mammalian advantage of being born to a mother who during gestation was suffused by hormones lowering her threshold for responding to sounds and smells of a warm, wriggling, fluid-covered baby. If only the newborn can make it to maternal nipples, root, suck, and stimulate lactation, ensuing surges in oxytocin and prolactin, further enhancing her nurturing impulses. With lactation underway, even an inexperienced first-time ape mother becomes increasingly bonded to this newcomer. But over the course of hominin evolution, increasing maternal reliance on allomaternal assistance would have rendered mothers increasingly sensitive to cues of available social support. In the absence of social support, the commitment of even the most experienced human mother falters (see especially Bugos & McCarthy, 1984; Hrdy, 1999, 2016b).

Over evolutionary time, more contingent commitment preadapted human mothers to become more discriminating than other apes. In addition to their parity, prior experience, physical condition, and likely social support, mothers began to respond to specific physical attributes of each infant. Consciously or not, each costly infant was in competition not only with still nutritionally dependent older siblings but also with subsequent infants a mother might bear under ecologically more opportune conditions if only she retrenched upon investment in this one, or bailed out altogether, and resumed cycling sooner. Over the course of the Pleistocene (perhaps earlier?), hominin babies came under increasing pressure to look good and sound vigorous right at birth, advertising that they were full-term, robust, good bets for survival, worth further investment. This challenge may help explain why, over the course of hominin evolution, fetuses began to stockpile adipose tissue at an unlikely time, just prior to squeezing through increasingly narrow birth canals. By now, human neonates are born much fatter than other apes (ca.10–14% body fat contrasted with 3–4% for chimpanzees). No doubt, an extra dollop of energy was initially beneficial for thermoregulation and fueling fast-growing brains, contributing to the emergence in mothers of sensory biases favoring plump babies (Kuzawa et al., 2014). Over time, plumpness may also have come to serve as an infantile equivalent of sex appeal seducing mothers into embarking on a long, exorbitantly costly, endeavor (Hrdy, 1999, chapter 21).

Once increasingly discriminating hominin mothers began to notice associations between birth weight and later outcomes, one of evolution's more consequential self-reinforcing feedback loops would be underway. With runaway social selection (sensu West-Eberhard) for neonatal plumpness underway, extra energy stores became available for brain development, in turn rendering allomaternal provisioning even more essential. Over generations, allomothers as well became attuned to cues of neonatal viability, adjusting levels of commitment accordingly (Hrdy, 2016b).

This brings us to the hominin infant's *second order of business*.

8.3.2 Attract Others

Because hominin mothers as well benefitted from allomaternal assistance, it behoved females to reside near trusted others, matrilineal kin and/or adult males who were probable fathers. Unlike exceedingly possessive Great Ape mothers, mothers in traditional human societies not only tolerate but often encourage postpartum contact with infants. Whether this shift was due to innately more tolerant temperaments, to greater autonomy in selecting who to live among, or both, is not clear. In any event, maternal tolerance facilitated intimate exposure of trusted group members to infantile smells and sounds, generating maternal-like affiliation-promoting neurophysiological transformations in male and female allomothers alike (Abraham et al., 2017; Bales et al., 2004; Carter & Perkeybile, 2018; Hrdy, 2009). Among humans, only a few hours of intimate contact with grandparents can be sufficient to produce surges in oxytocin and reorder priorities (Hrdy, 2019). (Among marmosets, similar oxytocin increases are found not only in mothers, but in all group members after the birth of new babies; Finkenwirth et al., 2016.)

But other factors also enter in, including the allomother's own physical condition and past caretaking experiences, alternatives available, as well as the infant's vulnerability and level of need. Facing this uncertainty, cues from infants themselves to elicit allomaternal involvement would again be paramount. Over time, human allomothers become sensitive to the same viability cues that mothers respond to. Magnetic resonance images of modern human brains reveal that even nulliparous women find the faces of plump, healthy-looking (read full-term) babies "cuter" and more rewarding to look at (Glocker et al., 2009). Not only physical viability cues but also behavioral interactions will attract caregivers. Humans are born with neurological capacities comparable to those of other apes, but differences soon emerge (Lonsdorf et al., 2010). At birth, both chimpanzee and human newborns seek out eyes, are capable of mutual gazing, and caught just right, may imitate someone else's outstretched tongue or other facial expressions (Myowa-Yamakoshi, 2010). Both species exhibit reflexive "fairy smiles," soon to be replaced by more open-eyed "social smiles" in response to someone else. Among newborn chimpanzees, that someone else would always be their own mother (Matsuzawa, 2010). In traditional human societies, however, blearily gazing newborns engage a wider audience (Konner, 1972, 2010). Over time as infants grow accustomed to and learn to trust specific allomothers, the sorts of emotional bonds primate infants forge with mothers prove sufficiently elastic to encompass multiple attachment figures, an average of six attachment figures among the Central African Aka hunter-gatherers Courtney Meehan studied (Meehan & Hawks, 2013). It is not known whether human infants are more prone to forge multiple attachments than are other apes if cared for by both mothers and others because nonhuman apes virtually never are.

A challenge unique to immatures of cooperatively breeding primates is that they are not in continuous contact with their caregiver. This can be buffered by proactive caregiving motivations by adults as in callitrichids where group members monitor babies on carriers eager to take over when necessary (Yamamoto & Box, 1997), or proactively announce that they have found food and are ready to share it. Such provisioning is different from food sharing patterns in other primates, where at most, immatures are passively tolerated when taking their mother's food (Brown et al., 2004; Jaeggi et al., 2010). Nevertheless, without being in constant body contact with a single caregiver, cooperatively breeding immatures face the chronic risk of being overlooked.

Among apes such as chimpanzees, gorillas, or orangutans, newborns constantly held by mothers in direct skin-to-skin contact have less need to smile or vocalize. Calling would only be useful if separated, or later, at weaning, as youngsters object to maternal rejections. Otherwise, low, scarcely audible sounds make more sense than loudly advertising to predators, "vulnerable baby here!" Among primates with shared care, life tends to be noisier. Infants need to stay "in touch without touch" and may complain to prompt maternal retrievals. Infant langur monkeys spend up to 50% of their first day of life being held and carried by females-other-than-mothers, calling incessantly (Hrdy, 1977).

Life is even noisier in animals with biparental and alloparental provisioning where babies beg for treats. This correlation is best documented in birds (Leighton, 2017), but it also holds for callitrichids and humans who fall among the most voluble of primates (Burkart et al., 2018b). Vocalizing starts early in marmosets and tamarins, becoming more frequent and specialized over the course of development. Begging calls spike around weaning when allomaternal provisioning is most critical (Brown et al., 2004; Rapaport & Brown, 2008). But these infants not only are noisy beggars but also engage in babbling-like behaviors, by producing repetitive, random-sounding streams of elements of adult vocalizations that can last for more than a minute. This babbling-like behavior comes with likely cost because it is noisy and makes infants conspicuous to predators. It peaks around weaning when allomaternal provisioning is most critical and turns out to be an effective attention getter, as adults are more likely to approach and interact with immatures that are babbling (Elowson et al., 1998).

Something similar goes on in humans. The onset of babbling roughly coincides with the time hunter-gatherer allomothers begin providing edible treats (discussed below). Within weeks of birth, human infants emit engaging noises. Learning progresses more rapidly if infants notice others reacting. By 10 weeks, some actually take turns vocalizing. The sound of a baby laughing generates an especially powerful stimulus, audible at some distance and signaling emotional engagement (Parsons et al., 2013; Riem Madelon et al., 2017). As babies put two and two together, conditioning plus early glimmerings of intersubjectivity (Trevarthen & Aitken, 2001) encourage them to incorporate sensory biases and preferences of potential caretakers into their own expanding repertoires for ingratiating themselves with others (Gopnik, 2020). By 9 months, little humans go out of their way to be helpful (Warneken & Tomasello, 2006). By 19 months, infants readily share, even offer delectable food items to someone else (Barragan et al., 2020). These human youngsters also care about what others think of their performance (Engelmann et al., 2012; Reddy, 2003).

8.3.3 Vocal Control and More Flexible Vocalizing

Old World monkeys and apes are sophisticated communicators. Vervet monkeys, for example, emit one kind of call to alert group mates of raptors, a different alarm call for terrestrial enemies. They are also sensitive to context, taking into account who is listening and who is out of range, modifying calls accordingly (Cheney & Seyfarth, 1990). Apes, particularly chimpanzees and bonobos, also make extensive use of hands and arms to communicate what they want, extending an arm palm up when requesting something. Even so, their vocal repertoires never achieve the richness, sophistication, and flexibility of their gesturing (Pollick & de Waal, 2007). Rather, nonhuman apes seem surprisingly limited in the kinds of vocalizations they emit (Slocombe & Zuberbühler, 2010), a marked contrast with humans who early in development increase vocal control and start to build larger and more flexible vocal repertoires (Zuberbühler, 2011). So how did this get started?

One important element developed elsewhere concerns the challenges that adults, rather than the immatures of cooperative breeders, are confronted with (Burkart et al., 2018b; Snowdon, 2001). They must increasingly coordinate their activities with others, as when transferring infants back and forth. Their prosociality motivates them to not only share food with others, but also provides information useful to them. Vocal communication is a prime candidate to provide solutions to such challenges. In line with this proposal, the large vocal repertoires of cooperatively breeding birds are driven by an increase in contact and alarm calls (Leighton, 2017). A critical element is added by immatures who grow up in an increasingly voluble environment.

From a comparative perspective, it seems clear that shared care with babies carried by others increases vocalization frequency. Allomaternal provisioning and contingent reinforcement raise the stakes, with begging leading to more calling, especially if immatures have to compete for rewarding attentions (Goldstein et al., 2003; Leighton, 2017). Through the expression of otherwise latent capacities and their subsequent shaping, attention-getting and begging set the stage for selection to favor enhanced vocal control accompanied by goal-oriented shaping of acoustic structure. Indeed, as in marmosets, vocal development in humans occurs earlier than motor development (Gustison et al., 2019). By contrast, infants in constant close contact with single-mindedly dedicated mothers (as in independently breeding species such as chimpanzees) would more often be called upon to cling than cry.

Experiments with marmosets undertaken by Asif Ghazanfar and his team demonstrate how contingent responsiveness by caretakers generates turn-taking and also speeds development of specialized, more mature-sounding calls (Takahashi et al., 2016). For 40 minutes a day during the first 2 months of life, each of a pair of marmoset twins was separated from their parents and allowed to call. Whereas one twin was provided consistent feedback from taped parental calls, the other twin received less consistent feedback. The more reliable the feedback, the more rapidly infants progressed from the coarse, random-sounding vocalizations typical of immatures to cleaner, more tonal, adult-like *phee* calls (Takahashi et al., 2016; Takahashi et al., 2017). By 2–3 months of age, their utterances resembled the turn-taking "conversations" human babies engage in with their caretakers. Chow et al. (2015) further showed that parents actively intervene when immatures make typical mistakes while learning to engage in turn-taking. If immatures get timing wrong and "interrupt" their parents, parents add an extra break before responding. When immatures respond with a wrong call type, the parents themselves interrupt them with the correct *phee* call. In another example of convergent evolution between human cooperative breeders and these tiny-brained, distantly related New World monkeys, Takahashi et al. (2017) noted that infant marmosets responding to contingent reinforcement rely on one of the same circuits to guide their *phee* calls that humans use in speech. The patterning of FoxP2 expression in marmosets' cortico-striatal circuit turns out to be analogous to that in both humans and songbirds. Moreover, a role of oxytocin has recently been proposed for the social motivation and evolution of vocal learning and language (Theofanopoulou et al., 2017), which is consistent with the increase of oxytocin in all group members after the birth of marmoset immatures (Finkenwirth et al., 2016) and its link with prosociality among group members (Finkenwirth & Burkart, 2017).

Observations of golden lion tamarins (*Leontopithecus rosalia*) in Brazil illustrate how these increasingly complex, two-way conversations function in natural habitats (Rapaport, 2011). Solitary adults traverse the treetops hunting for spiders, insects, and small frogs, prying prey from inside holes or tangled foliage. Youngsters learn to locate, stalk, and dexterously extract and dispatch struggling, sometimes biting or stinging, prey. Learning takes time and practice as immatures grow more adept at responding to adults volunteering prey. Deliveries peak near the end of weaning when up to 90% of their diets are provided by (mostly male) allomothers (Rapaport, 2011). Food transfers are often initiated by youngsters begging. But when adults locate food, provisioners too emit staccato "food-offering calls." Mothers, probable fathers, and other helpers extract the food and call the infant to come and get the food out of their hands. As prey-catching efficiency improves, but before youngsters reach adult proficiency, mentors switch from "come and get it" calls to "hey, look here!" calls. Adult calls direct older immatures' attention to a particular patch of substrate where prey have been detected. The finder then waits nearby while the young locate and extract the prey for themselves. Such adjustment of adults to immature skill levels has also been found in other callitrichids in captive studies (cotton-top tamarins, Humle & Snowdon, 2008; common marmosets, Chow et al., 2015; Dell'Mour et al., 2009). As infants increasingly associate an allomother's particular call with a particular reward, they register regularities in how others respond to particular sounds they themselves make.

Opportunities to link own vocal productions to regularities in how others respond to them are particularly evident for babbling (humans) or babbling-like behaviors (callitrichids). In humans, babbling emerges spontaneously at around 5–7 months, about the same time as the emergence of milk teeth, which among hunter-gatherers often coincides with allomothers beginning to offer premasticated and other (sometimes "kiss-fed") treats to infants (Hrdy, 2009). At some level (consciously or not), children recognize that babbling attracts rewarding attention. This may help explain why older children revert to "baby talk" after the birth of a younger sibling (S. Hrdy, personal observation 2019). Interestingly, babbling in marmosets not only attracts caregivers but also speeds up the acquisition of adult-like forms of vocalizations. Moreover, babbling similarly can resume and spike among juvenile marmosets following the birth of new infants in their group (Snowdon & Elowson, 2001). Apparently the same message is being conveyed: "pay attention to *me*!"

"If babbling changes adult behavior in predictable, infant-oriented ways," as Goldstein and colleagues propose, "infants should be able to recognize changes in others' actions as a result of their vocalizations" (Goldstein et al., 2003, p. 8034), launching more goal-oriented vocal control. As with other apes, humans are born with limited motor control over articulation, but beginning around 6 months, humans gain increased vocal control, including more tongue involvement, with vocal tracts continuing to develop over the first 15 months, contributing to greater vocal flexibility and larger vocal repertoires in humans than other apes (Zuberbühler, 2011). Impressed by the coincidence in timing between increased vocal control and the transition from baby-calls to babbling-like streams of consonants and vowels, Klaus Zuberbühler makes a compelling case that increased control derived from hominin infants' need to attract allomaternal attentions (Zuberbühler, 2011, pp. 71, 77–79). Although "babbling" is widely assumed to have first emerged in human children in preparation for the acquisition of spoken language – akin to Mother Nature adding training wheels on a bicycle – it makes more sense (and is far less teleological) to consider the initial emergence of traits like babbling as byproducts of infantile needs to attract caregivers. A key innovation here was increased motor control over articulation. Once vocalizations become subject to voluntary control, they can be shaped via conditional reinforcement, critical preadaptations for the eventual evolution of spoken language.

8.3.4 Incorporate Others' Preferences

These novel capacities emerged within broader sociocognitive contexts where apes were already endowed with rudimentary Theory of Mind (Herrmann et al., 2007; Krupenye et al., 2016; Tomasello, 2019), already utilizing rich gestural repertoires (Pollick & de Waal, 2007), already employing tools and devising new modes of extracting food. At a social level, we suspect new modes of interpreting the preferences of others were also emerging, including new modes of emotional and perspective taking. This could help explain why even though locomotor abilities develop faster in chimpanzees and other extant apes, little humans are the precocious ones in terms of sociocognition and interactive communication. For example, even though chimpanzee infants are gamboling with others and playing much earlier than human children, human babies start to laugh much earlier, by 4 months of age compared to 12 months among wild chimpanzees. More complex social interactions, such as offering comfort, with one individual consoling another with a hug, are seen as early as 13 months in human toddlers, not before 2.4 years in chimpanzees (Bründl et al., 2020). In other words, human infants not only test better than other apes in sociocognitive realms (Herrmann et al., 2007), they develop these prosocial and subjectively interactive capacities early (Wobber et al., 2014), long before they could be any practical use in cooperative foraging or group defense (see Buttelmann, Chap. 13, this volume).

These are early days in the comparative study of anthropoid brain development, but in this context, it is worth noting the unusually early development in human infants of brain areas implicated by inter-personal assessments and decision-making related to social interactions. Initial results from magnetic resonance imagining of developing chimpanzee and human brains suggest that when controlled for absolute size, white matter in the frontal cortex develops more rapidly in humans than in chimpanzees (Sakai et al., 2010, and especially Sakai et al., 2011). By the second half of the first year of life, this rapid trajectory of growth in parts of the brain linked to discriminating between or assessing others is already underway, continuing to expand to age three (see Wilder & Semendeferi, Chap. 8, this volume). Such precocity contrasts with slower maturation in other neural systems such as those controlling locomotion and physical coordination which proceed faster in infant chimpanzees who literally can run circles around their human counterparts. This raises the possibility that even though human infants are notably helpless at birth and through the first months of life, their altriciality is selective. Human infants develop at a slower pace than other primates in physical and locomotive domains, but their capacities for assessing motivations and preferences of others and for intersubjective communication, mature faster (Hrdy, 2014).

By the Late Pleistocene, selection pressures from a range of new subsistence and socioecological challenges would have favored ever greater inter-individual coordination among adults (Boehm, 2012; Tomasello, 2018; Tomasello et al., 1993). But we propose that more other-regarding impulses provided the underpinnings for coordinated behaviors such as group hunting and were already present, having begun to emerge during childhood earlier in the Pleistocene. It is within this broader context that recent proposals linking cooperative breeding not only to the evolution of enhanced capacities for joint attention (Ben Mocha et al., 2019), but also for language, need to be understood (Burkart et al., 2018b; Knight, 2016; Zuberbühler, 2011).

Social selection favoring more flexible communication coincided with other co-evolving feedback loops. But by themselves, neither larger brains nor increased uses for cooperation are sufficient to explain the evolution of language. As psychiatrist Peter Hobson reminds us, "before language there (had to be) something else … that could evolve in tiny steps … that something else was *social engagement with each other*. The links that can join one person's mind with the mind of someone else are, especially to begin with, emotional links" (Hobson, 2004, p. 2, emphasis in original). But what about the foundational steps? Klaus Zuberbühler's speculations point us in a promising direction: "Once vocal control has evolved to help infants secure care, it is only a small step to producing utterances in context-specific ways" (Zuberbühler, 2011, p. 80). But, Zuberbühler adds, such a transformation "may only be possible against a background of other psychological skills, such as the ability to share intentions and attention (Tomasello, 2008), and well-developed comprehension" (Zuberbühler, 2011, p. 80). He expands on Tomasello's insight regarding a "major difference" (Tomasello, 1999) between humans and other primates, involving (as Tomasello would later phrase it) capacities for "intersubjective sharing" (Tomasello & Carpenter, 2007, pp. 121–22).

Eagerness to ingratiate themselves with others would be enhanced by allomaternal care, an interpretation consistent with observations of captive chimpanzees who when co-reared by responsive human caretakers (allomothers of a different species) as well as their mothers, become more eager than wild chimpanzees are to engage in targeted helping of others (Bard, 2012; Yamamoto et al., 2012; reviewed in Hrdy, 2016a). Even though human-tended chimpanzees do not acquire spoken language and other distinctively human traits, they nevertheless develop greater concern for the intentions and goals of others, learning the power that particular gestures, facial expressions, and utterances exert on others. For example, human-reared chimpanzees point to what they want in ways that wild apes almost never do (Tomasello, 2019). The expression of such interactive potentials in ape phenotypes would increase opportunities to share and increase effectiveness of helping. Over the course of human evolution, such opportunities may have increased selection favoring neuroendocrine systems conducive to prosocial responses including the increasingly "dopamine dominated" striatal systems being documented by paleontologists working in concert with neuroscientists (Raghanti et al., 2018). Interactions with processes that opened parental neural care systems to a wider range of social stimuli might have resulted in more unsolicited food sharing and general prosociality (Numan, 2014). Apes who needed to be more interested in the preferences of others would also find it more emotionally rewarding to do so. This chain of admittedly speculative reasoning brings us to a key component to the hominin infant's to-do list.

8.3.5 Add Psychological Dimensions to Kindchenschema

Like all anthropoid primates, apes in the line leading to the genus *Homo* would grow up keenly aware of kin ties, alliances, statuses, and friendships. They would also be alert to competencies and reliability of group mates (Cheney & Seyfarth, 2007; Perry, 2020). The quantitative skills and manipulative capabilities of a chimpanzee or orangutan fall in the same ballpark as those of two-and-a-half-year-old humans. They too exhibit rudimentary capacities for theorizing about what others know (Herrmann et al., 2007; Krupenye et al., 2016; Tomasello, 2020). Our Last Common Ancestors with these apes were already beginning to register what others intended or wanted.

So, imagine such an ape growing up *reliant on* the competencies and motivations of others. If contingent reinforcement from allomothers encourages turn-taking and speeds up acquisition of adult vocalizations in tiny-brained marmosets with only minimal awareness of what another marmoset knows (Burkart & Heschl, 2007; Burkart et al., 2018b), how much more sensitive to the thoughts and preferences of others would apes already attuned to the thoughts and intentions of others become? Contingent allomaternal responses generate new psychological dimensions to *Kindchenschema* as apes growing up this way are conditioned to become more aware that others have preferences worth appealing to.

Youngsters would be conditioned to not only monitor the intentions of others but increasingly to probe their thoughts and feelings so as to better conform to their preferences. Over time, learning which facial expressions, sounds, or conversational rhythms result in solicitude would mature into more sophisticated understanding of how others perceived their own intentions, behaviors, and thoughts and to begin to care about their "reputations."

8.4 New Dimensions to Social Learning

8.4.1 Expanded Avenues

All apes are endowed with inordinate behavioral flexibility along with aptitudes for manipulating objects and imitating others. In the case of chimpanzees and orangutans, knowledge about what to eat, where to find, and how to process it is transmitted vertically during 5–8 years of intimate association with one other trusted individual, their mother. Mothers set the stage for socially induced independent practice (Jaeggi et al., 2010; Schuppli & van Schaik, 2018; Whiten, 1999) or, as in the case of chimpanzee nut-cracking, very occasionally make helpful adjustments (Boesch, 2012; Matsuzawa, 2010). The processes by which little apes copy and learn from others are, however, primarily self-initiated (Humle et al., 2009). Provisioning and shared care broaden this initial context for social learning.

From an early age, youngsters with shared care observe a wider range of role models. For example, cooperatively breeding magpie jays with many helpers become more adept at harvesting arthropods than jays growing up with few helpers (Langen & Vehrencamp, 1998). Furthermore, demonstrators among cooperative breeders tend to be more prosocial, even deliberately helpful (Burkart et al., 2009; Burkart & van Schaik, 2010). Recall that golden lion tamarin allomothers (often probable or possible progenitors) provide the majority of food for nearly weaned infants. Adults call when they have food to offer, but with older immatures, they call them to places where prey is hidden and then immatures have to extract it for themselves. As performance levels plateau, food calls cease. Rapaport (2011, p. 746) compares this progressive, developmentally sensitive behavior coupled with vocalizations that track the needs and skills of youngsters to “teaching-like” behavior on the part of allomothers providing foraging assistance to youngsters (cf. Thornton & McAuliffe, 2006 for cooperatively breeding meerkats).

Incorporating situation-dependent vocalizations enhances effectiveness of these demonstrations while contingently delivered edible rewards rivets the attention of mentees. Anyone who has ever tried to habituate wild creatures, or even skittish domestic ones, knows that food rewards provide the quickest shortcut to taming or training them. Now add to this prosocial-provisioning-vocalizing mix mentalizing mentees eager to accommodate their mentors. Possibilities for information transfer expand exponentially.

8.4.2 Emotionally Modern and Mentalizing Mentees

Even in the absence of detectable Theory of Mind, tiny-brained marmosets prove remarkably prosocial, sharing food or rushing to assist others. Marmosets coordinate with others to crack open tough fruits. They take babies from mothers, then voluntarily return them for nursing (Burkart et al., 2009, 2014; Garber, 1997).

Tamarins even use guided demonstrations accentuated by vocalizations to transmit age-appropriate information (Rapaport, 2011). In this respect, tiny-brained callitrichids converge on something close to what ethnographers studying hunter-gatherers term "natural pedagogy" (Hewlett et al., 2011). Yet, even as tamarins adjust demonstrations to the skill level of pupils, they do so without mentalizing what another knows. Marmosets who readily follow the gaze of another individual do so without registering *what* that individual is seeing (Burkart & Heschl, 2007).

So, what would happen if instead of the reflexive responsiveness of marmosets, the primates undertaking shared care and provisioning of young were already larger-bodied, bipedal, tool-users possessed of rudimentary Theory of Mind, with brains in the process of doubling from the 400 cc of chimpanzees or australopiths to the more expansive brains typical of *Homo erectus*? And what if novel contexts for social development coincided with new foraging tactics, more valuable food packets, and with these, a raised "grey ceiling" so that over time whenever – and for whatever reasons – they became favored, even costlier brains could evolve (Isler & van Schaik, 2012a, 2012b)? Little hominins growing up as cooperative breeders would have opportunities to observe group members of different ages and sexes (Deffner & McElreath, 2020; Gurven et al., 2020; Hawkes, 2020), trust them as their mothers do, gauge their competencies and intentions, decide who was likely to be helpful or not – something modern humans begin to do from as early as 3 months old (Hamlin et al., 2007, 2010). And what if at the same time these infants were beginning to monitor the intentions of others, seeking to conform to their preferences, even beginning to internalize their preferences and at the same time also developing larger and more flexible vocal repertoires?

Many factors were involved in the evolution of language (see Locke & Bogin, Chap. 10, this volume). Some clearly had to do with the unusual way apes in the line leading to *Homo sapiens* were reared. Learning language is a highly social endeavor. Anyone who has ever spent time with babies knows that their mother is not the only person who speaks to them in high-pitched "motherese." It is from eagerly listening to others that youngsters acquire new phonemes and words. Immatures learn new sounds better in the presence of someone else than when by themselves. As young as 9 months, babies watching instructive videos more readily discriminate sounds and learn foreign phonemes if another child is present (Lytle et al., 2018).

Not only current interactions but also past experiences with others influence children's readiness to mentalize what someone else knows. When experimenters set up a computer game where 5-year-olds must explain to someone else where to collect a digital prize, they were told that the unseen other (really the experimenters' confederate) was either a toddler or another 5-year-old. Subjects adjusted instructions accordingly. When told their partner was a toddler, subjects spent longer explaining the game than when they assumed the other child was older. The more days between birth and age four that the subject had spent with others in daycare, the readier that child was to take the other's level of understanding into account, mentalizing what they were likely to already know (Stolk et al., 2013).

8.4.3 Concern for Reputation and Learning

Within the first year of life, hominins approaching this level of emotional modernity would, like behaviorally modern humans today, actively seek to become the object of someone else's attention, feel at least a glimmer of pride when approved of, shame when disapproved of (Reddy, 2003; Trevarthen & Aitken, 2001). After a year or so, these youngsters may have already been disposed to spontaneously offer something interesting or desirable to someone else, the way 14-month-old behaviorally modern humans do today, even proffering an item differing from their own preference (Repacholi & Gopnik, 1997). Although it has long been assumed that the ability to reason about what others are thinking (Theory of Mind, TOM) does not develop until around age 4, as early as 2.5 children clearly have learned how to conform to the preferences of others. Capacities for intuiting the perspectives and preferences of others appear to be supported by different, independently maturing, brain networks. Recent research using magnetic resonance imaging points to different areas of the brain involved in later developing more verbal and explicit TOM. These largely preverbal capacities involved in "implicit theory of mind" emerge earlier in development than do verbal capacities (Wiesmann et al., 2020).

In any event, today's behaviorally modern Western children readily absorb and follow normative rules (Gopnik, 2010, pp. 224–25), expect others to do so, and care desperately about their own reputations (Engelmann et al., 2012). When someone is trying to teach them something, children not only feel pride at success, but want others to know "I did it!" Experiments comparing preschool children with chimpanzees show that the former are far more concerned with managing their reputations. Children, for example, are more likely to share, less likely to steal, if they are being watched by a peer. In contrast, chimpanzees behave the same way whether observed by a groupmate or not (Engelmann et al., 2012).

Equipped with sophisticated language, behaviorally modern children employ flattery to cultivate the goodwill of others as early as 3 or 4 years of age (Fu & Lee, 2007). By early adulthood, behaviorally modern humans in developed countries today find it so pleasurable to talk about themselves that it stimulates the same neural regions as anticipating something delicious to eat would (Tamir & Mitchell, 2012). This concern with presentation of self, reputation, and impressing others may fuel tendencies to register the intentions and preferences of others who are modeling behavior and then conform. This may explain why human children, but not other apes, do not just imitate, they often "over-imitate." Children add all the same ritualized bells and whistles as a demonstrator used even if these are far in excess of procedures needed to accomplish the task (Gopnik, 2010; Nielsen et al., 2014; Whiten et al., 2009). Acute sensitivity to the intentions, thoughts, and preferences of others, eagerness for their approval and a rush of dopamine and other neurochemical rewards when sensing approval, add new dimensions to social learning.

Primatewide, youngsters learn to conform to social rules while growing up. Monkeys and children alike internalize proper etiquette for approaching a dominant group member. But human youngsters display a special eagerness to ingratiate themselves with others and internalize their preferences, adding subjective dimensions to this quest. Evolutionary psychiatrist Randolph Nesse hypothesizes that runaway social selection favoring self-consciousness and concern with reputation in creatures already interested in mentalizing what others think helps to explain why our ancestors evolved the internal self-monitoring we call "a conscience" (Nesse, 2007, 2019).

Whether or not such ingratiating tendencies encourage humans to behave in fair, generous, or civic-minded rather than more self-serving ways is another matter. It probably depends more on socioecological contexts and immediate goals than on what are sometimes taken to be hard-wired moral sensibilities (Bloom, 2013; Hamlin et al., 2010; Hamlin & Wynn, 2011). As early as 6 months, long before language, infants exhibit preferences for helpful versus hurtful others (Hamlin & Wynn, 2011). However, it is unclear how prosocial versus self-interested such preferences are. In experiments simulating *voir dire* in an imaginary courtroom, Melnikoff and Baliley (2018) asked adult subjects who they would prefer in the jury, depending on whether they served as lawyer for the defense or for the prosecution. The researchers were struck by how conditional on peoples' current goals their preferences for moral vs. immoral actors could be. Whatever standards prevail, quests to demonstrate mental and behavioral responses conforming to others' preferences pave the way for internalizing group norms (Gavriletes & Richerson, 2017) and for behavior that group members consider "moral" (Boehm, 2012; Tomasello, 2016). It is exactly this third-party perspective that is so strikingly deficient in nonhuman primates (Burkart et al., 2018a), absent in creatures who otherwise exhibit many critical building blocks for morality (de Waal, 2006; Silk & House, 2016). Other primates may conform to local traditions, but they do not seem to care much if *others* do so or not, and even unusually prosocial primates such as marmosets do not manage their reputations by increasing their helpfulness when observed by others (Burkart et al., 2018a). But like great apes, early hominins would almost certainly have been able to theorize about what others knew (Krupenye et al., 2016) and over the course of human evolution became distinctively motivated to care about their reputations. This same aptitude would presumably have been advantageous for cooperatively breeding marmosets as well, but they may have simply lacked the cognitive infrastructure to register how they appear to others.

8.5 Conclusions

Across taxa, earlier weaning, shorter inter-birth intervals, and longer spans of postweaning (or in the case of birds, post-fledging) dependence are predictable corollaries of cooperative breeding. In the case of the cooperatively breeding apes in the line leading to the genus *Homo*, reliance on care and provisioning from alloparents as well as parents, conditioned dependent immatures to develop an un-ape-like eagerness to monitor and care about the intentions of others, mentalize what they were thinking and feeling, and seek to ingratiate themselves with them leading to the expression and refinement of otherwise latent ape potentials. This novel context for development and social learning coincided with directional social selection (West-Eberhard, 1983, 2003) favoring youngsters best at ingratiating themselves with protectors, mentors, and providers. By 2 million years ago, this combined process of development-plus-social selection was already contributing toward the emergence of cognitive and emotional phenotypes in hominins that were very different from those among our Last Common Ancestors with chimpanzees and other great apes.

Without any foresight on Mother Nature's part concerning how important questing for intersubjective engagement and escalating concerns with reputations would eventually turn out to be, *Homo erectus* infants would have been conditioned to monitor and care about what others were thinking, including thinking about them. They would have been rewarded for internalizing their preferences in ways other apes are not. Resulting concerns with reputation make having a conscience increasingly useful. Long before the emergence of *anatomically modern* big-brained humans by 300,000 years ago (Hublin et al., 2017), or before behaviorally modern humans with symbolic thought and language, these emotionally different apes were already eager to appeal to and help others. Although activities such as group hunting or inter-group warfare are frequently cited as the contexts in which greater inter-individual cooperation, communication skills, and helpfulness evolved, such explanations do not fit with the observation that helpful tendencies emerge early and in both sexes, with girls if anything better able to interpret others' expressions and feelings than boys (Geary, 2018).

By the Late Pleistocene as cooperative hunting of big game, division of labor, and sharing of food became more important, hominins of both sexes must *already* have become predisposed to read the intentions of others in order to coordinate with and help them (Hawkes, 2014; Hrdy, 2009, 2016a; Tomasello & Gonzalez-Cabrera, 2017). By the time coordinated hunting of large animals was established in the human repertoire – whether by 400,000 years ago as in Tomasello's reconstruction or closer to Chris Boehm's "magic number" (Boehm, 2012, p. 313) of 250,000 years ago – it was probably accompanied by "punitive social selection" against stingy or overly domineering men as documented for hunter-gatherer societies (Boehm, 2012, p. 164; Tomasello, 2016, 2018). If so, these members of the genus *Homo* would have already become motivationally very different from their more self-centered, solipsistic ape ancestors. In Boehm's account, sanctions against bullies could extend to exile or even execution of offenders, pressuring them to conform to and adopt group norms, behave in a "moral" way. We suggest that with internalization of norms underway, archaic humans would already have been, from an early age, sensitive to what others felt and thought about them, concerned about personal reputations, and eager to cooperate. Hominins were preadapted to internalize ways of behaving and expressing themselves that others preferred.

The higher-quality food and multiple provisioners that buffered weanlings from recurring food shortages in the Late Pleistocene would have lifted the gray ceiling limiting energy available for brains. The stage was set for these *emotionally modern* early humans to meet new social and ecological challenges in ways that would favor the evolution of even more costly, *anatomically modern*, brains. Expanding social networks and accompanying motivations would also encourage the emergence of more sophisticated modes of vocal communication that would vastly expand both the ability to learn from multiple others (via gossip and teaching) and expand the reach and importance both of normative ways of doing things (Richerson & Boyd, 2020) and of reputations. Such processes would stress conformity and further favor the internalization of group norms and human indoctrinability, hallmarks of *behaviorally modern* humans.

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Chapter 9
Evolutionary Perspectives on Infant-Mother Conflict

Catherine Salmon and Jessica Hehman

The image of mother and child is often celebrated in artistic depictions as a harmonious unit with mother willing to sacrifice all for the well-being of her child. At first glance, it appears to be a relationship that begins in perfect harmony. Images, fictional accounts, and other artistic descriptions of the synergy between mother and child are ubiquitous across time and culture. Historically, they have typically focused on doting adoring mothers and helpless infants, such as in *The Adoration of the Child* by Correggio or *L'Innocence* by William Adolphe Bouguereau, while reports of mothers who risk their own lives by delaying cancer treatment while pregnant are not uncommon in modern news. And yet the harmony often depicted also seems at odds with the modern image of typical parent-child relationships as full of strife. Is either accurate? While mothers typically invest a great deal in their offspring and are often highly devoted (Salmon & Hehman, 2021), the image of the all-sacrificing mother is certainly not always accurate, as data on child neglect, abuse, and infanticide reveal (Daly & Wilson, 1980, 1984, 1988).

From an evolutionary perspective, offspring are the vehicle of parental fitness and, as such, parent-child interactions can be highly cooperative, but they can also involve significant conflict (Salmon, 2008; Salmon & Malcolm, 2011). While there may be agreement about the general goal of offspring fitness, conflict can arise over allocation of investment in one offspring versus another. Activities that advance the fitness of one offspring can potentially reduce the lifetime reproductive success of the mother and vice versa. As a result, we would expect individuals to allocate their parental investment among their offspring in ways that optimize their own inclusive fitness. All other things being equal, parents are equally related to each of their offspring (Daly & Wilson, 1980; Kilner & Hinde, 2008; Trivers, 1974). However, we would expect individual offspring to have somewhat different perspectives as they are more closely related to themselves than their siblings and thus might benefit

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from extracting more than their share of maternal resources (Godfray, 1995; Hinde et al., 2010). In addition, maternal circumstances can impact offspring fitness in ways that may shift maternal investment away from offspring and toward maternal somatic investment or future reproductive success.

In this chapter, we will examine areas of conflict between mothers and infants, beginning with a review of the relevant theoretical literature, and continuing with a focus on both prenatal and postnatal conflict. Some areas in need of further exploration will also be addressed.

9.1 Theoretical Approaches to Mother-Offspring Conflict

From the parental perspective, each individual's overall reproductive effort is a combination of mating effort (time spent obtaining a mate, etc.) and parental effort or investment. Trivers (1972, 1974) defined parental investment as any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive potential) at the cost of the parent's ability to invest in other offspring (either current or future). In many species, it involves such things as food provisioning and protection from predators. In humans, it can involve much more, though for infants pre- and postnatal, food and protection are major components. In general, an offspring's fitness increases with the amount of parental investment it receives. In species with parental care, we can assume that extremely low levels of parental investment may result in offspring loss because a certain amount of investment is necessary for survival. However, a point of diminishing returns is also eventually met at very high levels of parental investment because offspring are unable to capitalize on investment over and above a certain amount. For most mammals, investment in offspring is substantially greater for females than for males (Babchuk et al., 1985; Clutton-Brock, 1991), starting with internal fertilization, gestation, and significant postnatal nutrition via maternal lactation. In fact, it is not an exaggeration to state that the most essential mammalian relationship is that between mother and offspring. Even for pair-bonding humans, where fathers could, and sometimes do contribute to parental care, mothers typically contribute 50% or more to direct infant care (Marlowe, 2005).

Hamilton's rule (1964) can shed light on how parents and offspring behave with regard to parental investment. Hamilton developed the concept of *inclusive fitness*, noting that when we assess the fitness of a trait or behavior, we need to consider its contribution to the reproduction of that individual and to whether it influences the reproductive prospects of its kin. The inequality that sums up the conditions under which a particular behavior would be expected to spread is $c < rb$, where c equals the fitness cost of the action (food provisioning) to the actor, b is the benefit to the recipient (food to eat), and r is the degree of relatedness between the actor and recipient (0.5 for parent and offspring, 0.5 for full siblings, 0.25 for half-siblings). Clearly, a parent's investment in its offspring provides a benefit to the offspring which in turn benefits the parent's inclusive fitness. As long as the cost of parental investment does not outweigh the benefit for the offspring times the degree of relatedness, it should continue. Similarly, in a brood of two equal siblings, A and B, from Hamilton's rule (1964), A should continue to take resources until its marginal gains drop to one-half those of B, who gets the remainder (Parker et al., 1989).

The key point is the degree of relatedness. A child shares a given gene with itself with a probability of 1.0, but it shares the same gene with its sibling with a probability of 0.5 (same as with each parent). As a result, a child is expected to try to obtain resources (or continue to monopolize them in the case of nursing) unless the value of that resource to that child drops below the value, multiplied by the degree of relatedness, of giving that resource to their sibling. Parents are equally related to all of their offspring and are therefore motivated to distribute resources equally unless a child is better able to benefit from the resource than others. Not all offspring are equally good fitness vehicles. As a result, selection has favored mechanisms of parental care that sometimes increase parental fitness by favoring investment in one child over another or by terminating investment entirely. (For a review of parent-offspring conflict in humans and non-human primates, see Maestripieri, 2002; Salmon & Malcolm, 2011).

Discriminative parental solicitude explains variability in mothers' responsiveness to their offspring across individuals as well as variability within individuals who have multiple offspring. That is, discriminative parental solicitude refers to factors that determine the quality and quantity of care a mother directs to her offspring. From an evolutionary perspective, it makes sense that natural selection would design mechanisms that allocate parental investment. Specifically, these mechanisms would allow parents to discriminate among neonates (i.e., identify their own offspring) as well as discriminate between their own potential offspring. Otherwise, there is the risk of misdirecting care and resources to (1) offspring that are not their own, and (2) offspring that are not likely to survive to maturity (Daly & Wilson, 1980; Wilson & Daly, 1994). Therefore, mechanisms that regulate parental motivation to care for any offspring should be sensitive to a host of different offspring, parental, and situational cues to the likelihood of the child surviving and achieving reproductive success. These cues include the reproductive value of the infant (e.g., health, cues to deformity); available resources (e.g., the mother's own health and ability to provide, social support); and potential costs of trade-off between investing in current offspring and investing in other current or potential future offspring (e.g., maternal age). In the rest of the chapter, we will explore how mother-infant conflict plays out in humans, focusing on prenatal and postnatal conflict and the factors that influence the degree of conflict.

9.2 Prenatal Conflict

Contrary to the idyllic perception of pregnancy as a time of ultimate harmonious cooperation between a mother and her offspring, substantial evidence indicates that pregnancy is a time of conflict. The two main sources of prenatal conflict are (1) the genetic quality of the fetus, and (2) the amount of maternal resources directed to the fetus. Examination of prenatal conflict demonstrates how mothers and fetuses have evolved adaptations to manage/balance their genetic interests during pregnancy. From the fetus's perspective, it is in its best interest to get as many resources as it can to ensure its survival, even at the cost of current and/or potential future siblings. From the mother's perspective, however, it is in her best interest to only direct her investment to viable offspring. Therefore, whereas the fetus has evolved ways to decrease the likelihood of spontaneous abortion and to increase the delivery of nutrients, mothers have evolved ways to "test" the genetic quality of fetus. Consequently, prenatal conflict reflects the interplay between a co-evolved system of adaptations for the fetus to signal its quality and avoid being aborted and for the mother to accurately assess the fetal quality and not be manipulated or tricked into the poor investment of her resources.

9.2.1 Genetic Quality and Spontaneous Abortions

The mother's first "test" of fetal genetic quality, as well as the first example of the fetus manipulating the mother's body for its own benefit, is the fetus's ability to overcome the mother's resistance (i.e., pending shedding of uterine wall with menstruation) and successfully implant in the uterine wall (Haig, 1993). In order to accomplish this feat, the developing embryo must produce *human chorionic gonadotropin* (hCG), a placental hormone. Before implantation, human embryos begin production and release of this placental hormone into the mother's bloodstream which serves to maintain levels of progesterone, thus, effectively preventing the shedding of the uterine lining and allowing for implantation of the embryo in the uterine wall. If the embryo is not able to produce adequate levels of hCG, menstruation would ensue and rid the mother's body of any fetal cells (Haig, 1993, 2010b). In situations where the mother would benefit more by investing in higher quality, existing or future, offspring and/or when environmental and social conditions are more favorable for the mother, this first early test of genetic quality to allow for implantation would be extremely important to minimize costs and prevent mother from carrying a fetus that is unlikely to survive and reproduce itself 1 day (Kotler, 2016). Beyond implantation, fetal production of hCG remains important throughout the pregnancy as progesterone is required to maintain the pregnancy. By the eighth week of gestation, the production of mother's progesterone is completely taken over by the fetus as a function of releasing hCG into mother's blood system (Dokras et al., 1991). Without fetal control, mother's progesterone levels would decrease and shedding of the placenta and uterine wall, along with any fetal cells, would occur.

Most early miscarriages (or spontaneous abortions) are genetic "quality control" in the sense that the fetuses show genetic abnormalities (Ellish et al., 1996; Forbes, 2017; Haig, 1993, 2010b; Kotler, 2016). Oftentimes, early pregnancy loss (EPL), spontaneous abortion that occurs within 14 days of conception due to failure to implant in the uterine wall cannot be distinguished from typical menstruation (Ellish et al., 1996). The likelihood of an EPL can be predicted by the level of hCG at implantation, with less hCG production linked to an increased likelihood of maternal rejection (Forbes, 2017). In a sample of 217 women (for a total of 1253 menstrual cycles) between the ages of 22 and 35 who were trying to get pregnant, urinalysis tracking of hCG levels indicated an EPL incidence rate between 17% and 27% where implantation would not have occurred (Ellish et al., 1996). A follow-up found approximately 14% of the confirmed pregnancies (i.e., where implantation had occurred) ended in a spontaneous abortion. The majority of these spontaneous abortions occurred between 7 and 13 weeks of gestation, but one occurred earlier at around 6 weeks of gestation and one occurred later at around 16 weeks of gestation. All of the observed EPLs and later spontaneous abortions were associated with inadequate fetal production of hCG (Ellish et al., 1996). An investigation of the genetic quality of fetuses spontaneously aborted within the first trimester indicated that up to 83% of the fetuses had chromosomal abnormalities that would have limited their ability to survive and reproduce (Strom et al., 1992). In fact, there is evidence to suggest that embryos with greater chromosomal and/or structural abnormalities are spontaneously aborted earlier than other aborted embryos (Forbes, 2017). To the extent that EPLs and spontaneous abortions minimize costs to the mother in terms of preventing investment in unfit offspring, EPLs and spontaneous abortions have been characterized as an adaptive strategy to increase female reproductive success (Kotler, 2016). Specifically, the adaptive response is to induce earlier reproductive loss to reduce the investment loss of the mother.

Prenatal conflict has been characterized as “cooperative conflict” and may play an important role in signaling information to mother and fetus (Haig, 1993). The fetus’s ability to overcome the mother’s tests and resistance signals its genetic quality and greater developmental competence to the mother; while the strength of the mother’s resistance signals to the fetus the cost of the demands being placed on the mother (i.e., greater maternal resistance indicates greater cost burden on the mother). Fetuses have been selected to demonstrate their genetic viability by the production of hCG, and mothers have been selected to demand certain levels of hCG to allow implantation and carrying of the offspring (Forbes, 2017).

Nausea and pregnancy sickness have also been linked to hCG levels and fetal adaptations to avoid spontaneous abortion. A popular explanation for this relationship is that hCG induces pregnancy sickness to protect the fetus from spontaneous abortion via maternal food aversions to dairy, meat, eggs, and seafood, which may carry pathogens or harmful toxins (Haig, 1993). Consistent with the fetoprotective explanation, for most women, pregnancy sickness is most severe (if not completely limited to) the embryonic stage of development. This is the stage in which the embryo develops all the parts, organs, systems, etc. required to make a viable human being. Based on the timing of pregnancy sickness, some researchers have suggested that pregnancy sickness evolved as an adaptive mechanism to prevent the mother from ingesting harmful substances that would interfere with the development of the fetus (Profet, 1988, 1992). Consistent with the idea that pregnancy sickness evolved to prevent developmental risks from teratogens, there is evidence that women who have pregnancy sickness are less likely to have a spontaneous abortion than those that do not have pregnancy sickness (Haig, 1993; Profet, 1992). Recent research suggests that the association between pregnancy sickness and spontaneous abortion increases with maternal age, and is strongest in mothers over the age of 35 (Forbes, 2017). While pregnancy sickness may be a fetal attempt to avoid spontaneous abortion, it has also been suggested that the severity of nausea and pregnancy sickness itself may be an indication of fetal genetic quality, with higher quality fetuses better able to manipulate the mother's system and induce pregnancy sickness than those of lower genetic quality (Haig, 1993; Forbes, 2017).

9.2.2 Genomic Imprinting

It is important to note that prenatal genetic conflict is not only between the mother and fetus, but also within the fetus itself (i.e., between genes inherited from mother and those inherited from father; henceforth, referred to as maternal and paternal genes). Genes that are expressed differently as a function of whether they were inherited from the mother versus the father are referred to as *imprinted genes* (Haig, 1993). This conflict arises due to the three different sets of genetic interests: mother's genes; maternal genes passed to the fetus; and paternal genes passed to the fetus (Haig, 1993, 2019). According to the parental conflict theory of genomic imprinting, differential expression of maternal and paternal genes evolved because levels of expression that maximize maternal inclusive fitness are not necessarily the same levels of expression to maximize paternal inclusive fitness (Haig & Wharton, 2003). Therefore, this theory predicts that maternal genes that benefit the offspring but pose costs to maternal reproductive value would be turned off; and paternal genes that benefit maternal reproductive value but pose a cost to the fitness of the offspring would be turned off. As pointed out by Haig (1993, 2019), this conflict is exacerbated when mothers have children fathered by more than one male. In such situations, paternal genes maximize their interests by ensuring investment in the current developing fetus, whereas maternal genes may maximize their interests by diverting the investment to either current or future offspring. Furthermore, there is evidence that maternal and paternal genes serve different functions essential for prenatal development, including placental development, implantation, and fetal growth and nutrition (Haig, 1993).

Evidence for the differential role of maternal and paternal genes largely comes from the investigation of atypical prenatal development. For example, abnormal embryo and placenta development have been linked to atypical ratios of maternal versus paternal genes (Haig, 1993). An overabundance of paternal cells is associated with placental overgrowth. The effect of paternal gene overabundance on the developing fetus ranges from the complete absence of embryonic fetal cells to a well-developed fetus with a proportionally small head. In contrast, an overabundance of maternal cells is associated with a smaller placenta and a fetus with an underdeveloped body and proportionally large head. These observations indicate not only the importance of paternal genes in the development of the placenta, but the delicate balance of the maternal and paternal genes required for optimal prenatal development.

Another aspect of prenatal development in which the genetic conflict between maternally and paternally imprinted genes can be observed is the implantation process. Greater invasion into the uterine lining is associated with greater blood flow (and thus, nutrients delivered) to the placenta and developing fetus. Upon implantation, the trophoblast burrows into the uterine lining until the cells begin to differentiate in the development of an embryo. While paternally imprinted genes increase invasiveness, driving the trophoblast to burrow further into the uterine wall by favoring delayed differentiation, maternally imprinted genes limit the invasion by favoring earlier differentiation of embryonic cells (Haig, 1993). Although further invasion into the uterine tissue allowing for greater blood flow and nutrients delivered to the placenta may be in the best interest of the fetus (and its paternal cells), it may be in the best interest of the mother to restrict resources and avoid costly over-investment.

The genetic conflict between imprinted genes is also observed in several imprinted-gene disorders. One such disorder is Beckwith-Wiedemann syndrome, which occurs with overexpression of paternal genes and underexpression of maternal genes (Haig, 2010a). Consistent with predictions that paternal genes would be selected to enhance patrilineal inclusive fitness at a cost to matrilineal inclusive fitness, Beckwith-Wiedemann syndrome is associated with fetal overgrowth. This overgrowth represents manipulation of the mother to receive more resources than necessary for typical growth and poses considerable health risks to the mother in supporting the fetus in utero as well as safely delivering a larger baby.

Imprinted-gene disorders associated with overexpression of maternal genes and underexpression of paternal genes include Silver-Russell syndrome, Prader-Willi syndrome, and Temple syndrome (Haig, 2010a). Contrary to paternal genes, maternal genes are selected to promote reduced demands on mothers. That is, the phenotypes expressed in imprinted maternal gene disorders benefit matrilineal inclusive fitness at the expense of patrilineal inclusive fitness. While the effects of Temple syndrome are largely observed in feeding behavior following birth (i.e., less intense sucking and earlier weaning), Silver-Russell syndrome and Prader-Willi syndrome influence prenatal development as well as postnatal behaviors (Haig, 2010a; Haig & Wharton, 2003; Kotler, 2016). Silver-Russell syndrome is associated with stunted uterine growth and shorter gestation periods (i.e., by about 2–3 weeks). While a longer gestational period would benefit the offspring's fitness, longer gestational periods pose an increasing cost to the mother's fitness (i.e., increased risk of birth complications). Prader-Willi syndrome is associated with low birthweight, though head circumference and length do not seem to be affected (Haig & Wharton, 2003). In fact, infants with Prader-Willi syndrome appear to develop normally until late in pregnancy when they do not store fat typical of that stage of development. The lack of typical fat store accumulation could be due to insufficient placental growth (i.e., not able to support increased nutrient needs at end of pregnancy) or because the fetus was not able to successfully override mother's system to increase the flow of nutrients (Haig & Wharton, 2003).

One of the clearest illustrations of the genetic conflict of interest between maternal and paternal genes comes from the comparison of Prader-Willi syndrome with Angelman syndrome. Both Prader-Willi and Angelman syndrome are imprinted-gene disorders involving the same chromosome, but have opposite effects on the developing phenotype depending on whether the maternal or paternal genes are expressed (Kotler, 2016). If missing the paternal gene, the Prader-Willi syndrome phenotype develops characterized by stunted growth (as described above). However, if missing the maternal gene, the Angelman syndrome phenotype develops characterized after birth as having increased sociality encouraging greater interaction with caregivers (Brown & Consedine, 2004). The opposite effects observed in Prader-Willi syndrome and Angelman syndrome as a function of which genes are expressed demonstrate that maternal genes have been selected to reduce costs to mother, whereas paternal genes have been selected to increase maternal investment (prenatally and postnatally, which would presumably also reduce the likelihood of maternal rejection following birth).

9.2.3 Fetal Microchimerism

Fetal microchimerism refers to the phenomenon in which a small number of fetal cells (i.e., of distinct genetic quality to that of the mother), transferred across the placental barrier during pregnancy, are found to persist in the mother's system for decades after she gives birth (Boddy et al., 2015; Glynn et al., 2018). Although the flow of maternal and fetal cells during pregnancy is bi-directional, the exchange of cells itself is asymmetrical. Specifically, more fetal cells are transferred to the mother (versus maternal cells to the fetus), and the transfer of fetal cells increases with gestational age. Once integrated into the mother's system, the fetal cells may then influence her physiology to enhance resource transfer during (and after) pregnancy in ways consistent with the genetic best interest of the offspring, and not the genetic best interest of the mother (Haig, 2019). In fact, menstruation and postpartum hemorrhage have been suggested to be adaptations to protect mothers from the invasive fetal cells that are capable of manipulating maternal behavior and physiology in ways that are not always in the mother's best interest (Abrams & Rutherford, 2011; Haig, 2019).

Although humans have the most invasive placenta physiology (relative to other placental mammals), and despite the great diversity in placental physiology and morphology among mammals, microchimerism is not specific to humans. Rather, microchimerism has been found to be common among placental mammals (Boddy et al., 2015). Diversity in placenta type across mammals is posited to reflect different selection pressures, including those arising from mother-offspring conflict, across that species' evolutionary past. The human invasive placenta type (i.e., hemochorial) serves the adaptive function of increasing nutrient transfer to the fetus and, in doing so, may also allow for greater transfer of cells between the mother and fetus (Boddy et al., 2015). Consistent with the proposed function of fetal microchimerism to increase fetal exploitation and manipulation of maternal resources, fetal cells have been identified in many organs and tissues throughout the mother's system, including sites of resource transfer (e.g., the breast, thyroid, and brain) and immune response (e.g., wound sites). The evidence regarding the effect of fetal microchimerism on maternal health, however, is inconclusive, with some studies finding positive effects on maternal health and others finding negative effects (Boddy et al., 2015).

Two factors that account for some of the discrepancies in findings regarding the effect of fetal microchimerism on maternal health are (1) the mother's own immune response (i.e., ability to limit the transfer of the fetal cells and the strength of the fetal cells' response to the mother's defenses), and (2) the location and specific function of the fetal cells (Boddy et al., 2015). Some fetal cells have been found to serve important functions in maternal wound healing, tissue repair, and replenishment of stem cells. For example, fetal cells have been observed in scar tissue following cesarean sections suggesting that they enhance maternal healing following pregnancy (Mahmood & O'Donoghue, 2014). Therefore, fetal cells that aid in somatic maintenance provide a benefit to maternal health. Fetal cells located in tissues and organs that regulate resource transfer (e.g., breast, thyroid, and brain) were predicted to have negative effects on maternal health, if the mother's system is exploited for more resources than what is in her best interest to provide (Boddy et al., 2015). Tests of this prediction in human studies have yielded inconsistent findings, both within the same resource transfer sites as well as between them.

9.2.4 Conflict Over Resources Directed to Fetus

The quantity and quality of resources delivered to the fetus are regulated by two factors of the mother's vascular system: (1) maternal blood pressure, with higher blood pressure associated with more resources, and (2) maternal blood glucose levels, with higher glucose levels associated with more resources (Arthur et al., 2018; Haig, 1993). Therefore, maternal blood pressure regulates the quantity of resources directed to the fetus; and maternal blood glucose levels regulate the quality of the resources directed to the fetus. The fetus gains control over the mother's vascular system upon implantation, with further invasion into the uterine tissue associated with greater fetal vascular control of maternal arteries responsible for sending blood and nutrients to the fetus (Haig, 1993).

Throughout pregnancy, conflict over maternal blood pressure is evident by the synchronous fetal production of vasoconstrictors (increasing blood pressure and delivery of resources to the placenta) and maternal counter-production of vasodilators (reducing blood pressure). In the beginning of pregnancy, maternal blood pressure tends to be low and tends to increase in the second half of pregnancy as the fetus exerts more pull on resources by increasing vascular resistance (and hence maternal blood pressure) as it grows larger (Haig, 1993). Fetal outcomes of gestational hypertension (high blood pressure during pregnancy without protein in the urine) include increased birthweight, enhanced fetal growth, and lower incidence of stillbirths and neonatal mortality (Haig, 1993). Gestational hypertension is not typically associated with other negative maternal health consequences, and maternal blood pressure typically returns to normal in a few weeks following birth. Therefore, the fetal benefit of gestational hypertension appears to be at a relatively low risk to maternal health.

Dysregulation of the conflict over maternal blood pressure, however, can lead to preeclampsia (high blood pressure during pregnancy accompanied with protein in the urine), which poses a significant health risk to the mother and potentially the fetus (Arthur et al., 2018; Espinoza, 2016). Worldwide, it is estimated that 10–19% of maternal deaths are due to preeclampsia (Brown et al., 2013). Some of the more threatening maternal complications include kidney failure, seizures, hemorrhage, and cardiac arrest (Brown et al., 2013; Haig, 1993). Potential fetal complications associated with preeclampsia include increased risk of low birthweight, prematurity, and stillbirth (Haig, 1993). In consideration of the substantial maternal and fetal risks, some researchers have proposed the fetal actions leading to preeclampsia (i.e., upregulation of vasoconstrictors to increase maternal blood pressure) may be an extreme survival tactic for an undernourished fetus to increase its chances of survival (Espinoza, 2016; Haig, 1993). Consistent with this suggestion, poor placental perfusion (indicative of less invasive burrowing at implantation and therefore fewer resources being delivered to the fetus) has been found to exist in many preeclamptic pregnancies (Arthur et al., 2018; Espinoza, 2016; Haig, 1993; Varas Enriquez et al., 2018). Together with the timing of preeclampsia (usually developing in the third trimester), this indicates that (1) poor fetal growth from lack of adequate resources may precede fetal actions leading to preeclampsia, and (2) those actions may indeed be an evolved “last chance” survival strategy to increase the amount of resources being delivered to the placenta (Haig, 1993).

It is important to note that in addition to fetal production of vasoconstrictors, there is evidence to suggest genomic imprinting also plays a role in the development of preeclampsia. A recent study found evidence of molecular genetic evolution indicating positive selection on a particular gene known to be strongly related to the risk of preeclampsia (Arthur et al., 2018). Arthur et al. (2018) proposed that the expression of the gene is triggered by the lack of sufficient embryonic invasion with implantation. Once triggered, the gene produces cytotoxins that damage the endothelial lining of maternal blood vessels. This damage causes the blood vessels to constrict, increasing vascular resistance and maternal blood pressure (Haig, 1993). It also causes serum proteins to leak out, leading to protein in the urine (Haig, 1993). Though research in this area is still somewhat limited, there is other recent evidence to suggest other genetic signaling mechanisms may be used by the fetus in an attempt to compensate for limited blood flow to the placenta (e.g., adenosine, a building block of RNA) (Espinoza, 2016). Therefore, in extreme circumstances of fetal undernourishment that are presumed to lead to preeclampsia, fetal control over the quantity of resources it receives appears to be accomplished through multiple mechanisms including the balance between fetal-produced vasoconstrictors and maternal-produced vasodilators as well as imprinted genes.

A main vehicle for fetal control of the quality of resources it receives is the placental hormone, human placental lactogen (hPL) (Haig, 1993). Along with hCG and other placental hormones, hPL passes through the placenta to the mother where it acts on maternal prolactin receptors and increases maternal resistance to insulin. Early in the pregnancy, maternal fasting levels of blood glucose start out low. After 6 weeks of gestation, fetal production of hPL begins (Di Cianni et al., 2003). Fetal manipulation of maternal metabolism then ensues for the remainder of the pregnancy as maternal glucose and insulin levels begin to not only increase, but also stay higher for longer periods of time (Di Cianni et al., 2003; Haig, 1993). This leads to more nutrient-rich blood being delivered to the placenta, and the fetus having longer to extract as many nutrients as it can. As fetal production of hPL increases, maternal production of insulin increases to compensate for (and fight against) the fetal pull on resources (Di Cianni et al., 2003; Haig, 1993). Across pregnancy, insulin sensitivity is estimated to decrease between 50% and 80% (Di Cianni et al., 2003). Similarly, insulin secretion progressively increases following the first trimester, peaking in the third trimester and returning to normal following birth (Di Cianni et al., 2003). Thus, this interplay provides yet another example of the intricate conflict and coadaptation between mother and fetus.

Gestational diabetes mellitus (GDM) is a metabolic condition in which pregnant women develop insulin resistance so that their glucose levels remain high for extended periods of time. In other words, GDM occurs when the mother is unable to upregulate her insulin production to effectively compensate for the fetal-induced insulin resistance (Haig, 1993). Recent estimates suggest that approximately 9.2% of mothers in the United States who gave birth in 2010 had GDM (De Sisto et al., 2014), though other estimates of GDM range from 3% to 14% of pregnancies affected by GDM (Giannubilo et al., 2018) with estimates of up to 20% in some cultures worldwide (Brown et al., 2013). While the actual prevalence of GDM is still unclear, the negative maternal and fetal outcomes are well known.

GDM is associated with increased pregnancy and delivery complications, including the need for cesarean delivery due to infant macrosomia where the fetus grows large for its gestational age (i.e., too large to fit through the mother's pelvis) (De Sisto et al., 2014; Di Cianni et al., 2003; Giannubilo et al., 2018). The longer and more severe the GDM, the larger the risk of cesarean delivery and infant macrosomia (Di Cianni et al., 2003). Because infants with macrosomia are too large to be delivered to through the mother's pelvis, before cesarean deliveries, mothers with GDM and their infants were not likely to survive (Brown et al., 2013). Other fetal outcomes associated with GDM include hypertrophic myocardiopathy, typically leading to cardiac arrest in the first few months of life; respiratory distress syndrome; hypoglycemia, hypocalcemia, and hypomagnesia (i.e., low levels of blood sugar, calcium, and magnesium, respectively); hyperbilirubinemia (i.e., elevated bilirubin levels); and hypoxemia (i.e., low blood oxygen levels) – all of which can significantly threaten perinatal outcomes (Di Cianni et al., 2003). Long-term effects on children of mothers with GDM include a higher risk for childhood obesity and diabetes later in life (Giannubilo et al., 2018). Long-term effects of GDM on maternal health also include a higher risk of developing Type II diabetes

(Giannubilo et al., 2018). Therefore, the fetal benefit of increased resources via this pathway comes at a high cost to both the fetus and mother, during pregnancy and beyond.

Similar to the mechanisms underlying conflict over maternal blood, hPL is not the only mechanism used by the fetus to obtain greater access to resources by influencing maternal metabolic functioning. Recent work found that, controlling for pre-pregnancy body mass index and other factors, women carrying male fetuses were significantly more likely to develop GDM than those carrying female fetuses (Giannubilo et al., 2018). While the mechanism by which fetal sex influences maternal metabolism is still unclear, some researchers proposed the prenatal production of testosterone by male fetuses may contribute to maternal insulin resistance (Giannubilo et al., 2018).

9.3 Postnatal Conflict

Of course, the conflict between mother and infant does not end after the baby is born. Just as there is conflict prenatally over the quality of the fetus itself and over the amount of resources it receives, there is postnatal conflict over whether resources should be allocated to the infant at all or if resources should be allocated, how much. This cost-benefit analysis can end in infanticide when, from the maternal perspective, investment is too costly.

9.3.1 Infanticide and Child Abandonment

Incidents and practices of infanticide and child abandonment have been examined across a wide range of human societies. In general, there are several factors that seem to influence the likelihood that the mother will cease investment in her infant. On one side of the equation, they include the quality or condition of the child. On the other side, there are maternal factors including mother's age, amount of social support she has, and resource availability. These relevant factors should not be surprising considering the earlier discussion of discriminative parental solicitude which theoretically varies according to not only relatedness, but with the phenotypic attributes of the child that are predictive of eventual fitness, situational predictors of offspring fitness, and alternative reproductive investment opportunities for the mother (Wilson & Daly, 1994).

A review of the ethnographic literature reveals a number of studies documenting the killing of infants (Daly & Wilson, 1988). In the Ayoreo, who engage in a mix for foraging and slash and burn horticulture, deformed or otherwise unwanted infants are buried immediately after birth (Bugos & McCarthy, 1984). Some of the women report in addition to deformities, a lack of paternal support, twins, or close birth spacing as reasons for infanticide. Daly and Wilson (1988) reviewed the Human

Relations Area Files (HRAF) and reported 112 infanticidal circumstances, 21 of which involved the killing or abandoning of infants due to deformity or severe illness. Fifty-six involved circumstances that were not favorable for child rearing including the birth of twins and a baby being born too close on the heels of an older sibling. Similar factors influence the occurrence of infanticide among the Tarahumara, an indigenous population of approximately 50,000 in the Mexican state of Chihuahua (Mull & Mull, 1987) as well as among the Australian aboriginal population (Cowlishaw, 1978).

Even in the modern western world, these fitness-relevant factors are connected to infanticide. A systematic review of the research on neonaticide, the killing of an infant within the first 24 h of birth, indicates that it is often committed by young, poor, and unmarried women (Friedman et al., 2005). These are mothers with little current access to the resources they need to raise successful offspring and at the same time the ones, due to their young age, with future opportunities to reproduce that might be more likely to improve their reproductive success (Wilson & Daly, 1994). Friedman and Resnick (2007) also highlighted the role of economic factors in maternal infanticide. Overpeck et al.'s (1998) analysis of deaths during the first year of life in the United States indicated that approximately half of these infanticides occurred within the first 4 months. The two most substantial risk factors were maternal youth and a lack of resources. In particular, the risk was substantially increased by being a second or later infant born to a mother less than 17 years old (compared to first infants born to a woman 25 or older), little prenatal care, and lower levels of education. An analysis of 110 cases of mothers killing 123 of their own offspring from 1976 to 2010 in Italy explicitly tested adaptationist theories of neonaticide, reporting that the neonaticidal mothers were relatively young, poor women with no partner support. They killed their offspring non-violently, either directly or through abandonment, and attempted to conceal the body (Ciani & Fontanesi, 2012). The researchers suggested that neonaticide is an adaptive disinvestment, designed to increase the biological fitness of the mother by eliminating an unwanted newborn and saving resources for future offspring born under better conditions. Similar results with regard to mothers being young, poor, and with little formal education were reported in a study of maternal infanticide in Fiji (Adinkrah, 2000).

Hrdy (2016) emphasizes the role of cues of social support in influencing maternal responsiveness, especially in cooperative breeders. In the majority of non-human primates, infanticide is committed by females other than the mother or by males (Hiraiwa-Hasegawa & Hasegawa, 1994). Hrdy (2016) notes that the only primate species where mothers are infanticidal toward their own offspring are those with allomaternal care, and that in callitrichids, a shortage of allomaternal assistance is the best predictor of maternal rejection. Human mothers also rely on significant allomaternal care from friends, family, and sexual partners. In the absence of cues of such support, despite the infants' own best interests, mothers may abandon or terminate their offspring in order to achieve greater reproductive success in the future. In a similar vein, Lycett and Dunbar's (1999) study of abortion rates suggests some of the same factors that influence postpartum maternal investment also impact the decision to terminate a pregnancy through abortion. Their data from England and Wales indicate that single women were more likely to abort than those ever married. In addition, younger single women, with their greater probability of future marriage than that of older single women, were more likely to terminate a current pregnancy than the older single women. Waiting for better future reproductive conditions seems to be playing a role in decisions to terminate pregnancies, especially for young women who may be lacking in social support.

9.3.2 Breastfeeding and Conflict

One of the core features of mammals is the provisioning of offspring with milk. Breastfeeding is one of the most energetically costly aspects of maternal investment post-birth (Konner, 2005; Prentice et al., 1996). While contemporary breastfeeding patterns vary widely across cultures (Scott et al., 2001; Sellen, 2009), human infants evolved under circumstances where their survival would have depended on the nutritional and immunological value of maternal breastmilk (Ballard & Morrow, 2013; Hinde & Milligan, 2011; Martin et al., 2016; Power & Schulkin, 2013; Volk, 2009). Extended breastfeeding is common in most contemporary hunter-gatherer or non-industrialized populations (Sellen, 2009), while frequency is less common and durations are much shorter in industrialized countries (likely influenced by outside-the-home work and the availability of breastmilk alternatives) despite frequent advocacy for breastfeeding (Endressen & Helsing, 1995; Obermeyer & Castle, 1996).

Because of the importance of breast milk to infant success, one might expect all mothers to provide as much as often as they can. However, because lactation is energetically costly and time-consuming, conflict can arise because of trade-offs between lactation/nursing and the mother's own somatic functions, investment in other existing or future children, and so on. This can occur while the mother continues to breastfeed as well as during weaning (the period of cessation of breastfeeding), which will be discussed with respect to weaning later in this chapter. This conflict can be seen at a biological and behavioral level.

One might assume that mothers would have the advantage in maternal-infant conflict over food and other resources once the baby is out of the womb. But the balance of power is not that clear cut, and both infant behavior and maternal biology seem to play a role. For example, a number of researchers have reported on how continued nursing is associated with lactational amenorrhea, which can result in higher infant fitness by delaying the arrival of their next sibling and the attendant dilution of resources (Haig, 2014). High-frequency continued nursing does this by suppressing the maternal hypothalamic-pituitary-ovarian (HPO) axis (Konner & Worthman, 1980; Vitzthum, 1994), influencing maternal hormone levels. From the current infant's perspective, they benefit from longer breastfeeding. From the maternal perspective, there is a trade-off as shorter breastfeeding duration can result in smaller infants at weaning (and possible increased infant mortality), but the next conception can occur sooner (Vitzthum, 1994, 2008). As a result, we would expect more conflict when there is a maternal advantage to an earlier next conception.

In addition, it has been suggested that maternal physiology has evolved to modify offspring behavior via components in milk influencing infant microbiota (Allen-Belvins et al., 2015). This conceptual model has bioactives in maternal milk directly influencing infant gut microbiota and neurobiology (as well as indirect infant microbiota impacts on developing neurobiology) so as to influence infant behavior (crying, nursing, other activity) and resulting mother-infant interactions. Studies have indicated that maternal-origin hormones ingested via milk shape growth and development in infants (Hinde et al., 2015) and that there are links between microbiota composition and infant temperament (Christian et al., 2015). While infants have behavioral tactics designed to elicit care and nutrition, sometimes more than is in mothers' best interests to provide, that can be seen as positive (smiling) or negative (crying), mothers have evolved countermeasures perhaps via their milk components in order to shape less costly phenotypes in their infants (Allen-Blevins et al., 2015).

As is the case for research on parent-offspring conflict in non-humans (Maestripieri, 2002; Salmon & Malcolm, 2011), there are several models of begging behavior that focus on infant attempts to influence parents into providing more nutrients, including blackmail, scramble competition, honest signaling of need, and honest signals of worth. Evidence from research on human infants suggests that suckling and crying signal nutritional need (and perhaps also thermoregulation needs) and worth to the mother (Wells, 2003). These cues can act at biochemical and behavioral levels. The role of imprinted genes in maternal-infant conflict has also been examined (Haig, 2014; Moore & Haig, 1991) with regard to the impact of paternally or maternally imprinted genes on resource transfer from mother to offspring as discussed previously. Moore and Haig (1991) predicted that some genes can influence the amount of resources transferred from a mother to current offspring at the expense of future offspring (who may not share the same father). Observations of the effects of a chromosomal deletion of 15q11-13 provide support for this prediction, in that maternal deletions are associated with Angelman syndrome while paternal loss is associated with Prader-Willi syndrome. The infant behaviors associated with these syndromes are discussed in the section on weaning conflict.

From the maternal perspective, lactation is a parental investment and as such, we would expect it to be allocated in ways that are consistent with fitness payoffs, as a current investment in lactation results in lower residual reproductive value for the mother, as well as post-partum amenorrhea (Margulis et al., 1993; Tracer, 1996). Tracer (2009) examined breastfeeding in terms of allocation of parental investment in Papua New Guinea, reporting high levels of maternal investment, and that when infants were fussing or crying, they were given the breast 30% of the time. However, in contrast to the prediction from parental investment theory that mothers should invest more in higher quality offspring, Tracer (2009) reported greater investment in offspring who were in poorer condition, perhaps because they were more likely to benefit from that investment than those already in good condition. Interestingly, a number of studies have indicated that allomaternal care reduces lactational demands and can reduce maternal-infant conflict due to helper at the nest effects (Kramer, 2010; McKerracher et al., 2017; Van Noordwijk et al., 2013). McKerracher and colleagues report in their study of rural Guatemalan Maya villages that mothers with more help, breastfed for shorter periods and that later infant birth order was associated with greater breastfeeding duration. This birth order effect is consistent with expectations from parent-offspring conflict theory. As mothers approach menopause, future reproductive opportunities decrease and mother and offspring ideal breastfeeding allocations converge.

9.3.3 Weaning Conflict

Weaning can be "defined as a process that begins with the introduction of nutritive supplemental foods and ends with the complete cessation of breastfeeding" (McDade, 2001, p. 10). Weaning is a major conflict point between mother and offspring in that the mother can end her lactational amenorrhea, increasing her likelihood of an additional pregnancy, while her infant is losing breastfeeding calories and starting to become nutritionally independent (though in humans, children are nutritionally dependent on parents to provide alternative foods for an extended period of time). In this sense, for humans, childhood is much longer than in the majority of mammals, but offspring are weaned at a relatively earlier age (Kennedy, 2005). Early weaning may have fitness benefits for mothers but longer access to breastmilk has infant fitness advantages, thus conflict is expected to occur over the timing of weaning, as there are costs and benefits to early versus late weaning. This maternal-infant feeding conflict can be seen in the influence of maternally and paternally imprinted genes (Haig, 2010a, 2014; Haig & Wharton, 2003). Maternally imprinted genes favor early maturation in offspring while paternally imprinted genes favor increased suckling. Mothers can benefit from having one infant nursing while another is more nutritionally independent, eating food (and receiving care) provided not only by the mother but by other alloparental sources, increasing maternal fitness (Bereczkei & Dunbar, 1997; Hrdy, 2005; Ivey, 2000; Kennedy, 2005; Kramer, 2005).

There are a number of strategies that infants employ to delay weaning. Studies of night waking indicate that it increases in the second half of the first year of infant life in breastfed infants. As previously mentioned, postpartum amenorrhea has a significant impact on the inter-birth interval in natural fertility populations (Thapa et al., 1988), and more frequent and intense nursing, particularly at night, is related to longer periods of infertility (Heinig et al., 1994). Haig (2014) has suggested the maternally and paternally imprinted genes influence the use of such strategies based on the study of infants with Prader-Willi and Angelman syndromes, which were previously discussed in terms of in utero effects. Prader-Willi syndrome infants are poor sucklers who sleep a lot while Angelman syndrome infants engage in greater suckling and night waking (poor sleepers). This suggests that night waking is an adaptive strategy on the part of infants to extend lactation amenorrhea and, as a result, delay the birth of sibling competitors.

Jealousy protest has been suggested as another offspring strategy to delay sibling competitors for maternal resources (Hart, 2015, 2016; See Hart, Chap. 12, this volume). While much of the study of jealousy as an adaptation has been concentrated on sexual or emotional jealousy in romantic relationships (Buss, 2017, 2018), jealousy is possible wherever conflict may arouse over investment allocation. This may be especially relevant for infants who are dependent on their mothers for nutrition and protection. Studies indicate that infants as young as 5–6 months show distress when their mother is positively interacting with another infant (Hart & Carrington, 2002; Hart et al., 2004) and by 10–12 months display distress and caregiving-directed bids for attention (Hart & Behrens, 2013). These behaviors characterize the outward manifestation of jealousy protest, "a constellation of caregiver-directed protests and attention-getting behaviors for protecting exclusive access to a caregiver" (Hart, 2016, p. 1). The characteristic onset around 9 months of age and peak around 20 months suggests that a problem infants needed to solve ancestrally was premature weaning due to the birth of another sibling and that jealousy protest evolved to defend against it. However, not all infants display indicators of jealousy protest around weaning, and future research should focus on what factors increase or decrease the likelihood of the use of jealousy protest by infants across cultures.

Because there are costs and benefits to exclusive breastfeeding, especially over the extended time, it is useful to consider the ecological conditions that may promote or delay the timing of weaning as well as who may be having more influence over the timing, mother or offspring. In general, it is in the best interests of mother and offspring to be sensitive to each other's needs and to modify their own behavior and demands accordingly so as to reduce the net costs of conflict. Although a great deal of attention has focused on the benefits of breastfeeding to child health, as well as the benefits of longer inter-birth intervals, somewhat less attention has captured the several ways breastfeeding imposes costs. We have already mentioned the delay in future conception caused by lactational amenorrhea, but there are also costs in terms of maternal nutritional depletion, as well as constraints of maternal activity, such as reducing foraging efficiency (McDade, 2001; Hawkes, 1996; Hurtado, et al., 1992). These costs and benefits vary across time. The relative benefits of breast milk decline over time for infants as consumption of solid foods increases as well as overall caloric requirements to support growth and development (Grammatikaki & Huybrechts, 2016; Koutras & Vigorita, 1989; Uauy & De Andraca, 1995); and they also vary by ecological factors such as pathogen exposure, maternal workload/subsistence type, availability of supplemental food, and alloparental support (Fouts et al., 2012; Hurtado et al., 1992; Konner, 2005; Morrow et al., 2005; Vitzthum, 1994).

A wide range of studies has looked at weaning conflict and the timing of weaning across a variety of cultures, in particular in non-western (in many cases not using modern contraception) populations. For example, Fouts and colleagues (Fouts, 2004; Fouts et al., 2005, 2012) have examined the contexts surrounding weaning among farmers and foragers in Central Africa. Consistent with Konner's (2005) assessment that foragers breastfeed longer than farmers, which is associated with longer interbirth intervals, Ngandu and Bofi farmers weaned offspring earlier than Aka and Bofi foragers. This highlights the role of subsistence type and attendant culture on weaning practices. Among the foragers, breastfeeding was also at more frequent intervals, the bouts were of shorter duration (Fouts et al., 2012), and the infants displayed less distress when weaning occurred. Any maternal-infant weaning conflict seemed ameliorated, at least in terms of obvious signs, in the foragers compared to the farmers. A study focusing specifically on the timing of weaning in Dominica reported that father absence was associated with early weaning but that the availability of alloparental care and household wealth was negatively associated with the age of weaning, and that the number of dependent children in the household was positively associated with the timing of weaning (Quinlan et al., 2003). These results emphasize the importance not only of focal offspring need but also the opportunity costs of prolonged nursing as well as the nature of reciprocal female labor and the value of paternal investment while nursing.

9.4 Conclusions

The research discussed in this chapter highlights the cooperation and conflict inherent in the maternal-infant relationship. Prenatal conflict demonstrates the evolutionary arms race between mother and fetus, in that the more elaborated the mechanisms for fetal exploitation, the more evolved the maternal adaptations for downregulation of response to fetal actions. This cooperative interplay of conflict between mothers and fetuses helps ensure successful outcomes for both mother and infant. This cooperative interplay continues postnatally with regard to nutrition and other forms of investment (bonding, attention, etc.). Even weaning, which has typically only been viewed as a zone of conflict, demonstrates cooperation and is influenced by ecological and cultural conditions.

Future research is needed to resolve a number of inconsistent findings. For example, some studies have found pregnancy sickness to be associated with elevated hCG levels, whereas others have found no associations. While descriptive work with mixed findings has been done, more research into the mechanisms underlying these outcomes is needed to clarify their functional nature. Research into genomic imprinting and fetal microchimerism has been limited in humans, yielding evidence suggesting both positive and negative effects on maternal health. Therefore, more human research in this area is needed to understand the long-term effects of these conflicts.

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Chapter 10
Niche Construction in Hunter-Gatherer Infancy: Growth and Health Trade-Offs Inform Social Agency

Paula Ivey Henry and Gilda A. Morelli

10.1 Introduction

One of the most challenging tasks for evolutionary research on human development is synthesizing the span of ecological processes responsible for its nature. New data and theory bring us closer to the consilience that ontogenetic explanations require, but often have equivocal relevance to the environments in which we evolved. Hunter-gatherers present an irreplaceable ecological venue to probe development in a more proximate niche to our evolutionary past (Blurton Jones, 1993; Hewlett & Lamb, 2005). Similarly, infancy is the most proximate period of development to that of other primates, as human postnatal altriciality, rapid brain growth, and early weaning relative to apes present a premature and energetically imperiled infant to the world (Hochberg & Albertsson-Wikland, 2008). Together, this developmental crucible of evolution is linked with adaptive features of human intelligence, parental pair-bonding and division of labor, central place foraging, food sharing, multiple dependency, cooperative reproduction,[1] and other biological and social

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[1] We use the term "cooperative reproduction" to describe the fundamental dependence of human reproductive success on the time and energetic contributions of other-than-parents to successfully rear young. It aligns with the interspecific construct of "cooperative breeding," but includes the broader and extended cooperative investments (e.g., food sharing, socialization, skills transfer) key to human developmental success. We prefer it, too, for interdisciplinary relevance, as the term *breeding* is used to describe artificial selection methods in other fields (e.g., genetics, neurosci-

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characteristics (Bjorklund, 2018; Hrdy & Burkart, Chapter 8, this volume; Kaplan et al., 2000; Konner, 2010).

In this chapter, we explore how ecological and somatic trade-offs within hunter-gatherer development inform the special social nature of human infancy. Like many of our colleagues studying hunter-gatherers, our research among Efe (pygmy) foragers of the northeastern Congo Basin (Democratic Republic of the Congo) finds that infants are highly active agents who acquire resources by increasingly sophisticated cooperative means (Morelli et al., 2014, 2019). We have identified resource and psychosocial implications of cooperative reproduction for infants as *cooperative development*, whereby human ontogeny *expects* the dynamic and multidimensional inputs of others (than mother) that prime developmental experience of discernment, synchrony, trust, and helping as precursors to a life dependent on sharing (Gurven et al., 2012).

Konner's (2005) review of hunter-gatherer childhood research illustrates regularities in developmental experience over the first 2 years of life: infants nurse frequently, their signals of distress are responded to quickly, and they experience extensive physical contact and proximity to others. Who cares for young and when, however, varies widely with local ecology, subsistence activities, and culture. Prominent themes of forager research include the explanatory role of infant allocare in human life history (e.g., Helfrecht et al., 2020; Ivey, 2000); lactation and weaning (e.g., Konner & Worthman, 1980; Meehan & Roulette, 2013); foodsharing (e.g., Morelli et al., 2019; Fouts & Brookshire, 2009); prosociality and attachment (e.g., Barlow, 2013; Crittenden & Marlowe, 2013); play and exploration (e.g., Kamei, 2005; Salali et al., 2019); and language and cultural acquisition (e.g., Gallois et al., 2018, Hewlett & Roulette, 2016).

This rich social view of forager infancy illustrates the ecological and biological substrates in which infancy evolved, and suggests that new insights can be gained from a closer view of *intra*-developmental processes and their trade-offs. Conceptualizing trade-offs in development moves us beyond constraint and risk models to probe the time and energetic costs and benefits of alternate pathways, and the co-acting nature of diverse processes that inform developmental adaptations (e.g., Bogin et al., 2007; Ellis & Del Giudice, 2019). Growth and mortality are perhaps the most reported features of forager infant biology (e.g., McDowell & Volk, Chapter 5, this volume; Ramirez Rozzi et al., 2015; Urlacher et al., 2015; Volk & Atkinson, 2013). Less frequent, but highly valuable, is research on forager infant physiological, motor, and neurobehavioral development (e.g., Kaplan & Dove, 1987; Takada, 2005; Tronick & Winn, 1992).

Elsewhere, evolutionary insights have been employed to examine infant developmental consequences of maternal energetic, stress, and immune transfers (e.g., Ellis & Del Giudice, 2019; Kramer & Veile, 2018; McDade et al., 2019; Sear & Mace, 2008). This progress frames infancy as a variable physiological, neuropsychological, and behavioral experience responsive to environmental features and social

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ence, and medicine). In addition, a primary life history trade-off is described as between "growth and reproduction," not "growth and breeding."

transfers to mothers and infants. Canalization protects this fragile period, but it also scaffolds phenotypic plasticity to better match and influence ecological and cultural experience in the developmental niche (Bjorklund, 2018; Chisholm, 2017).

Today, a new generation of "-omic" and other assay data offers new perspectives on forager infancy (e.g., Han et al., 2016; Meehan et al., 2018), although the integration of genetic, epigenetic, microbiome, and other -omic data with ecological and health evidence is still cautiously mapped territory under the most favorable circumstances (Subramanian et al., 2020). In spite of challenges, including the few foragers from which measures can be obtained, the intense environmental and social experience of forager infancy warrants explorations in this direction. These insights have special value to the expanding fields of evolutionary medicine and evolutionary developmental ecology, where they can deepen our understanding of neurobehavioral plasticity and social agency as biological and health processes (Kuzawa, 2012; Trevathan & Rosenberg, 2016).

The first quantitative descriptions of Efe infancy probed the biosocial intersection of this challenge. Tronick et al. (1987) hypothesized that Efe allonursing in the first few months of life enhances immune and regulatory development via shared antibodies and fluids, as well as nutrients. Efe also adjusted allocare to accommodate lower birth weight and fussing infants suggesting strategies to manage early physiological and neurobehavioral processes. These and other care patterns demonstrate sensitive and shared investments in infant health and growth, with infants over time playing an increasing role in soliciting the care they receive (Morelli et al., 2014, 2019). Their activity serves them well as they mature beyond the energetic threshold of lactation in the first year, when they need additional food from others (Kuzawa et al., 2014).

We return our attention to early characterizations of Efe infancy that weave together biology, cooperation, and infant sociality as interdependent features of evolutionary, ecological, and cultural experience. Here, we (1) briefly describe theoretical constructs framing the multileveled, interactive systems view of processes in Efe infancy; (2) describe ecological resources and risks in the Efe niche as prevalent opportunities and pressures on infants and others; (3) explore emerging phylogenetic, genomic, and epigenetic data regarding adaptive variation of Congo Basin hunter-gatherer (CBHG) biology; (4) consider evidence of Efe growth, health, and life history trade-offs; and (5) discuss how these insights inform Efe care, attachment, and social agency.

It is highly unusual to have this opportunity: few populations have as long and discreet an endemic evolutionary and ecological history as do African indigenous hunter-gatherers, such as the Efe, Aka, !Kung, and Hadza. This facilitates an extended view of biological canalization and plasticity and the mapping of social development to both. Opportunities to fill gaps in hunter-gatherer data are limited by the very few who remain mobile as coherent residential units dependent on hunting and gathering, even while attaining food by horticulture, trade, and other means (Marlowe, 2005).

10.2 Organizing Constructs in Evolution, Ecology, and Development

It is not surprising that Niko Tinbergen (1963) studied ontogeny, compelling the integrative explanatory framework of behavior that remains so productive today. Human development by necessity favors an ambitious causal scope that spans dynamic evolutionary, adaptive, proximate, and ontogenetic processes, in addition to cross-cultural and cross-disciplinary views (Amir & McAuliffe, 2020; Bjorklund & Ellis, 2014). In that spirit, but scaled, we bring together diverse perspectives and data to reconstruct, in part, the richly complex developmental niche of Efe infancy. Human infants are vulnerable and demanding, and hunter-gatherer environments make these risks substantially more challenging (Helfrecht et al., 2020). How do forager adaptations to ecological and social variation and uncertainty inform the capacity of human infants and their caregivers to mitigate harm and to thrive? We briefly describe central constructs that guide this review, and in service of space, refer the reader to detailed descriptions of theory elsewhere, including other chapters in this volume.

10.2.1 Developmental Niche Construction (DNC)

Niche construction (NC) describes evolutionary ecological feedback processes of phenotype-environmental interactions, whereby organisms directly and indirectly influence the parameters of their own environmental experience, and therefore, the subsequent ecological conditions they encounter (Laland et al., 2016; Odling-Smee, 1995). For example, many animals construct special habitats to protect young, thereby generating new conditions to which offspring must adapt (Clutton-Brock, 1991). These feedback systems between individual and habitat interact as adaptive processes on proximate to evolutionary scales, and within and across systems, for example, physiological, psychological, behavioral, and cultural. If stable over extended time, the shifted phenotype may become embedded in the genome, further influencing the coevolution of traits, and direction and strength of selective processes (Clark et al., 2010). Nature is stochastic, yet niche feedbacks help to stabilize an inherently dynamic process, increasing the predictability and efficiency of environmental experience, and channel *phenotypic plasticity*, the organism's adaptive range (Bruijning et al., 2020).

Developmental niche construction (DNC) is special form of NC during ontogeny. It describes ecological feedbacks inherent in developmental processes that bias ontogenetic trajectories, stabilizing outcomes (e.g., maturation, timing, and structure of traits), and response variability described as *developmental plasticity*, or ontogenetically mediated phenotypic plasticity (West-Eberhard, 2003). These multisystem interactive processes increase the predictability and efficiency of resource and risk adaptations during the unique period of growth and development by producing a set of reaction norms that are environmentally contingent (Matthey Doret et al., 2020). DNC characterizes adaptation without inferring trait selection at an evolutionary scale, although they may be related (Stotz, 2017), as research here suggests.

Somatic and extrasomatic feedback processes of DNC enable human young to manage the variable experience of mother and others' time and energetic allocations as physiological and psychosocial cues of resource availability and risk (Ellis & Del Giudice, 2019; Kramer & Veile, 2018). And, as infants and children grow, they face a diverse and changing set of problems to solve to secure adequate food and care, including the competitive and cooperative experience of each other (Gurven & Walker, 2005; Hart, 2015; Chapter 15, this volume; Kramer et al., 2016). We argue that DNC processes are evident in both the evolutionary and ecological synchrony of Efe infant growth and physiology to their energetic and health environment, and the synchronization of biobehavioral processes between infant and caregivers that facilitates predictability and security in Efe relationships as adaptations to resource and risk uncertainty.

10.2.2 Human Developmental Ecology (HDE)

Human development ecology (HDE) is the complementary examination of variation in processes and outcomes as they play out in a specific niche. Most critically, it heeds empirical demands to attend to local environment and history, and context-specific biological and behavioral trade-offs in the complex, integrated, and self-generating processes of development (Bjorklund & Ellis, 2014; Gurven, 2018). For example, it extricates the construct of child *resilience* from conventional trait and impairment models by probing alternative and adaptive developmental pathways (Ellis et al., 2017; Macrì, 2013). As such, resilience is conceptualized not only as an individual process, but a social one in a specific niche of affordances and constraints (Júnior et al., 2015). DNC and HDE stimulate questions of multiple processes at play in any outcome of interest, and facilitate the integration of alternative theories to explain variation within it.

10.2.3 Problems and Methods in Hunter-Gatherer Niche Reconstruction

Hunter-gatherer researchers have been careful to frame measures and interpretations of infant development in ways they see as salient to contexts they observe. They are often reluctant to generalize findings, precisely because the ecological variation and richness of forager experience is so entangled in the details and dynamics of their biology and behavior. This risks a fragmented view, but underscores the diversity of infant experience less appreciated from a canonical frame. The situation is hardly hopeless; researchers are keen to summarize and compare data (e.g., Hewlett, 1991; Konner, 2005), and one of the most successful approaches has been to narrow the ecological lens by comparing forager development to neighboring groups, often horticulturalists, who share a broader habitat (e.g., Kramer & Greaves, 2007; Meehan, 2009; Morelli et al., 2019).

The challenge of aligning disparate data informing ecological processes in hunter-gatherer development is complicated by the very few forager groups from which new data can be collected, the fragmented scope of historic and emerging data, and many difficulties of hunter-gatherer fieldwork. For the Efe, a decade of war and insurgency still prohibit the safety to collect data (Wilkie, 2005). These problems require casting a wider net to reconstruct the forager infant niche. Here, we review diverse data available informing Efe development, giving primacy to the northeastern Ituri Efe reported in our prior studies. We also include research on nearby Andiri Efe and Wamba Mbuti whose clans frequently intermarry with them, contiguous Mbuti and Asua/Sua in the Ituri forest, other eastern CBHGs (Batwa), and western CBHGs as appropriate. Diverse data sources present a challenge to the usual business of comparative validity that we recognize and forewarn. It also presents an opportunity to bring as much of the story of Efe infant development together, as a quantitative-driven historian or ethnographer might do (Kraft et al., 2020), where the merits of each can be considered more specifically. Especially, it allows us to see the outlines of the Efe evolutionary setting and infant developmental niche.

10.3 The Ecological Niche of Efe Hunter-Gatherer Development

The Efe are indigenous (pygmy) bow hunters whose population has been well described in the northeastern Ituri (Bailey & DeVore, 1989; Bailey & Peacock, 1988, Ellison et al., 1986), and adjacent south (Andiri) (Terashima, 1983; Terashima et al., 1988). We refer readers to these and other research for details on the environmental, demographic, economic, and reproductive lives of Efe, and here describe features of local ecology and adaptation that proximately shape development.

Efe reside in groups of about 15–30 people, but camps can vary widely in composition with each move of every 4–6 weeks. This shuffling of the infant's social world is in response to rhythms of climate and forest resources, demography (e.g., mortality, marriage, fostering, and migration), and intermittent access to neighboring Lese farmer cultivans by clearing gardens and harvesting rice (January) and peanuts (June). As such, Efe infants are exposed to the variable presence and routines of others, along with changes in residence often from one month to another (Morelli et al., 2014).

Over the last decades, infrastructure deterioration in the region reduced the only road to a footpath by the early 1990s (Wilkie & Morelli, 1997). With poor market access, Lese gardens retracted to subsistence levels, greatly diminishing Efe' access to labor and farmed carbohydrates. In 1988–89, only 1% of observations of 1-year-olds, who still nurse frequently, were located in gardens or villages. In spite of constraints on carbohydrate and fat intake, Efe consume a diverse diet high in protein, fruit, and honey, and with the exception of anemia in reproductive-age women, neither adults nor children show signs of nutrient deficiencies (Dietz et al., 1989). Independent of body size, the average daily calorie intake of Efe falls well within forager variation, and higher than the San, Hiwi, Onge, Anbarra, and Mbuti net-hunters (Jenike, 2001). Unlike many CBHGs, rather than plant gardens themselves, northeastern Efe have responded to nutritional uncertainty by increasing the extraction of wild yams and other tubers, and hunting and trade of bushmeat for scarce cultigens (Wilkie & Morelli, 1997).

Conditions that have weakened Efe' access to horticultural foods present an opportunity to think more broadly about CBHG ecology in the past (e.g., Ichikawa, 2012). The Ituri is the most diverse rainforest in Africa, but resources are often temporally and spatially unpredictable in distribution. Ethnobotany inventories of Andiri Efe and Mbuti reported over 100 species of forest plants used (Ichikawa, 1999; Terashima et al., 1988), and in the northwestern Congo Basin, over 88 species of 61 genera and 43 families of wild edible plants were identified by the Baka (Billong Fils et al. 2020). In the heavy rainy season of 1989, many Efe complained of scarcity, but an old woman proudly displayed to the author (PIH) her basket brimming with an array of fruits, nuts, tubers, crustaceans, and fish, saying "the young women have forgotten where to find all the food." Securing food in the distant past required higher information and travel demands for women.

Efe and other CBHGs share much in common regarding their forest and social environments, along with many features of an extensive and sensitive infant allocare system. But not all. For example, Efe infants experience much lower direct paternal care (Hewlett, 1991; Tronick et al., 1992) and a briefer period of allonursing (Hewlett & Winn, 2014, Ivey Henry et al., 2014). Additionally, economic differences influence CBHG's access to food and care in important ways. Efe archers achieve higher hunting returns than Mbuti net-hunters overall, but experience much greater variation in day-to-day intake (Wilkie & Curran, 1991). The uncertain nature of bow-and-arrow hunts, prescribed butchering and distribution, rather than the pooling and equalization of net returns, and sharper sexual division of labor (Efe women and children rarely participate in hunts) reflect a more unpredictable energy budget for Efe archers than CBHG net-hunters (Bailey, 1991a; Meehan, 2009). Women's foraging and fishing returns are also variable and narrowly shared (Bailey & Peacock, 1988). Few Efe in the region, and no subject families in our research, planted gardens, and thus mothers could not readily buffer their own and their children's energetic variation.

10.3.1 A Phylogenetic View: Reconstructing the Efe Evolutionary Niche

Looking up through a porthole in the canopy, it may be that as Efe infants grow, they see the same complexly structured forest view as their ancestors in millennia past. Three rock shelters in the Efe region, and still used by them, suggest that the Ituri has long been occupied as Pleistocene and Holocene forests expanded and contracted, producing an archipelago of forests with savanna and woodland corridors between (Mercader et al., 2001). Such findings among CBHGs, together with early *Homo* occupation of Asian rainforests, reframe these habitats as central to the human story (Oslisly et al., 2013; Wedage et al., 2019).

Over the last decade, genomic studies have begun to lift the veil on the prehistory of CBHGs. Pygmies were long considered homogenous remnants of a continuous population, but genetically, geographically, and culturally they are diverse (Anagnostou et al., 2013; Bahuchet, 2012). An ancestral population of central African hunter-gatherers diverged from the shared !Kung line 48–60 kya, and split again around 30–20 kya (coincident with the last glacial maximum) into two distinct clusters – eastern (e.g., Efe, Mbuti, Asua, Sua, and Batwa) and western (e.g., Aka, Baka, and Biaka), with little subsequent exchange between them. CBHGs extended separation, and convergent adaptions are evident in genetic, epigenetic, and phenotypic patterns between the two groups; with Efe distinct in the lowest level of admixture with horticultural neighbors (Fagny et al., 2015; Perry et al., 2014). The Efe also retain the use of ancestral bow-and-arrow technology and have minimal access to market economies (Bailey & DeVore, 1989). Like other CBHGs, their indigenous association with the forest raises unique questions concerning plasticity in human growth and development (Migliano et al., 2013).

10.3.2 An Adaptive View: Genetic and Epigenetic Signals of CBHG Development

Primary interest in CBHGs has long focused on the question of small body size. Adaptive hypotheses are typically framed in terms of adult traits and functioning associated with mobility (Jang et al., 2019), thermoregulatory advantages (Cavalli-Sforza, 1986), low food supply (Bailey et al., 1989), pathogen costs (Perry et al., 2014), and a life history pattern associated with high mortality (Migliano et al., 2007). But, small body size during development presents a very different set of vulnerabilities than for adults, requiring a closer view of the infant niche and diverse developmental systems influenced in tandem with ecological experience. Genetic enrichment in eastern CBHGs include sites related to sensory perception (e.g., olfactory, taste, and myopia), neurodevelopment (e.g., neurogenesis, prefrontal cortex), morphological (e.g., adiposity, skeletal density, cardiovascular, muscle, and reproductive), and immune functions (e.g., antiviral signaling pathways, pathogen-specific responses) (Harrison et al., 2019; Lopez et al., 2019; Perry et al., 2014). These point to multiple adaptive systems at play in habitat responses over evolutionary time.

New insights are also emerging from epigenetic analyses informing CBHG's adaptations. Fagny et al. (2015) found that developmental processes dominate CBHG DNA methylation enrichment profiles, including gene sites associated with brain and neural development, growth factor binding, morphogenesis, locomotion, and a broad set of immune processes. Many sites are associated with embryogenesis and fetal development, but the timing of other signals remain unclear. Broad postnatal neural and physiological exposures, and later reproductive shifts underscore the extended importance of many (Gao et al., 2017; Kuzawa et al., 2010). (See Fig. 10.1 for genetic, epigenetic, and observed evidence reported in this chapter).

We do not speculate on specific associations between CBHG variants and outcomes in Efe development; phenotypic interpretations remain conditional on additional research on pathways and plasticity involved (Hoban et al., 2016). But, salient traces of ecological variation are evident in these patterns, offering clues of evolutionary to proximate developmental adaptation.

10.4 Developmental Plasticity and Somatic Capital – Forager Infancy in an Evolutionary Ecological Niche

Infancy is a transformative period of the most rapid postnatal growth (Locke & Bogin, Chapter 6, this volume; Bogin, 1999) and the period of strongest selection pressure in humans (Jones, 2009; Volk & Atkinson, 2013). In addition to evidence above, Efe infancy exhibits a biophysiological tuning of size and growth as features of adaptive biology. The Efe have the lowest average adult stature of any population (mean 143 cm males, 136 cm females), in a pattern evidenced from birth. Efe infants' average weight is 2.4 to 2.6 kg at birth, that is, a weight near or below the 5th percentile of NCHS standards and considered low birth weight (LBW) (Bailey, 1991b; Tronick & Winn, 1992).[2] Mbuti infants in the Ngayu region of the eastern Ituri weighed 2.6 kg at birth ($n = 40$) (Vincent et al., 1962), and were among 29 other populations with average birth weights below 3.0 kg in a global survey of neonates from 1945–1965. Only newborns among the Lumi of New Guinea were similar or smaller (mean = 2.4 kg) (Meredith, 1970).

Many LBW infants experience a period of rapid "catch-up growth" in the first year of life (Kuzawa et al., 2010); however, longitudinal measures of Efe from birth to 5 years demonstrate an increasingly negative rate of growth (i.e., increasing z-scores) compared to Lese and NCHS standards (Bailey, 1991b). Hunter-gatherers,

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[2] We report Efe growth comparisons according to the original analyses of respective authors who use NCHS (CDC) standards. Both NCHS and current WHO standards for low birth weight are 2.5 kg. Our discussion of postnatal growth trends relies on comparisons to neighboring farmers rather than external standards alone.

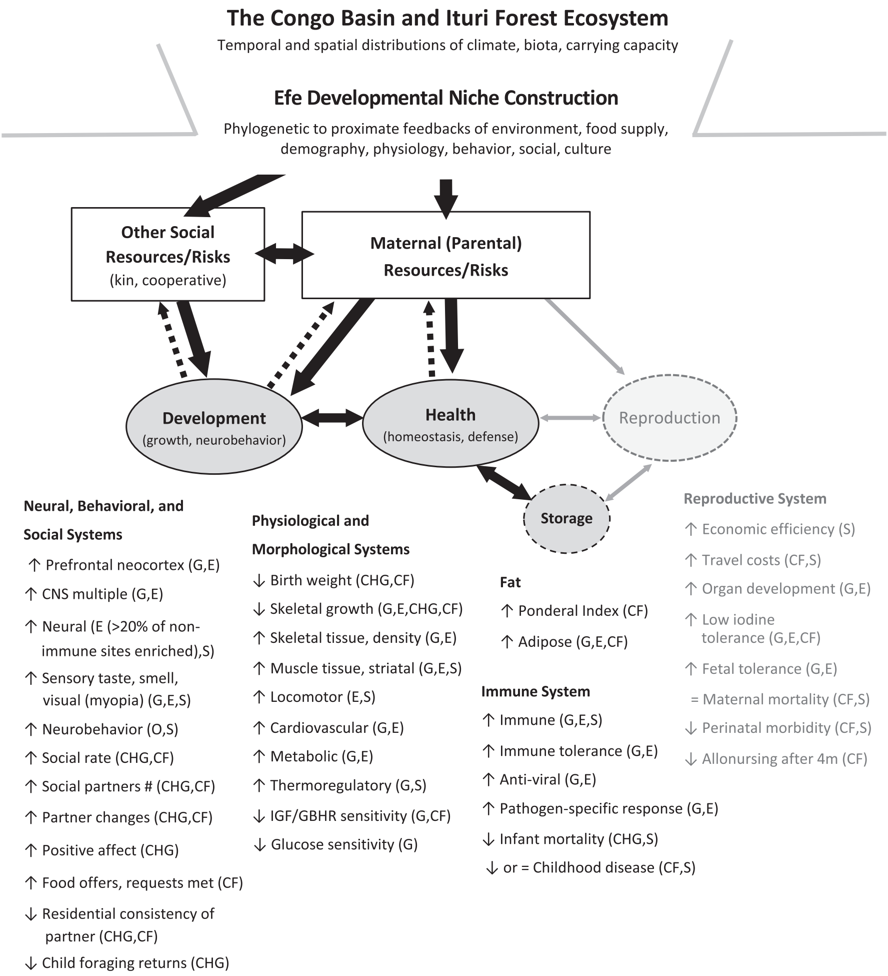

Fig. 10.1 A niche construction model of Efe development summarizing evidence of tradeoffs and enrichment from the following: (CHG) = Compared to several or mean of hunter-gatherers; (CF) = Compared to neighboring Bantu or Sudanic farmers; (E) = Epigenetic enrichment; (G) = Genetic enrichment; (S) = Social enrichment and support. Shaded circles represent life-history tradeoffs in development. Dark arrows show resource and risk flows, dashed arrows show developmental feedbacks. Light arrows and text represent current and predicted tradeoffs and investments in Efe reproduction. See citations in text for sources and details

including those with higher birth weights, generally converge on slower rates of growth than observed in other populations (Walker et al., 2006), and the small adult size of !Kung and Hadza leaves open the hypothesis that small size represents an ancestral phenotype (Howell, 2010; Little, 2020). In addition to this pattern, smaller body phenotypes than the hunter-gather average have emerged independently in a number of tropical forest peoples, with adaptive hypotheses similarly aligned to those described for CBHGs above (Amorim et al., 2015; Migliano et al., 2013).

Developmental plasticity in infant size and growth in the hunter-gatherer niche is likely to differ from LBW and slow growth among impoverished agricultural groups, where macro- and micronutrient scarcity and poor maternal health result in poor fetal growth (e.g., Rickard et al. 2012). In resource abundant settings, meta-analyses demonstrate that LBW in infants born ≥37 weeks gestation was not associated with childhood hypertension, obesity, cognitive impairment, or psychiatric diagnoses as predicted by a simple rendering of the developmental health constraint hypothesis (Malin et al., 2015). In these settings, where the most intensive research has been conducted, adverse LBW-associated outcomes involve additional signals of interuterine growth restriction (IUGR) (e.g., early gestation, very low birth weight [VLBW]) and compounded risks of economic, psychosocial, and environmental adversity (Aizer & Currie, 2014, Gage et al., 2010). Some etiological processes and risks (food insecurity, social, and immune stress), though, may be shared (Akombi et al., 2017; Wells, 2019).

10.4.1 *Trade-Offs in Growth and Health: The Hungry Immune System*

Coupled maternal and offspring energetic effects should be especially evident in high pathogen environments (McDade et al., 2019), and the endocrinological *resistance* to growth in CBHGs (Becker et al., 2013) implies serious disadvantages of rapid growth or larger size. Forager mothers must manage energetic and immune challenges through subsequent pregnancies, while enhancing the energy available for her offspring's own investments in growth and defense (Gurven & Walker, 2005; McDade et al., 2019). Efe and other hunter-gatherer infants are at special risk in the pathogen-rich niche of tropical forests. Immune activation can disrupt child growth across even the short span of a few months (McDade et al., 2008), and the exceptional diversity of forest pathogens implies higher costs of managing complex trade-offs *within* the maturing immune system (e.g., allocations to innate versus acquired, sensitivity versus specificity, and tolerance versus elimination responses) (McDade et al., 2016).

Infections are most costly to the young, and an early survey of Ituri Mbuti net-hunters found that children under 15 years of age had a higher prevalence of parasites than did adolescents or adults (Mann et al., 1962). Yet, compared to Lese farmers, Efe children aged 2–18 years experienced a lower frequency of every disease and symptom assessed, including anemia, splenomegaly, hepatomegaly, diarrhea, cough, and chills/fever, although differences did not reach significance (Dietz et al., 1989). Efe children spend most of their time in the forest setting, suggesting greater pathogen exposure (Mann et al., 1962). But, although they are smaller, and grow more slowly than Lese at every age, immune allocations and enrichment appear to buttress the forager child's health. Efe infants have other tools in the toolbox, as well.

10.4.2 Trade-Offs Within Growth: A Different Investment in Size

An important context of Efe’ adaptation to immune and other energetic threats is suggested by a different measure of infant size – Ponderal Index (PI = kg/cm^3). Mean Efe PI at birth of 2.93 places them in the 90th percentile (Tronick & Winn, 1992). Thus, relative to size, Efe neonates are heavy, recasting their LBW as an adaptive feature of developmental biology (e.g., Hochberg & Albertsson-Wikland, 2008). Maternal investment in fetal adipose tissue is associated with environmental disease risks (Kuzawa, 1998), and in a country-level comparison, Thomas et al. (2004) found that birth weight was positively related to the prevalence of parasitic disease. Efe birth weight runs counter to this trend, but fetal adiposity suggests such buffering. The Efe infant mortality rate of 14–20% (Bailey, *unpublished data*; Ivey, 2000) is below the hunter-gatherer mean of 26.8% (n = 18) (Volk & Atkinson, 2013). LBW alone poorly captures ecological processes in infant growth. Rather than a deficit, Efe trade-off responses suggest resilience.

Infant fat is critical for expensive postnatal growth of the brain, and Efe biology may specialize in this protective evolutionary feature. Efe head circumference (a metric of brain growth) and weight for height (an indicator of fatness and nutrition status) remained within standards through infancy and childhood (Dietz et al., 1989). Even as infant fatness mediates the tight somatic trade-offs of neural development, health, and skeletal growth, Efe experience a comparative slowing of growth such that most of the relative height difference between Efe and other populations is accounted for by 5 years of age (Bailey, 1991b). This period aligns with the high glucose demands of the growing brain, which increase 2.5 times from birth to 4 years of age (Kuzawa et al., 2014). Linear growth slows precipitously, but as genetic and epigenetic enrichments suggest, other developmental systems are fully at play. And, the protective relevance of fetal adiposity may extend well beyond infancy, enhancing resilience to energetic demands in the reproductive years (Jasienska et al., 2006).

10.4.3 Life History Trade-Offs of Small Size and Slow Growth

Small size, fast growth, and early reproduction has been proposed as a mortality-associated life history pattern for CBHGs (Migliano et al., 2007; Ramirez Rozzi et al., 2015). However, the Efe average 15.5 years at menarche, 19+ years age at first birth (Bailey, *unpublished data*), and interbirth interval of 3.2 years (Ellison et al., 1986; Ivey Henry, *unpublished data*) all align with a slower growth-later reproductive pattern. Efe are consistent with Aka birth spacing (mean 3.5 years) (Hewlett, 1991), and analyses of Gawlik and Hochberg (2012) showing longer interbirth intervals associated with smaller body size among foragers and other small-scale societies. As with Efe development, genetic signals of reproductive enrichment may be protective, rather than accelerate these systems. For example, unlike the Lese, Efe exhibit fewer signs of iodine deficiency, which is associated with adverse developmental (e.g., congenital malformations, cognitive deficits) and reproductive (e.g., anovulation, fetal loss) outcomes (Dietz et al., 1989; Dormitzer et al., 1989).

Maternal constraints on Efe reproduction and infant care are suggested by lactation patterns, a critical energetic transfer from hunter-gatherer mothers to growing young (Sellen, 2007). In spite of extended and intensive assistance in infant care, Efe do not allonurse beyond the first months of life (Ivey Henry et al., 2014). Nor do they have consistent access to cultivans and fats to speed the weaning process (see Meehan & Roulette, 2013). They do benefit greatly by a flexible allocare system that lessens maternal work conflicts with nursing (Ivey, 2000), with increasing food sharing by others as infants grow (Morelli et al., 2019). The substantial expense of Efe young, however, extends well beyond weaning. Like other CBHGs, Efe children face poor prospects of meaningful returns of forest foods well into their second decade (Hagino & Yamauchi, 2016). But, unlike juvenile CBHG net-hunters, Efe children can provide little in the way of direct assistance to archers in the hunt. Their primary contribution to parental provisioning is infant care (Ivey Henry et al., 2005). Similar to traditional !Kung, unpredictable food returns, high maternal travel demands, and low provisioning capacity of young are a substantial constraint on maternal condition, favoring small size and slow growth independent of rainforest environments (e.g., Blurton Jones et al., 1994; Howell, 2010).

Few hunter-gatherer infants survive their mother's loss (Trevathan & Rosenberg, 2016), and childbirth is a risk to all hunter-gatherer mothers. Births recorded among neighboring Asua Mbuti in the Ituri from 1956 to 1959 found no significant differences in the ratio of infant size at birth to maternal size, or infant or perinatal mortality between pygmy and Bantu mothers. Mbuti births, however, experienced a significantly lower rate of dystocia (1% versus Bantu 12%), suggesting some advantage to mothers and infants of small size at parturition (Vincent et al., 1962). No data exist on Efe or other forager gestational age at birth, but would be advantageous to further understand hunter-gatherer plasticity in early development (e.g., Williams & Drake, 2019). These comparisons of Efe infant and maternal health suggest fewer costs to small size than expected.

10.4.4 How Can a Small Hunter-Gatherer Infant Compete?

A LBW, fat, slow-growing child is still small, and at great risk if they cannot garner attention required from energetically stressed mothers and others to survive, and to respond adaptively to the variable natural and cultural environments in which they find themselves. How well infant neurobiological systems are organized is important to their ability to secure resources (Bell et al., 2008). Often, LBW infants rate poorly on measures of neurobehavioral competency and coordination, but this is not evident in Efe infancy. Over the first 2 weeks of life, using the Neonatal Behavioral Assessment Scale (NBAS), Tronick and Winn (1992) noted:

> Efe infants stilled and focused on visual and auditory stimuli. They tracked and followed these stimuli, moving their eyes and head in smooth arcs. Efe infants managed extended periods of well-modulated alertness and in general experienced few dramatic changes in state. When they did become upset or fussy, they were easily quieted, sometimes with the assistance of the examiner, but often they quieted themselves. Their motor tone was in the normal range and for the most part unremarkable, both when lying alone and when handled. They had few startles, and tremulousness was only observed during the more stressful segments of the examination. Repeated measures analysis of variance (ANOVAs) on each of the cluster scores failed to uncover changes in performance on any of the cluster scores over time (all $F < 1.0$, $p > .5$). (p. 442)

Efe infants' neurobehavioral organization is comparable to healthy average weight Caucasian samples, with none of the weak indicators found in symmetrical growth-restricted full-term infants of similar birth weights. And, rather than more irritable and reactive, they are calmer and more easily settled than these samples. Efe newborns also differ from the NBAS performance of Gusii infants (Kenya), who are higher in lability of state, inanimate visual, and motor maturity measures than Efe (Tronick & Winn, 1992). The NBAS performance of Efe in early infancy may present an additional phenotypic advantage suggestive of variation among hunter-gatherer infants, and underscores the need to further test the assumed costs of being small and growing slowly.

In sum, the somatic and neurobehavioral assets of Efe infancy are many: lower than expected mortality given birth weight, environment, and hunter-gatherer mean; higher PI at birth, higher relative weight for length and head circumference (within NCHS standards) for size (weight or length) during infancy and childhood; lower or equal childhood disease than farmers; and better neurobehavioral performance than expected for size. Efe genetic and phenotypic enrichment also suggests developmental enhancement of morphological, neural, sensory, motor, and immune facilities to environmental signals that favor their survival. Rather than small size as a consequence of lower investment per offspring, these developmental qualities suggest other infant and intergenerational investments that standard growth comparisons overlook.

10.5 The Sociocultural Niche of Efe Hunter-Gatherer Development

So far, our inquiry into Efe phylogenetic and ontogenetic adaptations have focused on infant growth, health, and emerging neurobehavioral processes. We add to this mosaic behavioral and psychosocial processes related to the culturally organized experience of others, in which care is a central part. Drawing on decades of research on Efe ecology and practices of infant and child networks, we see these early relationships as critical to both their health and the development of social agency in a dynamic and often unpredictable physical, energetic, and social environment. An infant's ability to weather social variability appears central to resource security, thus, the somatic demands of Efe infancy are tethered to the intimate biophysiological and psychosocial experience of care.

Tronick et al. (1987) proposed that Efe regulatory vulnerabilities are managed by care characterized by near constant physical contact, frequent nursing of short durations, and social stimulation. These protective features typify hunter-gatherer systems of care (Konner, 2010), and are prescribed in Western settings as interventions to mitigate the adverse physiological performance of preterm and LBW infants (Campbell-Yeo et al., 2015; Kubota et al., 2019). In forager care contexts, infant biosocial systems appear organized to the rhythms of the developmental niche, while also priming their capacities to take advantage of it. For Efe, this involves a diverse set of people approaching, moving, and engaging an infant throughout the day.

Efe social experience is surprisingly broad and rapidly paced from infancy into childhood. First reports found that from birth to 4.5 months, Efe had an average of 14.2 different caregivers, and the rate of infant transfer between caregivers increased from almost 4 to 8 times an hour (Tronick et al., 1987). Rather than heightening risks, in addition to physiological supports, these practices protect infants by moving the child, oftentimes, to unencumbered (i.e., relatively relaxed and undistracted) caregivers (Ivey, 2000; Ivey Henry et al., 2005). Increasing the likelihood that infants spend time with less burdened, and, therefore possibly more attentive caregivers, may mean infants experience social movement positively. They get extensive practice with social variability in a protective niche, allowing them more easily to attend to and learn from their social partners. Features of the Efe infant neurobehavioral system – well-modulated alertness and high thresholds for state dysregulation – assist with this learning. In time, infants develop skills to manage these fluid social scenes with their myriad characteristics, permanency, and interests.

10.5.1 Socially Distributive Care and Changing Infant Capacities for Agency

With improved technology, later research recorded continuous focal observations in real time, and found that while there continues to be a steady increase in unique partners across infancy, the rate of partner changes was higher than evident by interval sampling. The rate of social partner change in a 2-h period averaged every 3 min from 5 months to 2 years, with only small differences in timing between ages. The stability of the pattern is evident in that infants between 7 and 11 months, comprising those who did not toddle independently about camp (and physically choose partners), engaged new partners every 2 min, while mobile infants from 12 to 15 months did so every 3 min, and from 18 to 21 months every 2 min (data were sampled in 15-min intervals from the infant's morning emergence from the hut to dusk) (Morelli et al., 2014). Achieving the capacity to locomote and approach others about camp, Efe infants mirror the social pace they experienced in more sedentary care. They sustained this pattern given the physical, cultural, and interpersonal factors that enable it, such as the public landscape in which most daytime events occur, the freedom they have to wander and approach others in camp, and their developing capacities for physical (e.g., motor, verbal) and social agency. We see this pace as evidence of attunement to a community-wide rhythm of sociality and care.

Attunement to a community and pace of engagement suggests a familiarity and stability of relationships that Efe infants may not experience as such. Camps were rarely in the same locale from one observation to the next, and partner consistency was dramatically affected by Efe mobility. For example, on average, ~70% of infant partners changed from one observation to the next (from 4- to 6-month-old to 7- to 11-month-old focal follows). While family members related r =.125 (e.g., first cousins) and higher were more consistently available than extended kin (e.g., clan) and non-kin, the latter groups represented 60% of nonmaternal care across all age ranges to 2 years of age (Morelli et al., 2014).

This care pattern would appear an unstable and insecure psychosocial experience for the child. We suggest otherwise. Efe infants are primarily positive in affect, and increasingly so over the course of the first 2 years (Morelli et al., 2014). There are also regularities in care across caregivers that infants learn to expect (e.g., experiencing a rapid response when distressed (within seconds), food sharing when a partner is eating). Additionally, caregivers are typically well known and trusted by mothers (e.g., friends, frequent camp residents), and the care they provide is important to their cooperative relationships with mothers. In fact, the number of allocaregivers experienced at 1 year of age was positively associated with Efe survivorship at 3 years (but not with group size or number of kin) (Ivey, 2000).

Another indicator of their empowerment is observed in infant and young children's success in securing resources. As clues to the rapid pace of infant social engagement, the relative percentage of successful requests to others was negatively associated with the interval (in minutes) between partners (Morelli et al., 2014). Brief multiple engagements may facilitate more solicitous responses. Positioning infants and young children as social actors in give-and-take interactions introduces them to cooperative acts, of which food sharing is one of the most important. They are initiated into food sharing mostly by offers of (rather than requests for) food, not only from family members, but from many others in the camp (Morelli et al., 2019). And, while they have little food of their own to share, before they begin to walk they are taught how to divide their small share and offer it to others. In this way, others recognize their capacity to make such choices, and when infants and young children are asked for food, they are likely to share it.

These experiences of meaningful exchange enhance the sense of solicitousness and obligations that others feel toward the child, and these early ties are often extended in relationships where children as young as 3 years old may sometimes sleep in the huts of especially close allocaregivers. As they grow, even young children may be found in different camps from their homes for a short period of time, and older children are often fostered for longer periods, especially if one or more parent has died (Ivey Henry et al., 2005). For Efe infants, the early development of especially familiar, comfortable, and cooperative relationships appears well-timed with the period of increasing energetic insecurity, as nutrition needs outstrip maternal milk supply, and linear growth slows precipitously.

10.5.2 Attachments and Synchrony: Biobehavioral Perspective

Infants and young children develop affiliative relationships with caregivers they perceive as trustworthy. As our research has demonstrated, there are many trustworthy caregivers who consistently and reliably meet their needs and keep them safe in contexts of threat. Given this, and infants' highly positive experience of others, we expect them to increasingly develop trust across many relationships. These are the caregivers with whom infants are likely to form attachments, which, we propose, are experienced as an integrated system of relationships, not as a collection of single attachments. For example, infants were not observed as engaged with every group member, but spent substantial time with many, and their positive affect was not associated with kinship (Morelli et al., 2014). We imagine their experience of trust radiates across the social landscape, rendering the camp as a whole a secure setting for them.

This inclusive, flexible, relational system of attachments is supported by relationship features common to all relationships people develop across the life span. One in particular stands out to us – synchrony. Synchrony refers to temporally coordinated process between social partners that takes place at the same time or close in time (Feldman, 2007). With regular experience of synchrony, biobehavioral systems become mutually attuned (e.g., mothers adapted their heart rhythms to that of their 3-month-olds, and vice versa, during gaze and vocal synchrony in face-to-face interactions (Feldman et al., 2011), and for infants, such attunement lays the basis for attachment relationships.

Morelli and Liu (2021) argue that Efe infants and young children experience high levels of synchrony with many who care for them. Frequently, care involves regulating infant state and establishing infant internal rhythms – indicators of synchrony. Sitting on the back and hips of caregivers who are involved in rhythmically repetitive daily activities are other ways to experience synchrony. Care is usually a multisensory experience with one – or several caregivers at the same time – singing to, patting, and rocking infants, and multisensory processing maximizes synchronous processes (Harris & Waug, 2002). In addition, infants experience synchrony with others with whom they are not directly involved in regularly occurring camp-wide activities characterized by rhythm and repetition, such as storytelling, singing, drumming, and clapping. Neurobehavioral organization of Efe infants and sensori-perceptual gene enhancements in CBHG development may aid this processing.

10.5.3 Developmental Niche Construction as a Synchronous Process

Synchrony across modalities and biobehavioral systems is a central dimension of developmental niche construction that generates expectations, predictability, and efficiency in relationships that facilitate and encourage social agency. When forager infants can anticipate the rhythm and responses of others, they can initiate actions and move more confidently in tune with them, and about the camp. Efe infant affect and the pacing of relationships suggest so, as they are passed, move, and engage social partners without obligating them for long periods of time, or pressing demands for more costly forms of care, or more food (Ivey, 2000; Morelli et al., 2014). Infant agency is built on such confidence, strengthening multisystem capacities to engage others and the world. These insights inform the evolution and development of human cooperation, as interpersonal synchrony in expectation and exchange, and the trust that grows from the sharing and reciprocity in which relationships develop, is foreshadowed by the growth, health, and social trade-offs that infants (and humans) must manage to survive an uncertain world.

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Chapter 11
Evolutionary Perspectives on the Role of Early Attachment Across the Lifespan

Jeffry A. Simpson and Margaret M. Jaeger

At its core, attachment theory is an evolutionarily based theory that articulates how people develop, both in terms of their personality and their social behavior, in response to significant environmental and interpersonal experiences throughout their lives. This development depends, in large part, on how they have been treated by close others (attachment figures) in different relationships and types of situations earlier in life. Indeed, it is difficult to fully appreciate attachment theory and all it has to offer without understanding its evolutionary foundations and purposes, both of which begin in infancy.

Over the past 30 years, a handful of attachment-relevant models of social development have utilized and expanded upon key connections between attachment theory and current theorizing in evolutionary psychology. As we shall see, much of this work has been guided by an overarching evolutionary framework known as *life history theory* (LHT). One of the primary goals of this chapter is to showcase these models and their underlying logic to not only reveal the fundamental role that attachment theory and research assume within them, but also to identify new directions in which future attachment research might head.

In this chapter, we begin by discussing some of the critical features of the physical and social environments in which our ancestors evolved, which ostensibly shaped the development of the attachment behavioral system in humans. We then discuss how and why attachment theory is considered a major, middle-level evolutionary theory and highlight a few of its normative (species-typical) and individual difference components, especially those that are relevant to the evolutionary-based social development models we review later in the chapter. Following this, we discuss some of the core tenets of LHT, after which we describe six evolutionary-grounded models of social development, each of which leverages ideas, principles, and processes from attachment theory as well as current evolutionary thinking to explain how and why people develop in different ways across their lives, starting early in infancy and childhood. We conclude by discussing some ways in which

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attachment theory and research might benefit from incorporating and examining additional constructs central to other major, middle-level evolutionary theories.

11.1 Key Features of the Social and Physical Environment of Evolutionary Adaptedness (EEA)

To appreciate the unique problems that the attachment behavioral system evolved to solve, one must understand the physical and social environments in which humans have lived during our evolutionary history. Attachment theorists beginning with Bowlby (1969/1982) have speculated some about what the physical *Environment of Evolutionary Adaptedness* (EEA) was probably like, but less attention has focused on the *social* EEA (see Simpson & Belsky, 2008).

Throughout most of evolutionary history, our ancestors hunted and gathered food in small, cooperative, and fairly well-coordinated groups (Cronk, 1999; Kelly, 1995). In all likelihood, most people were biologically related to other members in their tribe, with strangers being encountered primarily during inter-tribal trading, social exchanges, or war (Wright, 1994). Although some people moved in and out of their primary (natal) groups, many stayed within the same tribe for most or all of their lives. For the most part, men and women established pair bonds (Cronk, 1999), but serial monogamy was probably also common (Fisher, 1992). Most children were born approximately 4 years apart and were raised with help from extended family members, including some biologically unrelated individuals (Wright, 1994). According to Hrdy (1999, 2005), humans were "cooperative breeders" who shared and distributed important tasks, one of which was child rearing (see Hrdy and Burkart, Chap. 6, this volume). Especially during the first few years of life, young children were socialized by older children, particularly older siblings, if the older children survived the many perils of childhood (Eibl-Eibesfeldt, 1989). Both men and women provided food to their groups and families, with men doing most (but not all) of the hunting, and with women doing most (but not all) of the gathering (Wood & Eagly, 2002).

The physical environments our ancestors inhabited also varied over time in both their harshness and predictability (Ellis et al., 2009), which made daily life and parenting challenging. The attachment behavioral system, therefore, most likely evolved to address the challenges posed by these conditions, balancing trade-offs between increasing the likelihood of infant survival while also ensuring as much as possible parents' own survival (Chisholm, 1996). Young children probably inferred what their current environment was like (e.g., its level of harshness and predictability) based on the quality of care they received from their primary caregivers (Simpson & Belsky, 2016). All of these probable features of our social and physical EEA must be considered when conceptualizing the purpose and functions of the attachment behavioral system in the context of an evolutionary framework.

11.1.1 Attachment as a Middle-Level Evolutionary Theory

Similar to almost all evolutionary theories, attachment theory has two primary components: (a) a normative component, which explains modal (species-typical) patterns, processes, and stages of attachment in humans (e.g., "How and why are attachment bonds formed in children and adults?"), and (b) an individual difference component, which addresses deviations from modal (normative) patterns, processes, and stages (e.g., "How and why do different patterns of attachment emerge in children and adults?").

According to Bowlby (1969/1982, 1973, 1980), the attachment system evolved to serve three basic functions: (1) to maintain close proximity between vulnerable infants and their stronger/older/wiser caregivers; (2) to provide infants a safe place to retreat for comfort and soothing when threatened; and (3) to provide infants a secure base within which to gain confidence and resume exploration of the world once threat abates. Bowlby believed that these three functions, if met sufficiently, should have, on average, increased the likelihood of infant survival and facilitated their social development, especially considering that humans are born in an underdeveloped physical state and must rely on caregivers to meet their basic needs for several years (Trevathan, 1987). This strong dependency makes it necessary for infants to maintain close physical and psychological proximity to their stronger/older/wiser caregivers. Close proximity allows caregivers to provide sufficient food, warmth, and safety to their vulnerable infants as well as a supportive place from which infants can explore their world and eventually pursue other important life tasks and goals.

For these normative (species-typical) features of attachment to emerge, however, there needs to be synchrony between caregivers and their infants. Evidence of such synchrony has been documented between caregivers and their young infants across many cultures (see Eibl-Eibesfeldt, 1989, for a review). Most caregivers behave in ways that facilitate emotional bonding with their infants from the opening days of life, such as emphasizing eye contact, automatically holding infants the ideal distance away for their infant's underdeveloped eyes to see clearly, and exaggerating facial expressions once eye contact is made with their infant (Hane & Fox, 2016). These and other forms of synchronization between caregivers and their infants also facilitate the continued development of the attachment behavioral system as infants transition to becoming young children.

Attachment behavior early in life develops across four stages, beginning at birth and continuing to approximately 3 years of age (Bowlby, 1969/1982; Main, 1990). During the first stage from birth to about 3 months old, most infants enact attachment-related behavior (e.g., being soothed by being held when upset) toward many different adults, showing little preference for a specific caregiver or a small set of caregivers. From about 3 months of age until approximately 7 months, most infants enter a second stage during which their attachment-related behaviors become specific to either one or a small set of caregivers with whom they regularly interact. During the third stage, which runs from about 7 months to 3 years of age, infants' internal working models (i.e., their general expectations about how their caregivers will respond to them) start to develop as the three primary functions of attachment (proximity maintenance, safe haven, and secure base) begin to emerge. At approximately age three and beyond, which marks the fourth stage, attachment processes begin to shift from a focus on physical proximity maintenance to a focus on psychological felt security (Sroufe & Waters, 1977) as children become more active and independent. During adolescence, most individuals gradually shift their attachment bonds from their primary caregivers to close peers (i.e., best friends) and eventually to long-term romantic partners.

Children, however, are exposed to different kinds of rearing environments and, subsequently, different styles and patterns of parenting. The Strange Situation Procedure, a lab experience in which infants are exposed to "danger cues" while their caregivers have an opportunity to comfort them, identifies stable individual differences in parent-child attachment relationships (Ainsworth et al., 1978). The manner in which the attachment behavioral system operates within a particular relationship can be categorized in one of four patterns: secure, insecure-anxious/resistant, insecure-avoidant/resistant (see Ainsworth, 1979; Main, 1981, 1996), and disorganized (see Lyons-Ruth & Jacobvitz, 2016).

Secure attachment patterns tend to emerge when caregivers behave in a warm, responsive manner to their distressed infants, routinely providing them with effective, soothing comfort. Infants and young children who are securely attached to their primary caregivers trust and rely on them to regulate their emotions, especially when infants are distressed. Insecure-anxious/resistant attachments usually emerge when caregivers do not respond to their infant's distress in a consistent or skilled manner, perhaps due to lack of parenting knowledge, under-involvement, or distractions. Infants with insecure-anxious/resistant attachments tend to be clingy, vocal, and difficult to comfort, particularly when they become upset. Insecure-avoidant/resistant attachments are typically witnessed when caregivers consistently push away or reject their infant's bids for comfort when infants are distressed, either because they do not like or want to be a parent or they feel overwhelmed by parenting responsibilities. Infants with insecure-avoidant/resistant attachments tend to be more independent, quieter, and less likely to turn to their caregivers for comfort when distressed. There is a fourth attachment pattern—disorganization—which usually emerges in response to parental abuse or mistreatment (Hesse & Main, 2000). Disorganized children often display strange or conflicting behavioral reactions when upset, revealing their lack of a coherent strategy to seek or maintain contact with their caregivers and utilize them as a source of safety and comfort.

Even though attachment insecurity tends to be associated with more negative psychosocial outcomes (Thompson, 2016), insecure-anxious/resistant and insecure-avoidant/resistant attachment patterns are adaptive in evolutionary meaningful ways (e.g., Main, 1981; Szepsenwol & Simpson, 2019). For example, the clingy, protesting behaviors commonly displayed by anxious-resistant infants help them to draw the attention of caregivers who are failing to provide consistent attention and care. Moreover, the standoffish behavior of avoidant-resistant infants keeps their potentially reluctant caregivers from feeling overburdened or overwhelmed, increasing the likelihood that such children are not abandoned. Secure attachment patterns also make evolutionarily adaptive sense, but primarily in benign environments that permit warmer, more responsive caregiving, which was by no means the norm in evolutionary history. These distinct attachment patterns and associated behaviors not only help children cope more effectively with their current environments; they also provide a glimpse of what children might eventually encounter in their own future environments. We now introduce a broad evolutionary framework within which attachment theory and its core principles are embedded.

11.2 Life History Theory

At its core, life history theory (LHT) addresses how and why individuals allocate time, energy, and resources to different traits, behaviors, and/or life tasks, given certain trade-offs that might affect their reproductive fitness (Del Guidice et al., 2016). Cast another way, LHT attempts to identify the selection pressures that would have influenced how our ancestors should have allocated their time, energy, and resources to physical development, growth, reproduction, body repair, or aging. Broadly speaking, individuals can increase their reproductive fitness in two fundamental ways: (1) they can “invest” (either consciously or unconsciously) in traits or attributes that affect the timing of their mortality (i.e., the age at which they die), or (2) they can “invest” in traits or attributes that influence the timing of their fertility (i.e., the age and rate at which they reproduce).

Many life history traits/attributes, however, have opposing effects on mortality and fertility (Del Guidice et al., 2016). For example, traits or attributes that improve fertility through more frequent or greater mating effort tend to shorten survival because many of the traits that make people (particularly men) more attractive to the opposite-sex compromise the immune system (Grafen, 1990). Moreover, the allocation of energy and resources to growth during development usually impedes fertility when individuals are younger, but enhances it after they reach sexual maturity (Charnov, 1993). As a result, individuals must make three basic trade-offs during their lives: (1) whether to invest in present (immediate) reproduction or future (delayed) reproduction; (2) whether to invest in higher quantity or higher quality offspring; and (3) whether to invest in mating effort or parenting effort. The way in which each trade-off is made should be contingent on many factors, such as the nature of the local environment (e.g., how difficult it is, the number of pathogens it contains, whether biparental care is necessary), an individual’s health, skills, and resources at a given time, the health, skills, and resources of others (e.g., kin, potential mates, competitors), and so on.

11.2.1 Lifespan Attachment-Evolutionary Models of Social Development

Attachment theory was developed in part to explain social and personality development across the lifespan (Bowlby, 1979). Early attachment theory and research, however, focused primarily on barriers to inclusive fitness, especially problems surrounding infant survival, rather than other major barriers to fitness, such as problems associated with mating and parenting later in life (for an exception, see Main, 1981). In fact, the possible evolutionary function(s) of childhood attachment patterns were not linked theoretically to the development of different adult romantic attachment and mating orientations until Belsky et al. (1991) published a groundbreaking model that conceptualized social development from an evolutionary/attachment perspective.

11.2.1.1 Belsky, Steinberg, and Draper's Model

Inspired by LHT and the effects of early father absence during childhood (e.g., Draper & Harpending, 1982), Belsky et al. (1991) outlined the first evolution-based, attachment-oriented lifespan model of human social development. According to this model, early social experiences "prepare" young children for the social and physical environments they are likely to inhabit across their lifetime. The model focuses primarily on the rate of development (faster vs. slower) and the trade-off between offspring quantity versus quality. As depicted in Fig. 11.1, the model suggests that: (a) early contextual factors in and around the family of origin (e.g., the degree of stress, spousal harmony, and financial resources) affect (b) early child-rearing experiences (e.g., the level of sensitive, supportive, and responsive caregiving they receive). These experiences, in turn, then shape (c) psychological and behavioral development (e.g., the development of specific attachment patterns and associated internal working models), which influence (d) somatic development (i.e., how quickly sexual maturation is reached) and ultimately (e) the adoption of faster vs. slower orientations toward both mating and parenting.

According to the Belsky et al. model, two developmental trajectories result in two phenotypically different reproductive strategies in adulthood. One strategy reflects a short-term, opportunistic orientation toward mating and parenting in which sex occurs relatively earlier in life, romantic pair bonds tend to be weak, fleeting, and unstable, and parental investment is lower. During our evolutionary past, this orientation would have increased the *quantity* of offspring, on average. The second strategy reflects a longer-term, more investing orientation toward mating and parenting in which sex occurs comparatively later in life, romantic pair bonds are stronger and more enduring, and parental investment is greater. Across evolutionary history, this orientation would have maximized offspring *quality*, on average. The most unique prediction stemming from this model is that early rearing experiences should alter the timing of puberty. Specifically, sexual maturation

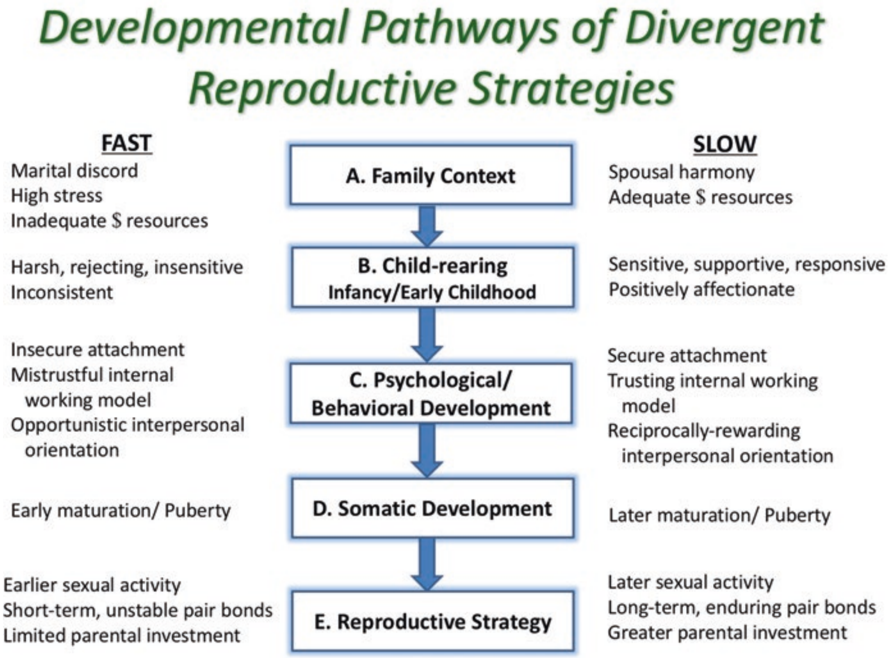

Fig. 11.1 The stages and pathways of Belsky et al.'s (1991) evolutionary model of social development

should occur earlier in individuals who develop on the "quantity trajectory" relative to the "quality trajectory."

A sizable amount of cross-sectional and more recently longitudinal research supports various stages of the Belsky et al. model (see Belsky, 2012; Simpson & Belsky, 2016 for reviews). For example, higher socio-emotional stress within families is associated with more insensitive, harsh, rejecting, inconsistent, and/or unpredictable parenting practices. Moreover, economic hardship (McLoyd, 1990), occupational stress (Bronfenbrenner & Crouter, 1982), marital discord (Emery, 1988), and psychological distress (McLoyd, 1990) are all related to more hostile or detached/indifferent styles of parenting. Conversely, greater social support and more abundant economic resources forecast warmer, more sensitive child-rearing practices (Lempers et al., 1989), most likely because parents who are less stressed tend to be more patient with or tolerant of their children (Belsky, 1984).

The hypothesized link between parental sensitivity and the psychological and behavioral development of children is also well established. For example, during the first year of life, insensitive and unresponsive caregiving predicts the development of insecure attachment patterns in children (De Wolff & van IJzendoorn, 1997), which forecasts more behavior problems later in childhood (e.g., Matas et al., 1978; Waters et al., 1979). During elementary school, for instance, insecure children typically display more behavior problems, especially involving aggression and disobedience (Lewis et al., 1984). These behaviors are presumably guided by their insecure working models, which "prepare" the child to engage in more opportunistic advantage-taking and less communal relationships later in life.

Belsky et al. (1991) also conjectured that children who are exposed to greater socio-emotional stress, have insecure attachment patterns, and display behavior disorders should reach puberty (i.e., reproductive capacity) earlier than children without these attributes. According to LHT (Chisholm, 1993, 1999), in environments where resources are scarce, relationship bonds are weak, and mortality risks are high, individuals should allocate more energy and effort toward physical development, earlier mating, and shorter-term romantic pair bonds because doing so would have increased the likelihood of reproducing before death in the EEA. Conversely, environments in which resources are plentiful and relationship bonds are stronger and more enduring should motivate individuals to channel greater energy and effort to somatic development, later sexual maturity, delayed mating, and longer-term romantic pair bonds that facilitate higher quality parenting. In these more benign evolutionary environments, reproductive fitness would have been enhanced by delaying reproduction until individuals acquired the skills and resources needed to ensure sufficient quality of each offspring, allowing offspring to benefit from the embodied capital that humans often require for successful reproduction.

Several studies have found evidence consistent with these expectations (Belsky, 2012; Simpson & Belsky, 2016). For example, greater parent-child warmth forecasts delayed pubertal development in both prospective longitudinal studies (e.g., Ellis et al., 1999; Graber et al., 1995) and in retrospective or concurrent ones (e.g., Kim et al., 1997; Miller & Pasta, 2000). Moreover, greater parent-child conflict and coercion predict earlier pubertal development in both prospective longitudinal studies (e.g., Ellis & Essex, 2007; Moffitt et al., 1992) as well as retrospective or concurrent ones (e.g., Kim et al., 1997). Furthermore, parents involved in happier, less conflict-ridden relationships tend to have daughters who reach puberty later, both in prospective longitudinal studies (e.g., Ellis et al., 1999; Ellis & Garber, 2000) and in non-prospective ones (e.g., Kim et al., 1997). In addition, attachment insecurity in the first 1–2 years of life prospectively forecasts the earlier age of menarche (Belsky et al., 2010). Not all studies, however, have documented puberty-related effects. Steinberg (1988), for instance, did not find associations between either the amount of family conflict or coercion and pubertal timing in a sample of girls. However, family experience/pubertal timing effects have emerged in studies capable of accounting for possible genetic confounds (e.g., Tithers & Ellis, 2008; Pesonen et al., 2008).

It is important to emphasize that all of these findings come from studies of girls, but not boys. What might explain this gender difference? One possible explanation is that the early versus later reproduction trade-off might be more important for females, whereas the trade-off between somatic development and reproduction might be more pressing for males, who often must engage in greater intrasexual competition in order to attract and retain mates (see James et al., 2012).

Evidence relevant to the final stages of Belsky et al.'s model comes from two sources: (1) research linking adult attachment orientations to mating and romantic relationship functioning, and (2) research linking adult attachment and parenting practices. Besides several cross-sectional studies that have confirmed these connections (e.g., Brennan & Shaver 1995; Miller & Fishkin, 1997; Simpson, 1990), recent longitudinal research from the Minnesota Longitudinal Study of Risk and Adaptation has provided fairly compelling support for the model. Simpson et al. (2007), for example, found that individuals who were insecure at age 1 in the Strange Situation experience and express more negative emotions in their romantic relationships 20 years later, an effect that is mediated through their lower social competence in grade school and their less-secure same-sex friendships at age 16. Additionally, Simpson et al. (2012) have shown that exposure to more unpredictable forms of life stress during the first few years of life predicts more risk-taking in early adulthood, as indexed by having more sexual partners and scoring higher on aggression, delinquency, and ties to criminal activity by the early 20s. Szepsenwol et al. (2017) have shown that being exposed to more unpredictable environments early in life predicts more unrestricted sociosexuality (i.e., the adoption of a fast life history strategy) in early adulthood. Finally, Szepsenwol et al. (2015) have found that men who are exposed to more unpredictable environments early in life have a more negative orientation to parenting at age 32, whereas women do not. Furthermore, men exposed to more unpredictable early environments are more likely to have received lower quality care from their mothers early in life, which in turn predicts them having more insecure attachment representations of their childhood in early adulthood. These insecure representations, in turn, predict having a less-positive orientation to being a parent at age 32.

11.2.1.2 Chisholm's Model

Chisholm (1993, 1996) proposed an alternate model of reproductive strategies, one that highlights the life history trade-off of immediate versus delayed reproduction. This model contains several novel features beyond those proposed by Belsky and colleagues. For example, the Chisholm model suggests that local mortality rates are the specific cues that children use to regulate the rate of their physical/sexual development as well as their adult reproductive strategies. The principle reason for this expectation is that higher mortality rates should have been a valid indicator of how difficult local environments were in the EEA, and they should also have been associated with poorer caregiving in our ancestral past. According to this model, parental indifference or insensitivity—which should have been valid indicators of higher local mortality rates—should have motivated children to develop avoidant working models and associated behavioral patterns, which in turn may have increased fitness in difficult environments. Lower mortality rates, indicative of more benign environments, should have generated better, more attentive caregiving in general. Sensitive parenting, in other words, should have "communicated" to children that premature death was less likely, instilling secure working models and behaviors that should have enhanced fitness in more hospitable environments.

Consistent with Chisholm's model, robust associations exist between having experienced more adverse life conditions and the expectations that people have for their longevity and the timing of their reproduction later in life (Nettle, 2010; Nettle & Cockerill, 2010). For example, when life expectancy declines on average within a geographic area, most women in the area reproduce at a relatively younger age (Wilson & Daly, 1997). Moreover, teen mothers who believe they will die at a comparatively younger age tend to have their children earlier in life (Johns, 2003). These findings are consistent with what is known as the "weathering hypothesis" (Geronimus, 1996), which suggests that having children earlier in life is an adaptive response when women believe they are less healthy than their same-aged peers. Viewed together, these findings support the premise that local mortality rates served as a valid cue that may shape alternate reproductive strategies in adulthood.

Chisholm's model also addresses time preference—people's tendency to discount the future by favoring small, immediate rewards now instead of large, delayed rewards later—as another psychological mechanism tying early childhood experiences with adult mating and parenting behavior (Chisholm, 1999). The rationale for this focus is that children raised in harsh or unpredictable environments, where waiting for rewards could result in leaving no descendants, should prefer immediate payoffs, even when delayed ones might be superior.

Finally, Chisholm's model devotes attention to two primary threats to the survival and growth of children in the EEA—a parent's *inability* and *unwillingness* to invest in their offspring—both of which children should have evolved to detect and try to counteract. Chisholm suggests that attachment security reflects an adaptation to a parent's ability *and* willingness to provide sufficiently good investment, as indexed by warm and sensitive parenting. He further proposes that attachment avoidance is an adaptation to a parent's unwillingness to invest (regardless of their ability), as indexed by cold and rejecting parenting. Finally, he claims that anxious attachment is an adaptation to a parent's inability to invest, as indexed by inconsistent, unpredictable parenting.

The Belsky et al. and Chisholm models are important because they have focused attention on how and especially *why* certain types of early experiences tend to shape development across the life course. Neither model, however, addresses some additional variables that may also influence the adoption of specific reproductive strategies in adulthood. Mate selection involves a host of other factors, such as a potential mate's compatibility, health, ability to accrue and share resources, and capacity to teach and socialize offspring (Gangestad & Simpson, 2000). Moreover, the early psychosocial acceleration models such as those by Belsky et al. and Chisholm did not address the unique reproductive roles of men and women (Buss & Schmitt, 1993; Geary, 2005). As discussed below, the most critical trade-off for most women is likely to be between early vs. later reproduction, whereas the most important trade-off for most men may center on growth versus reproduction. Despite these limitations, both models have significantly advanced our understanding of attachment and social development across the lifespan.

11.2.1.3 Del Giudice's Model

Del Giudice (2009) formulated a model that directly addresses sex differences within an attachment/evolutionary framework. A reasonably large body of cross-cultural research has revealed that boys are somewhat more likely to be avoidantly attached in middle childhood, whereas girls tend to be somewhat more anxiously attached (Del Giudice, 2009; van IJzendoorn & Bakermans-Kranenburg, 2010). According to Del Giudice's model, sex differences in attachment patterns beginning in middle childhood could have been evolutionarily adaptive if they reflect the initial enactment of sex-specific life history strategies. In particular, early psychosocial stress and insecure attachment patterns may serve as external and internal cues of heightened environmental risk, which shift development toward reproductive strategies that facilitate current reproduction over later reproduction and/or prioritize mating effort over parenting effort. In line with the well-documented sex differences in mating and parenting effort (see Geary, 2005), more insecure males tend to be avoidantly attached, whereas more insecure females are anxiously attached, with each of these behavioral strategies increasing investment from the kin and mates of males and females, respectively.

Perhaps the most novel element of Del Guidice's model is the assertion that sex differences in attachment should emerge during middle childhood rather than earlier in life, contrary to what psychosocial acceleration models anticipate. According to his model, adrenarche (the early stages of sexual maturation) is a "developmental switch-point" that reorganizes attachment starting in middle childhood, which then has noteworthy developmental implications later in life. During early middle childhood, for example, insecure attachment patterns become sex-biased, shunting reproductive strategies down somewhat sex-differentiated developmental pathways. To the extent that attachment security (versus insecurity) was a valid indicator of the amount of risk in a child's immediate environment in the EEA, it could have been retained by evolutionary processes to function as a stable and adaptive behavioral trait. Of course, strategies adopted earlier in life can be altered later during the course of development, especially if earlier strategies no longer address environmental demands later in development. This flexibility is important because avoidant and anxious attachment patterns appear to have different adaptive values for boys and girls, particularly with regard to successful competition within same-sex peer groups during middle childhood (Del Guidice, 2009).

Indeed, the strongest selection pressure on attachment patterns during middle childhood may well have stemmed from intrasexual competition within peer groups as children begin competing with one another for status, attention, and resources. Successful negotiations within peer groups ought to be particularly challenging for insecurely attached children, who cannot necessarily turn to nuclear family members to buffer them from many of the stresses and failures that occur when children enter grade school. The avoidant behavioral pattern, which is characterized by higher levels of aggression, strong self-reliance, and inflated self-esteem, tends to be used more effectively by males as they attempt to gain higher status and popularity within their middle-childhood peer groups (Benenson, 2014). Girls, on the other hand, shift toward the anxious behavioral pattern, which helps them utilize "tend-and-befriend" tactics (Taylor et al., 2000), which result in greater success within female peer groups.

11.2.1.4 Ellis' Model

In developing their evolutionary model of reproductive strategies, Ellis and colleagues (1999; Ellis & Garber, 2000) borrowed concepts from work on father absence (Draper & Harpending, 1982) along with parental investment theory (Trivers, 1972) to examine the unique role that fathers play in the emergence of reproductive strategies in girls. Whereas Belsky et al. (1991) viewed early father absence as a marker of stress mainly within the family of origin, Ellis (2004) proposes that father absence (or stepfather presence) is its own powerful evolutionary cue communicating low, unpredictable, or declining paternal investment.

There is abundant prospective evidence showing that father absence predicts accelerated pubertal development in most girls (e.g., Campbell & Udry, 1995; Ellis & Garber, 2000; Ellis et al., 1999). Similar effects, however, have not been found in African-American samples (e.g., Campbell & Udry, 1995; Rowe, 2000), and studies have not always revealed stronger effects for fathering (or the quality of the father-child relationship) versus mothering (or the quality of the mother-child relationship) (e.g., Ellis et al., 2011). What there is consensus on is the robust finding that the earlier father absence takes place (particularly within the first 5 years of a child's life), the more powerfully it predicts the earlier age of puberty in girls (e.g., Ellis & Garber, 2000; Quinlan, 2003). Furthermore, the presence of stepfathers also influences pubertal timing in girls, which might explain some prior father absence effects (Ellis, 2004). Supporting this assertion, greater conflict between the mother and stepfather in conjunction with earlier stepfather presence appears to accelerate pubertal development in girls (Ellis & Garber, 2000). Finally, pubertal development in girls tends to be delayed the longer fathers care for their daughters during the first few years of life and the more fathers have warm, supportive relationships with their daughters early in life (Ellis et al., 1999).

11.2.1.5 Hazan/Zeifman's and Kirkpatrick's Models

Other models have focused more squarely on adult romantic pair bonds from an attachment/evolutionary perspective. One such model, proposed by Hazan and Zeifman (1999; Zeifman & Hazan, 2008), suggests that adult romantic relationships represent a unique type of attachment bond, which has some similarities with parent–child attachment bonds (see Shaver et al., 1988). Both young children and adults, for example, express similar reactions to separation from or the loss of their attachment figures. Furthermore, both children and adults behave in somewhat similar ways when seeking physical contact, expressing emotional intimacy, and displaying affection toward their attachment figures.

Hazan and Zeifman (1999) hypothesize that the basic evolutionary purpose of forming secure attachment relationships in adulthood is to promote stable, enduring pair bonds between mates so they can support one another and provide better care to their children (Zeifman & Hazan, 2016). Pair bonding, in other words, may have evolved to facilitate the reproductive fitness of *both* parents and their children (see also Fletcher et al., 2015). Supporting this account, adult mating strategies are associated with the pair bond status of one's parents in that father absence and greater marital discord in one's family of origin both forecast earlier sexual maturation, enacting short-term adult mating strategies, and having less stable marriages (Belsky, 1999). Children with pair-bonded parents who are likely to be securely attached, in contrast, are more inclined to adopt longer-term mating strategies and place greater emphasis on investing in their children (Hazan & Zeifman, 1999). Pair-bonded partners also contribute to their own reproductive success by providing more support to one another, which tends to be associated with better physical and mental health (Zeifman & Hazan, 1997).

Kirkpatrick (1998) has offered an alternative view of the evolutionary function of adult romantic attachment and its ties to specific reproductive strategies. Similar to the models proposed by Belsky et al., Chisholm, and Del Guidice, Kirkpatrick conjectures that adult romantic attachment orientations (secure, avoidant, and anxious) evolved to enhance reproductive fitness in relation to early childhood experiences. As discussed earlier, the allocation time and energy to mating effort versus parenting effort is one of the critical life history trade-offs. Kirkpatrick (1998) and others (e.g., Gangestad & Simpson, 2000) have proposed that, during evolutionary history, it may not have always been adaptive for women and men to pursue long-term, monogamous mating strategies. If so, adult attachment orientations could have provided a way to adopt the best mating strategy depending on one's childhood experiences, especially the quality of early parental care and investment received. On average, individuals who received consistently good, sensitive, and responsive parenting should have developed secure working models and should have pursued long-term, more committed mating strategies. Indeed, secure adults do usually report higher levels of trust, intimacy, and commitment in their romantic relationships, and they tend to become involved with secure partners, which further promotes the stability of their relationships (Feeney, 2016). Avoidantly attached adults, by comparison, tend to have less trusting, less intimate, and less committed relationships, and they are more likely to engage in short-term mating strategies, which result in less stable, less satisfactory relationships (Simpson et al., 2004). Most anxiously attached adults claim that they want long-term mates, but their strong need to please and be desirable to potential romantic partners frequently leads them into short-term romantic relationships that tend to be unstable (Kirkpatrick, 1998).

11.3 Stepping Back: How Attachment Theory Can Benefit from Incorporating Elements of Other Evolutionary Theories

Considered together, these early life attachment-based evolutionary models of social development illustrate the complex interconnections between an infant's early rearing environment, their experience of receiving care, and the internal working models that eventually guide their social development, starting in infancy and stretching across their lives. In the same way that each of these models has benefited from the incorporation of attachment principles to stipulate how developmental processes are likely to be affected by certain environmental conditions, attachment theory might also benefit from incorporating some key ideas and principles underlying LHT (Szepsenwol & Simpson, 2021).

Take, for example, the different forms of attachment insecurity. Attachment theory and research suggest that anxious and avoidant attachment patterns in children stem at least in part from differences in caregiver sensitivity, with anxious attachment occurring in response to inconsistent or unpredictable care, and with avoidant attachment being generated in part by consistent parental rejection or rebuffing. As reviewed above, a great deal of evidence has documented connections between the nature of the early caregiving environment and the degree of parental sensitivity. Much less work, however, has examined whether and how other features of the early environment shape the development of these insecure attachment patterns.

Chisholm (1993, 1996), for example, discusses two primary reasons for insensitive parenting: a parent's *inability* to provide care in a sensitive and responsive manner, and a parent's *unwillingness* to do so. He posits that caregivers who have neither the skill nor the ability to parent a child sensitively, but would be willing to do so if circumstances were different, are likely to engage in less predictable caregiving, which typically should result in anxious attachment. On the other hand, caregivers who are simply unwilling to parent sensitively and responsively should display colder, more disengaged caregiving, usually culminating in avoidant attachment. These ideas—linking the ability versus the willingness to parent with the quality of parental care in response to specific features of the local environment—have received insufficient empirical attention to date.

Furthermore, even though there is good empirical evidence that environments affect parenting behavior, the unique effects that the predictability or harshness of the local environment has on specific modes of parenting and infant attachment patterns have not been extensively examined (for an exception, see Simpson, 2019). Do unpredictable environments encountered early in life reliably produce inconsistent caregiving, which results in anxious attachment patterns in young children? Do harsh environments early in life reliably generate more rejecting caregiving, which results in avoidant attachment patterns in young children? Do extreme levels of unpredictability *and* harshness encountered early in life interact to predict other forms of attachment insecurity, such as the disorganized pattern? And what role does the sensitivity of parenting play in moderating (or mediating) these associations? All of these questions deserve examination.

11.4 Conclusion

As noted at the beginning of this chapter, attachment theory is a major, middle-level evolutionary theory (Simpson, 1999), one that provides an underlying current that links all of the evolutionary theories and models summarized in this chapter. Thus, understanding the nature of our earliest attachment relationships—especially those in infancy—is key to understanding the implications of each of these theories and models, including the mechanisms through which they operate across the lifespan. Early attachment patterns and their associated internal working models shunt individuals down different developmental trajectories, shaping how they respond to future attachment-relevant relationships, environments, and events.

Nevertheless, as evolutionary approaches advance, so too must attachment theory. One promising avenue forward would involve devoting greater attention to understanding *how* critical features of the early rearing environment, such as its degree of harshness and/or predictability, impact the ability and/or willingness of parents to provide sensitive, responsive care to their children. It will also be important to document how these variables are prospectively related to the consistency with which parents enact sensitive/responsive versus insensitive/non-responsive care across time as their children grow and develop. Addressing these issues will advance not only our understanding of the origins and nature of parenting, but of attachment theory, as well.

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Part IV
Cognitive and Social Cognitive Development

Chapter 12
Beyond the Language Module: Musicality as a Stepping Stone Towards Language Acquisition

Hirokazu Doi and Nobuo Masataka

12.1 Presumed Dissociation of Music and Language

Music is among the most ancient forms of art in human history (Masataka, 2010). The universality of music suggests that music has served some functional roles in increasing the survival odds of mankind. However, specific advantages of music conferred to human survival remain elusive. Existing theoretical and empirical studies show that music enhances group cohesion and helps emotional regulation (Tarr et al., 2014). In contrast, some theorists see no survival benefit in music, a view which is championed by Steven Pinker's famous characterization of music as "auditory cheesecake" (Pinker, 1997).

There has been a long-standing debate over whether music and language processing share the same processing stages and recruit the same neural regions. Recent studies challenge a simple dichotomy between music and language processing by showing activation of overlapping neural regions by music and language (Koelsch et al., 2002; Yu et al., 2017; but see, Peretz, et al., 2015) and impaired processing of linguistic prosody in amusic patients (Thompson et al., 2012). Thus, the linguistic ability is not as impermeable as presumed and shares part of the processing stages with music.

Interestingly, it has been reported that long-term musical training enhances language processing at various processing stages (Zhao & Kuhl, 2016), including fundamental frequency (f_0) extraction at the brainstem (Wong et al., 2007). Therefore, it seems only natural to postulate that machinery recruited in music processing has

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facilitated the evolution of language and helps in language acquisition in human infants (Masataka, 2008).

In this chapter, we first discuss the commonalities in processing stages recruited between music and language. Among the perceptual functions presumably recruited in both musical and linguistic domains, a substantial amount of knowledge has accumulated about the perception of frequency structure and rhythmic pattern. Thus, in the second section of this chapter, we provide an overview of empirical data on the developmental course of these perceptual functions in musical and linguistic domains in human infants. In the last section of this chapter, we propose a hypothesis regarding the evolutionary roots of musicality that is utilized in language acquisition in human infants today.

12.2 Commonality Between Music and Language

Language can transmit messages that are far more semantically complex than music. However, the sound stream of language shares many acoustic characteristics with musical sounds. First, vowel sounds have similar spectral structures as musical chords. When pronouncing vowels, the power of different frequencies is modified by resonance in the vocal tract, and consequently, some of the frequencies become prominent in vocal sound. Such peaks in spectral power in a few frequency ranges, called formants, define the perceived vowel category. Thus, analysis of the relative relationship between formant frequencies is required in vowel categorization. The similar ability of relative pitch perception is indispensable in music perception because the perceptual quality of musical chords is also determined by the relationship between the pitches of musical notes played simultaneously.

Second, both music and language are characterized by a hierarchical structure (Jackendoff & Lerdahl, 2006). Language is governed by grammatical rules that define the ordering of words in a hierarchical manner. Similarly, identical sound sequences are played repeatedly within a music score and are grouped into larger motifs hierarchically. Thus, the ability of perceptual grouping together with the statistical analysis of repeated sequences are valuable in analysing the global structure underlying the sound stream in both music and language.

Third, pitch contour, the temporal course of pitch change, is essential in processing both musical and linguistic sounds. Pitch contour creates a musical melody that induces vivid emotional reactions and even conveys semantic information (Koelsch et al., 2004). Likewise, linguistic prosody plays an important role in conveying emotional and semantic information (Doi et al., 2013). The human linguistic system interprets the meaning of identical sentences differently depending on the pitch contour, as in the case of pitch change at the end of utterances in declarative sentences and yes-no questions. Further, pitch contour sometimes specifies a structurally important location, e.g., phrasal boundary, in the linguistic stream.

Fourth, both music and language have a culturally transmitted rhythmic structure. Folk music in several regions has a unique metric structure that is different from those seen in other regions of the world. Likewise, some researchers claim that language can be grouped into families according to its rhythmic structure (Nazzi & Ramus, 2003). Culture-specific patterns of auditory rhythms exert such strong influences on the perceptual system through postnatal exposure that adults have difficulty detecting slight changes and reproducing rhythmic patterns with culturally unfamiliar metric structures (Hannon & Trehub, 2005a; Collier & Wright, 1995).

12.3 Contributions of Musicality to Human Language Acquisition

Given the close similarity between music and language as described above, neural mechanisms recruited in musical processing could help in processing linguistic materials as well. Infants at the prelinguistic stage are faced with the task of analysing sound streams and grasping their underlying structure without any prior knowledge (but see Chomsky, 1965). The primary tenet of the *prosodic bootstrapping hypothesis* of language acquisition is that prosodic information, such as lexical rhythm and melodic contour in the linguistic sound stream, scaffold infants' analysis of the mother tongue. Prosodic cues are loosely related to grammatical structure. Therefore, prosodic information, a collection of musical properties of language, can help infants learn their mother tongue.

Studies on auditory perception in the fetus raise the appealing possibility that prosodic bootstrapping of language acquisition starts during the prenatal period. Fetuses are exposed to environmental sounds in the womb. However, the abdominal wall filters out high-frequency components of external sounds, and consequently, phonemic information is almost lost. Salient information contained in the filtered sound heard in the womb is mainly a prosodic pattern of language. In DeCasper et al. (1994), mothers read target rhymes each day for 4 weeks during pregnancy. Researchers then measured the fetal heart rate when hearing the target rhyme and an unfamiliar rhyme. There was a more notable deceleration in heart rate when hearing the familiar rhyme, indicating that fetuses can learn the prosodic pattern of mother's speech.

In this section, we discussed how musical functions could assist language acquisition by reviewing empirical evidence on the developmental course of these abilities. We focused especially on the perception of rhythm and frequency structure and examined whether there are any parallels between the developmental courses of these abilities in the musical and linguistic domains.

12.3.1 Perception of Frequency Structure

12.3.1.1 Musical Chord and Formant Perception

In musical chord perception, the auditory system must analyse the relationship among f_0 of simultaneously played musical notes. The difference of one-semitone in one note comprising a chord changes the perceived quality of a musical chord, from major to minor chords or vice versa. Further, adherence to certain mathematical rules creates a consonant chord, while violation of it results in a dissonant one.

There has been a debate over the innateness of chord processing ability, especially whether the preference for consonance over dissonance is acquired through cultural assimilation. Empirical studies generally favour the innateness of consonant chord preferences (Masataka, 2006). A functional magnetic resonance imaging (fMRI) study revealed differential activation of the newborn's brain in response to consonant and dissonant chords (Perani et al., 2010). An event-related potential (ERP) study indicated that newborns could discriminate between a consonant and dissonant as well as between major and minor chords (Virtala et al., 2013). These findings indicate that the infant brain is innately endowed with the capacity to analyse the pitch relationship of multiple sounds being played simultaneously.

The formant structure in vowel sounds has some resemblance to the spectral structure in musical chords. In vowel categorization, the auditory system must analyse the peak frequencies of at least three formants simultaneously. Since everyone has different exposure to f_0 depending on their gender, age, and height, the formant frequencies of identical vowel sounds differ among individuals. Despite this, identical vowels uttered by different individuals are perceived as such, a phenomenon called *speaker invariance*. Thus, what counts in vowel perception is the analysis of the relationship among formant frequencies rather than the absolute values of each formant frequency.

Behavioural studies on infant vowel categorization have shown that even neonates can discriminate between different vowel sounds (Cheour-Luhtanen et al., 1995). Vowel categorization is tuned by postnatal exposure to the mother tongue. Interestingly, some studies even argue that the tuning process starts in the womb (Moon et al., 2013). Therefore, as in the case of musical chord perception, the nascent ability of formant perception functions from the very initial stage of development.

12.3.1.2 Melody and Pitch Contour Perception

Melodic contour is created by the temporal sequence of musical notes f_0. Melody will sound the same when the notes are transposed or played in different keys (Mottron et al., 2009). This illustrates that the primary determinant of musical melody is not the absolute value of pitch but the contour of the temporal sequence of relative pitches that unfolds as the music is played.

Studies on the early development of melodic perception have shown that infants as young as 5–10 months old can detect violations of melodic contour irrespective of transposition (Trehub & Hannon, 2006). Plantinga and Trainor (2009) showed that even 2-month-olds could discriminate melodies of different songs, although the musical materials used in this study were not well controlled for low-level auditory features.

It is widely acknowledged that infants use pitch contour as a cue to analyse the grammatical structure. One example is the use of lexical stress in word segmentation (Jusczyk, 1999). Lexical stress is characterized by high pitch, long duration, large amplitude, and vowel quality. Among these acoustic cues, the human auditory system is quite sensitive to pitch change; humans can discriminate lexical stress patterns (trochaic or iambic) of nonsense syllables based on pitch-cue alone (Hoeschele & Fitch, 2016). Infants as young as 8 months can use lexical stress cues for segmenting sound streams into words (Jusczyk, 1999). In English-speaking countries, infants usually segment sound streams into units with strong-weak stress patterns. However, the 7-month-olds in Thiessen and Saffran's (2007) study switched this stress-based strategy and started extracting words with weak-strong (iambic) stress patterns after repeated exposure to word sequences of the iambic stress pattern. Thus, infants can flexibly modify their stress-based word-segmentation strategy through experience.

Another well-studied example is infants' use of pitch contour information as a cue for boundary detection. In speech, boundaries between phrases and clauses are often marked by pitch change and a long duration of syllables followed by a brief pause, which is observed cross-linguistically. Infants as young as 6 months have been shown to rely heavily on prosodic pattern for boundary detection (Seidl, 2007). Wellmann et al. (2012) investigated the acoustic characteristics that 8-month-old infants rely on in boundary detection. Pitch change or long duration alone were not sufficient for infants to detect a phrase boundary. However, the combination of long duration and pitch change enabled infants to find boundaries without pause cues. Similar results have been obtained in 6-month-olds as well (Seidl, 2007).

These studies indicate the primary importance of pitch contour in linguistic sound in order for human infants to be able to segment grammatical units. Interestingly, these studies revealed the emergence of the ability to use pitch contour in sound segmentation around 6–10 months (Thiessen & Saffran, 2007; Seidl, 2007; Wellmann et al., 2012), which roughly corresponds to the age when infants acquire the ability to process melodic contour (Trehub & Hannon, 2006). Comparisons of the developmental courses of pitch change in musical and linguistic materials also support a domain-general pattern of development (Chen et al., 2017). Indeed, such coincidence alone should not be deemed as definitive evidence, but it is quite conceivable that the maturation of identical neural mechanisms underlies the development of the ability to process pitch contour in both musical and linguistic materials.

Infants' sensitivity to pitch contour is effectively used in parental vocalizations directed towards infants. When talking to infants, adults modify their manner of speech so it differs from speech that is used with adults (Kuhl, 2007; Masataka, 2003). Such infant-directed speech is mainly characterized by high-pitch and exaggerated intonation (Doi, 2020). High-pitched voice is effective in grabbing an infant's attention, possibly due to its emotional connotation (Corbeil et al., 2013). Likewise, exaggerated intonation makes it easier for infants to extract pitch contour, which assists infants in word segmentation and boundary detection. Thus, the domain-general ability of relative pitch perception as well as social input provided in infant-directed speech interactively scaffold infants' language acquisition (Doi, 2020; Sulpizio et al., 2018).

12.3.2 Rhythm Perception

Rhythm perception can be both objective and subjective (Iversen et al., 2009). A strong beat is often marked by large sound amplitude. At the same time, people sometimes perceive strong and weak beats in the repetition of monotonous sounds without any acoustic marks.

Rhythmicity in synchronized bodily movement is observed in as early as the neonatal stage, which is thought to reflect the activity of the central pattern generator. As for the perception of musical rhythm, an ERP study by Winkler et al. (2009) showed evidence of beat perception in neonates. In their study, neonates were exposed to a sequence of percussion sounds with a hierarchical metric structure. They were repeatedly exposed to standard sounds that lacked sound at a weak beat location. Within the sequence of standard sounds, the target sound, in which sound was omitted at a strong beat (downbeat) location, was presented with low frequency. They focused on a newborn's homologue of mismatch negativity (MMN). MMN is an ERP component usually elicited by deviant auditory sound that is presented with low frequency, embedded within a sequence of standard sounds. MMN is elicited even when a subject is not directing attention to the sounds. Thus, MMN is accepted as a reliable indicator of the ability to discriminate deviant and standard sound at the pre-attentive perceptual stage. The main finding of Winkler et al. (2009) was that the target sound elicited MMN in neonates, indicating that even neonates can discriminate weak and strong beats.

The innate ability of beat perception prepares infants to process rhythmic structures in incoming auditory information. This ability is shaped further by postnatal exposure to environmental sounds. Folk music of Eastern European countries such as Bulgaria and Macedonia has a complex metrical structure that differs from the simple metric structure in Western music. Twelve-month-olds reared in the United States, who probably had almost no experience of hearing music with a complex metre, could not detect slight changes in complex metres of Eastern European folk music (Hannon & Trehub, 2005b), while 6-month-old infants could (Hannon & Trehub, 2005a). In phoneme perception, the neural system is plastically tuned to process phoneme categories in mother tongues through postnatal experience, while losing the ability to discriminate phoneme categories that do not exist in the mother tongue (Kuhl et al., 2011). Likewise, infants lose their ability to discriminate unfamiliar types of faces, e.g. faces of different species and unfamiliar races (Pascalis et al., 2002). The studies by Hannon and Trehub (Hannon & Trehub, 2005a, b) indicate that a similar process of perceptual tuning is at work in the development of musical rhythm; infants lose their ability to process unfamiliar rhythmic structure through postnatal exposure to their musical culture.

Linguists have raised the possibility that languages can be classified into several families according to their rhythmic structure, e.g. stress- and syllable-timed languages (Nazzi & Ramus, 2003). In stress-timed languages, such as English, the timing of the successive stressed locations in utterances are kept fairly constant, while in syllable-timed languages, such as French and Italian, syllables are uttered with constant timing. Nazzi et al. (1998) tested whether neonates could discriminate unfamiliar low-pass filtered foreign languages. Low-pass filtering eliminates high-frequency components of linguistics sound. Consequently, phonemic information is almost lost in low-pass filtered language, which makes it impossible for infants to use phoneme distribution as a clue to discriminate two languages. Interestingly, neonates in this study could discriminate unfamiliar foreign languages in different rhythmic families but not in the same rhythmic family. Thus, infants can detect rhythmic structures in languages as well as in music from the neonatal stage.

Nazzi and Ramus (2003) proposed the *rhythm bootstrapping hypothesis,* which proposes that human infants rely on rhythmic structure in language as a clue to segment grammatical units. Adults who speak syllable-timed languages use segmentation strategies in online language processing which differ from those of individuals whose mother tongue is a stress-timed language (Cutler et al., 1986). Therefore, speakers of both syllable- and stress-timed languages adopt a word segmentation strategy suited to their mother tongue. Lexical stress often signals the onset of a single word in English, but stress is less likely to be a marker of a word boundary in syllable-timed languages. Such language-specificity in word-segmentation strategies presents infant with a problem of deciding which acoustic cue to rely on in word segmentation. The rhythmic bootstrapping hypothesis suggests that the rhythmic structure of language gives infants a clue to discover the most efficient strategy, syllable- or stress-based, in word segmentation.

Most evidence for rhythm bootstrapping comes from studies on infants in an English-speaking environment. The aforementioned studies on infants learning English show that infants as young as 8 months segment words by lexical stress (Jusczyk, 1999; Thiessen & Saffran, 2007). Further, when the cues of transition probability and lexical stress are incongruent, 9-month-old infants treat lexical stress as a primary cue over transition probability in word segmentation (Thiessen & Saffran, 2007). As for syllable-timed languages, Nazzi et al. (2006) reported that French infants segmented words using a syllable-based strategy. These results, together with the early emergence of the domain-general ability to perceive rhythmic structure (Nazzi et al., 1998; Winkler et al., 2009), provide partial support to the rhythm bootstrapping hypothesis. The reason remains elusive why human infants, who are innately endowed with the ability of rhythm processing (Winkler et al., 2009), do not show evidence of language-specific segmentation strategies until around 8 months. One possible reason is that infants do not learn to associate perceived rhythmic structure with word segmentation strategy until around this age.

12.4 Evolutionary Roots of Musicality and Its Relationship with Language

Perceptual systems recruited in music processing can be used to analyse the linguistic stream and grasp its grammatical structure. The parallel development of corresponding functions in the musical and linguistic domains indicates the possibility that the maturation of domain-general functions recruited in both music and language processing assist language acquisition in human infants. This line of reasoning further raises the possibility that the evolution of musical functions has prepared the basis of the evolution of language in humans.

The burgeoning ability, or precursors, of music processing can be seen in birds, rodents, and non-human primates as well (Doi, 2020). However, their musicality does not match that of humans in its refinement. Considering this, the gap in musicality between humans and non-human species might constitute part of the reason why only humans have a sophisticated ability for language processing and speech communication. This section reviews the existing findings on musical abilities in non-human species and discusses the evolution of language from the perspective of phylogenetic roots of musicality.

12.4.1 Frequency Structure Perception

12.4.1.1 Analysis of Musical Chords and Vowel Formants

Chord perception and vowel categorization require the ability to grasp the relationships of peak frequencies. Interestingly, behavioural and electrophysiological studies have revealed close similarity in musical chord perception between non-human primates and humans (Izumi, 2000). For example, Fishman et al. (2001) measured electrophysiological responses in neurons of the primary auditory region in macaque monkeys and humans to dissonant and consonant chords. This study revealed that neurons in homologous regions in macaque monkeys' and humans' brains represent dissonance levels of musical chords.

Instrumental and vocal sounds contain harmonics of f_0. Here, harmonic means sound with the frequency of integer-multiple of f_0. When a sound composed of harmonics of the same f_0 is presented, one perceives a sound with the f_0, even when the sound lacks spectral peak in f_0. This phenomenon, called *missing fundamental*, is deemed as the expression of the superb ability of the human auditory system to analyse harmonic structure, and human infants as young as 3 months old show signs of missing fundamental perception (He & Trainor, 2009). Bendor and Wang (2005) measured activations of frequency-sensitive neurons, neurons that are activated by sound with specific frequency, in the auditory cortex in marmosets. They found a set of neurons that were activated by both pure tone with f_0 and the sound composed of harmonics of f_0 without spectral peak in f_0. These findings indicate that marmosets possess the ability to analyse fundamental frequency in complex harmonic sound. Behavioural studies have revealed the ability to perceive missing fundamentals in other species as well (Cynx & Shapiro, 1986; Heffner & Whitfield, 1976).

These electrophysiological and behavioural studies (Bendor & Wang, 2005; Fishman et al., 2001) indicate that the basic functions for analysing the relationships of peak frequencies are phylogenetically old. Considering the spectral similarity between vowel formants and musical chords, it is possible that non-human species also possess the basic ability of vowel categorization. Direct evidence for vowel categorization has been obtained in several species (Hienz et al., 1981, 1996; Ohms et al., 2010). Among these species, songbirds show the most prominent resemblance to humans in their ability to categorize phonemes. Ohms et al. (2010) found that zebra finches could learn to discriminate vowels and generalize this discrimination to vowel sounds uttered by opposite-sex speakers despite the difference in the absolute height of formant frequencies. Thus, the findings of Ohms et al. (2010) support the view that zebra finches can analyse the relative relationship of formant frequencies in a manner closely similar to that of humans.

12.4.1.2 Analysis of Pitch Contour

In ecological settings, animals transmit many messages by modifying their vocalizations either voluntarily or involuntarily. A well-known example is the innate association between arousal level and high-pitched voice. In a highly aroused state, vocal folds vibrate at a higher frequency, which generates voices with higher f_0 in many mammalian species including humans (Bachorowski, 1999; Filippi et al., 2019; Kamiloğlu et al., 2020). In addition to the absolute height of f_0, a substantial number of studies have revealed that context-dependent messages and emotional states are encoded in the pitch contour in animal vocalizations (Briefer, 2012; Filippi et al., 2019). Therefore, the ability to analyse pitch contour must have been essential for survival.

The neural system must extract the temporal course of pitch change irrespective of the absolute pitch in the perception of pitch contour. Independence of absolute pitch and pitch contour perception is well illustrated in a phenomenon called *octave-generalization* which states that melodies sound the same when transposed by an octave. Absolute pitches of all musical notes change after transposition. Despite this, the human auditory system perceives an identical melody after transposition, which indicates strong reliance on the pitch contour, or relative pitch change, in melody processing (Mottron et al., 2009). A study by Wright et al. (2000) tested octave generalizations of musical chords in rhesus monkeys. Their main finding was that the monkeys showed signs of octave-generalization; the monkeys perceived the identical tune played in different octaves to be the same when tonal music was used as the musical material. Thus, similar to humans, rhesus monkeys also rely heavily on pitch contour rather than absolute pitch in perceiving sound sequence.

In songbirds, Spierings and ten Cate (2014) revealed that zebra finches treat prosodic patterns more heavily than structural cues in discriminating multisyllabic sequences. Among three stress cues manipulated, i.e., pitch contour, amplitude, and duration, pitch was the most salient one to the songbirds, indicating the basic ability to discriminate rising and falling pitch contour in this species. The same group also showed that zebra finches could learn to discriminate trochaic and iambic stress patterns by pitch cue alone, but not by duration and sound amplitude cues (Spierings et al., 2017), showing the prominence of pitch contour in stress detection in zebra finches.

The number of laboratory studies reporting pitch contour perception ability in non-human species is relatively small, compared to studies on musical chord and formant perception (Fishman et al., 2001; Hienz et al., 1981, 1996; Izumi, 2000; Ohms et al., 2010). This could be because the analysis of pitch contour might be actually more difficult for non-human species than chord and formant perception; the analysis of the temporal course of pitch change requires additional functions, such as working memory, compared to the analysis of pitch relationships among simultaneously played sounds. At the same time, the prevalent use of pitch contour in the wild (Briefer, 2012; Filippi et al., 2019) indicates that lack of ecological validity in laboratory settings might have prevented researchers from finding signs of pitch contour perception in the laboratory (see Hoeschele et al., 2014, for similar discussion).

12.4.2 Rhythm Perception

Rhythm perception is closely linked to motoric functions. Indeed, human fMRI studies revealed activation of motoric regions, such as the premotor area and basal ganglia, in rhythm and beat perception (Grahn & Brett, 2007). When listening to ambient music, humans spontaneously make bodily movements in tune with the perceived beat of the music. Spontaneous entrainment to rhythm is ubiquitously observed in humans but is relatively rare among non-human species (Patel et al., 2009; Schachner et al., 2009). Even in those species showing signs of rhythmic entrainment, the temporal precision of their movement is far lower than that of humans (Hattori & Tomonaga, 2020; Patel et al., 2009).

Lack of spontaneous entrainment to rhythm does not necessarily mean the lack of ability to produce and perceive rhythmic patterns. The production of rhythmic patterns is often tested by the synchronization-continuation task (SCT). In SCT, an animal is first required to make bodily movements, usually tapping movement, in synchrony with an auditory or visual stimulus appearing at constant intervals (synchronization phase). In the continuation phase, external stimulation is eliminated and the subject must continue making bodily movements at the same pace as the synchronization phase.

An electrophysiological study using the SCT paradigm found a subgroup of neurons representing action timing in the medial premotor cortex of rhesus monkeys (Merchant et al., 2011). The firing rate of one group of neurons changed according to the elapsed time from the last action, while the other group of neurons represented the remaining time until the next action. Thus, there are several systems for time keeping in the brain of rhesus monkeys, enabling them to make externally and internally paced actions.

However, the ability to make rhythmic movements in rhesus monkeys is not the same as that in humans. Zarco et al. (2009) compared the behaviour in SCT between rhesus monkeys and humans. After training, rhesus monkeys learned to make paced movements, but detailed analysis revealed substantial differences in the pattern of action timing between rhesus monkeys and humans. First, humans made the actions synchronously with or slightly ahead of external stimulation, indicating anticipatory preparation of timed-action. In contrast, the action timing of rhesus monkeys lagged behind external stimulation, though the action timing was faster than that in the serial reaction time task. Second, the variance of action timing was drastically larger during continuation than in the synchronization phase in rhesus monkeys at long intervals, but no such trend was found in humans. These findings raise the possibility that the mechanism for generating internally timed movements in rhesus monkeys is qualitatively different from that in humans.

Regarding the purely perceptual aspect of rhythm processing, Honing et al. (2012) measured MMN-homologue elicited by deviant stimuli in rhesus macaques using the same paradigm as Winkler et al. (2009). As explained above, a deviant sound sequence, in which sound is omitted at the downbeat location, elicits MMN in human newborns. However, the same stimuli did not reliably elicit MMN-like responses in rhesus macaques, indicating a lack of beat perception in this species.

Though several avian species show rhythmic patterns in their vocalizations, there are only mixed results on the ability of these species to perceive rhythmic structure (ten Cate & Spierings, 2019). European starlings are reported to be capable of discriminating rhythmic and arrhythmic patterns (Hulse et al., 1984). Pigeons are reported to show the ability to discriminate different metric structures only under severely limited conditions (Hagmann & Cook, 2010).

12.5 Evolutionary Roots of Language from the Perspectives of Musicality

Many species, including songbirds and non-human primates, show human-like abilities of frequency structure perception. Some species can apply this ability to process materials taken from human language (Hoeschele & Fitch, 2016; Ohms et al., 2010; Spierings & ten Cate, 2014). Further, cotton-top tamarins and rats are reported to be capable of discriminating unfamiliar languages based on prosodic cues (Ramus et al., 2000; Toro et al., 2003). Considering these, it seems likely that phylogenetically old functions are recruited in both music processing and prosodic bootstrapping of language acquisition in human infants in a domain-general manner.

In contrast to the cross-species prevalence of frequency structure perception (Briefer, 2012; Filippi et al., 2019; Fishman et al., 2001; Wright et al., 2000), few species show the ability to perceive and produce rhythmic patterns. To obtain a full picture of the evolutionary roots of prosodic bootstrapping in language acquisition, it should be clarified how only humans acquired sophisticated rhythmic abilities. This is still a contentious field of debate, but we summarize below a tentative scenario based on existing evidence.

Schachner et al. (2009) analysed the characteristics of species that show signs of rhythmic entrainment and claimed that most of the species capable of rhythmic entrainment are also vocal learners/imitators, species that possess the ability to mimic and reproduce environmental sounds and conspecific vocalizations (Egnor & Hauser, 2004). Because both rhythmic entrainment and vocal learning require a linkage between auditory and motor systems, Patel proposed that increased functional and anatomical linkages between motor and auditory regions underlie the evolution of both vocal learning and rhythmic entrainment (Patel, 2014; Patel & Iversen, 2014). Songbirds, primates, dolphins, elephants, and bats use vocal imitation for authenticating group membership, territorial defence, adjustment of social relationships, and courtship behaviour (Coleman et al., 2007; Doi, 2020). Thus, refinement of vocal learning/imitation, hence the development of auditory-motor coupling, had conferred clear adaptive benefits to these species.

Ethnographic research on existing hunter-gatherer societies indicates the primary roles of vocal imitation in cooperative behaviour (Boyd, 2018; Lewis, 2014). Accumulation and sharing of knowledge about the surrounding environment among group members increase the odds of survival. Initiated males of the Bakaya Pygmy group achieve this by narrating their experience and knowledge through multimodal channels, including sophisticated imitation of environmental sounds as well as gestures and facial expressions (Lewis, 2014). Therefore, representing external entities by mimetic sound might have served as an efficient tool of communication in *Homos* throughout evolutionary history (Boyd, 2018). The adaptive benefit of sound-mimicking ability must have led to a closer and stronger coupling between motor and auditory regions in the human brain.

Though somewhat speculative, auditory-motor coupling may have paved the way for the emergence of fine-motor control of the vocal apparatus required in speech communication (Kearney & Guenther, 2019). The evolution of language made auditory-motor coupling even more valuable for humans, further strengthening the anatomical and functional association between these neural regions. In other words, auditory-motor coupling underlying the refinement of vocal learning/imitation prepared the basis for the evolution of speech communication. Thereafter, the survival benefit of language and speech communication in turn strengthened this coupling further.

The evolution of tight auditory-motor coupling (Rauschecker & Scott, 2009) has been driven first by the survival benefit of vocal learning/imitation and then speech communication. As a by-product of this process, humans have acquired superb ability for rhythm processing. Interestingly, neuroimaging studies indicate that motoric regions as well as auditory cortices contribute to the perception of rhythmic (Grahn & Brett, 2007) and prosodic information (Brown & Martinez, 2007; Reiterer et al., 2007; Belyk et al., 2016). Further, several studies revealed an association between the strength of auditory-motor coupling and linguistic processing ability (Yu et al., 2017). Thus, it seems to be the case that the human brain found a way to utilize strong auditory-motor coupling to process acoustic information and hence bootstrap language acquisition during infancy.

12.6 Conclusion

Human infants are faced with the daunting task of analysing the underlying structure of linguistic sound streams. Due to the lack of any language-specific knowledge, linguistic sounds must be almost indistinguishable from music for infants. Therefore, it is natural to think that infants first apply their ability for musical processing to linguistic materials.

Indeed, existing studies point to the possibility that domain-general abilities of frequency structure and rhythm perception contribute to language acquisition during early infancy. Infants start applying these abilities to analyse linguistic sound streams almost coincidentally with the emergence of corresponding abilities in the musical domain. Such cross-domain similarity in the developmental course provides partial support for the view that domain-general functions assist language acquisition. However, this view should be validated empirically by future studies that investigate whether identical neural structures are recruited in processing musical and linguistic materials in prelinguistic infants.

The abilities for musical chord and pitch contour perception can be seen in many non-human species. Further, the species can apply these perceptual functions to analyse linguistic materials as well. In contrast, animals do not match humans in their ability to perceive and produce rhythmic patterns. Considering these, what separates humans from non-human species in terms of language evolution seems to be the emergence of tight coupling between auditory and motor regions in humans that engendered both speech communication and refined rhythmic ability.

The emergence of language made auditory-motor coupling more beneficial for humans. The strong auditory-motor coupling has brought up musical and linguistic abilities to even higher levels in humans, thereby enabling infants to use these domain-general functions to analyse linguistic sound streams in the process of language acquisition.

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Chapter 13
What Is Unique in Infant Thinking About Others? Infant Social Cognition from an Evolutionary Perspective

David Buttelmann

Based on the idea that the mental abilities of all beings were subject to evolutionary continuity (Darwin, 1859, 1871), this chapter explores the uniqueness of human infant social cognition. Focusing on infants in this regard makes sense, because as soon as children reach preschool age, most tasks they are presented with in order to evaluate their social-cognitive abilities involve verbal responses and require sophisticated levels of other cognitive abilities such as attention and memory (see specific sections below). Thus, my approach is to compare human infant social cognition to that of our closest relatives, the nonhuman great apes – chimpanzees, bonobos, gorillas, and orangutans. This comparison is the most fruitful given that great apes are closely related to humans phylogenetically. The high degree of genetic relatedness (*Homo sapiens* and members of the species *Pan* share between 98.3% and 98.7% of their DNA; e.g., Wildman et al., 2003) suggests that differences in other areas, such as cognition, might also be smaller than expected.

In this chapter, I summarize empirical findings on human infants and great apes for their understanding of the mental states of goals, intentions, desires, and beliefs, examining whether human infants and great apes share an understanding of the mental state in question. If we identify a social-cognitive ability that only human infants possess but other great apes lack, this might be the key to human uniqueness and, consequently, a hint toward which abilities evolved specifically in humans and equipped our species with the tool kit needed to cooperate and build the kind of sophisticated culture we see in modern humans.

Reading others' mental states helps individuals to explain and interpret others' behavior (Premack & Woodruff, 1978), and, in consequence, to regulate one's own intentional actions in accordance to the mental states underlying others' actions. Thus, understanding that others act according to how they *represent* the current (and future) world equips individuals with a tremendous advantage. Although several

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authors have claimed that humans are unique in how they deal with others' psychological states compared to all other animals (e.g., see Call & Tomasello, 2008; Povinelli et al., 2000; Tomasello & Rakoczy, 2003), in recent years comparative research has demonstrated that humans might not be the only species that discerns what others perceive, intend, desire, and believe when reasoning about others.

13.1 Understanding of Others' Desires

The term *desire* has been used differently by different authors (e.g., Repacholi & Gopnik, 1997; Schult, 2002; Searle, 1983). What all explanations have in common is that desires are considered mental states that cause people to act to bring about changes in the world. Following Repacholi and Gopnik's (1997) use of the term "desire," it could easily be exchanged with other terms that describe an individual's attitude toward outside entities (e.g., the term "preferences"). Such use allows us to differentiate desires from goals. At least in humans, an individual's desire typically is reflected by emotional expressions (e.g., a happy face when liking an object).

13.1.1 Understanding Others' Desires in Human Infants

The development of infants' understanding of emotional expressions seems to start early in ontogeny. By 4 months of age, human infants discriminate between some facial expressions such as fear and happiness (Nelson, 1987). Repacholi (1998) tested 14-month-olds' understanding of emotional expressions and found that the infants understood both the directedness and the valence of emotional signals. In this study, infants saw an adult approach two boxes, open each one in turn, and show an emotional expression according to the content of each box (either happiness or disgust). When handed both boxes afterward, the infants correctly interpreted the available emotional expressions which was shown by them, predominantly opening the box to which the adult had responded with a happy expression.

By 18 months of age, infants understand that an individual's emotional expression toward an object can be considered an indicator of the individual's desire (for this particular object). In their study, Repacholi and Gopnik (1997) showed that 18-month-old infants, after viewing an adult's emotional responses to different food items, responded to the adult's ambiguous request gesture by handing over her preferred food item even when it did not match their own preference. They thus demonstrated that 18-month-old infants understand that desires are mental states underlying behavior and action. Specifically, infants at this age – but not 14-month-olds – have a non-egocentric understanding of the differences between their own desires and those of others.

13.1.2 Understanding Others' Desires in Nonhuman Great Apes

Nonhuman great apes have shown some ability to discriminate the emotional states of conspecifics (Parr et al., 1998) and are also able to match videos with emotional content (e.g., a conspecific being injected) to the appropriate conspecific facial expression (Parr, 2001). Apes thus can differentiate emotional expressions. Only a little research has investigated their understanding that emotional expressions reflect internal states (i.e., desires) directed referentially to outside entities. In one study (Buttelmann et al., 2009a, Exp. 1), behavioral settings previously presented to infants were modified and presented to great apes of all four species. As in Repacholi (1998), the authors had an experimenter emote neutrally or with disgust to the content of one box and with a happy emotional expression to the content of another box. At least for disgust versus happiness, the apes significantly preferred the box associated with the happy expression. Although this does not yet demonstrate that the apes considered emotional expressions as indicators for desires, it at least demonstrates an understanding of the valence and directedness of emotional expressions. To check whether apes indeed chose the happy box and did not just avoid the disgust box, and to see whether the apes used emotional expressions to infer desires and to interpret consequent behavior, the authors modified Repacholi and Gopnik's (1997) procedure (Exp. 3). First, the experimenter hid two high-value food items in each of two containers. He then emoted to the content of each of the two containers: to one with an expression of happiness and to the other with an expression of disgust. Out of apes' view, he then took the food out of the "happy box" and pretended to eat. Thus, when subsequently given a choice between both containers, the apes had to choose the disgust box in order to retrieve a food item. Although the effect was not too big, this is what the apes did. This research indicates that non-human great apes, like human 18-month-olds, can use the experimenter's emotional expression to infer his desire.

13.2 Understanding Others' Goals

As with the term desire, the use of the term *goal* provoked several misunderstandings (e.g., see Want & Harris, 2001). In general, there are two main ways this term is used in the developmental literature. On the one hand, authors talk about goals when referring to a certain state of the environment; i.e., a person's desired result as a state in the world. On the other hand, the term goal is used as referring to an internal representation of this desired state in the world that guides a person's behavior (Tomasello et al., 2005). Since this chapter deals with infants and nonhuman apes' understanding of others' mental states, the term "goal" refers to this mental representation of the desired state in the world.

13.2.1 Understanding Others' Goals in Human Infants

Understanding others' intentional actions in terms of goals tells the observer what an organism is trying to do. Thus, this mental state derives from a desire and forms a more concrete representation that affects the organism's behavior. Several types of tasks have been used to investigate goal understanding in human infancy. A very prominent task is the habituation-dishabituation paradigm that measures infants' looking time at video scenes in which an actor acts according to his or her goal versus performs an action that is not directed at his or her goal. Using this paradigm, research has shown that human infants seem to understand others' goals from a very early age. For example, Woodward (1998) presented 6-month-olds with an actor who repeatedly reached for one of two objects that were always positioned next to each other (with each object staying at the same position during familiarization). At test, the two objects were switched, and the actor reached either at the old object (following a new path) or followed her previous path but consequently reached for the alternative object. Results indicated that 6-month-olds understand others' actions as object-directed: The infants looked at the scene longer when the actor reached for the alternative object (although the path was identical to the previous one) compared to when she reached for the old object (although she had to use a new path).

In related research, a number of subsequent studies have provided evidence that infants between 6.5 and 12 months already understand that agents pursue goals around obstacles (e.g., Csibra et al., 1999; Gergely et al., 1995). Watching a computer screen, infants are habituated to an animate dot jumping over a wall and approaching another dot on the other side of this wall. When the wall is then removed in the test trial, infants seem to expect the dot to approach the other dot directly (e.g., horizontally, without a jump), which is interpreted from their longer looking times at the screen when the dot in the test trial continues the previous jumping action although it is now not necessary (violation of expectation).

Another clever task to measure whether human infants have an understanding of goal-directed actions is to investigate how they segment others' actions (e.g., Baldwin et al., 2001; Saylor et al., 2007). Both on video and live, infants in the last quarter of their first year of life observed a human (or a human-like array of light dots) perform a continuous everyday action sequence. These action sequences were then interrupted, either at a point at which a goal-directed action was finished or at a point at which a goal-directed action was still in the process. What was measured was how long infants looked at these interruptions. Infants demonstrated their understanding of goal-directed actions when they looked longer at the interruptions when they stopped a goal-directed action from being fulfilled than at an interruption that appeared after a goal-directed action has been fulfilled.

Beginning in the second half of infants' first year of life, their goal understanding starts to guide their behavior: 7-month-olds imitate an actor's goal-directed actions in a differentiated manner. That is, they performed modeled actions only if these actions were goal-directed (Hamlin et al., 2008). Around their first birthdays, infants use their understanding of others' goals when imitatively learning from others and copying others' actions selectively according to the others' goals. In one series of studies, participants were presented with an experimenter performing two identical but differently marked actions on a novel apparatus. Infants tended to imitate the action that was vocally marked as intentional (e.g., by the word "There!"), whereas they ignored the same action when marked as an accident (e.g., by the word "Whoops!") by the experimenter (e.g., Carpenter et al., 1998; Olineck & Poulin-Dubois, 2005). In another set of imitation studies, 18-month-old infants even imitated an actor's intended goal after they had only seen the actor's failed attempt to achieve her goal (e.g., Bellagamba & Tomasello, 1999; Carpenter et al., 2005; Meltzoff, 1995).

Finally, studies testing infants in interactive non-imitative settings found that at around their first birthdays, infants start to understand that others persist in pursuing their goals when they are not achieved, for example, in the case of failed attempts or accidents. For example, Behne et al. (2005) presented infants sitting at a table with an experimenter handing over objects to the participants in two different ways. Infants from 9 months of age onwards became more impatient (reaching, banging on the table, turning away) when the experimenter was unwilling to pass over the object, e.g., by holding it out and moving back in a teasing fashion, than when the experimenter was unable to do so, e.g., because he accidentally dropped it during the attempt to hand it over to the participant. Further, infants infer an actor's goal when presented with referential gestures, such as gazing and pointing in combination with intentional reaches for or graspings of an object, with some studies also including emotional cues (see previous section) (e.g., Moses et al., 2001; Phillips et al., 2002; Sodian & Thoermer, 2004). Taken together, there is an abundance of experimental evidence that shows that human infants have a relatively complex understanding of others' goals by around their first birthdays.

13.2.2 Understanding Others' Goals in Nonhuman Great Apes

Studies investigating the understanding of others' goals in great apes apply different types of paradigms. In the first kind of study investigating goal understanding in great apes, a human experimenter communicates the location of hidden food to the subject by using various gestures (e.g., head orientation, pointing at the container) to show the subject which of these containers is baited. Across different studies, great apes show variable performance. Some studies indicate that, despite their ability to follow a human's gaze (Call et al., 1998), chimpanzees still fail to use human pointing or gazing cues in such tasks (e.g., Call & Tomasello, 1994; Itakura et al., 1999; Tomasello et al., 1997). Other studies, however, indicate that chimpanzees, orangutans, and gorillas are all successful at using at least some of these cues, such as pointing, head and eye orientation, or a physical marker put intentionally on top of the baited container by the experimenter to locate hidden food (Barth et al., 2005; Byrnit, 2004; Call & Tomasello, 1998; Itakura & Tanaka, 1998; Miklósi & Soproni, 2006). However, it should be mentioned that in most cases when subjects did use these cues successfully, they first experienced extensive training where they might have learned the cues.

The fact that in this task subjects are presented with communicative cues such as pointing, tapping the container, or gazing in a cooperative setting might account for the apes' failures to apply social cognition spontaneously (see also Herrmann et al., 2007). While all of these communicative cues are common behaviors for humans, they may not normally be used between conspecifics in other primate species (Goodall, 1986; Menzel, 1973). Yet great apes may be able to interpret others' goals when observing them act in a more non-cooperative context, such as food acquisition or food processing. Unlike communicative cues, such behavioral cues consist of fully functional behaviors and do not reflect the actor's intent to communicate specific information to other individuals (Buttelmann et al., 2008a). Indeed, several studies involving more behavioral cues provide evidence for great apes' ability to understand the actions of others in terms of the goals they are pursuing. For example, although chimpanzees fail to retrieve the container with food in object-choice tasks that are set-up in a cooperative situation, i.e., when it was indicated by a communicative cue, they could successfully use a very similar behavioral cue to locate the hidden food in a competitive context, namely a human or conspecific reaching for the baited cup but not paying attention to the subject (Hare & Tomasello, 2004). Thus, even though both cues involve a very similar arm movement, subjects differentiated these two cues. However, there are also mixed findings with non-cooperative object-choice tasks. For instance, Bräuer et al. (2006) presented chimpanzees and bonobos with two behavioral cues: a cue in which the experimenter attempted to remove the lid from the baited cup, and the reaching cue from Hare and Tomasello (2004), and subjects failed to use these cues when choosing between locations. One important difference between this study and the one by Hare and Tomasello (2004) may account for the subjects' failures in the reaching condition – in Hare and Tomasello's study the experimenter first established a competitive relationship with the subject before the cue was given; such a relationship was not established in the Bräuer et al. study. This competitive context may have especially motivated the subjects. We will later come back to this point.

As with children (e.g., Behne et al., 2005), some studies also used natural interaction paradigms to investigate great apes' ability to understand others' goals. For example, Call et al. (2004) had a human experimenter repeatedly give chimpanzees food through a glass panel. Then, on some trials, the experimenter did not give the food. The experimental manipulation was that sometimes the experimenter did not give food because he was unwilling to, whereas other times he did not give it because he was unable to do so. Unwillingness was expressed in one of three ways: the experimenter either simply stared at the food on the table in front of him without giving it, he ate it himself, or he teased the chimpanzee with it, pulling it back when the chimpanzee reached for it. Matched with each of these three unwilling actions were two unable actions that resembled fairly closely their counterpart behaviorally – with respect to how and where the food was moved and where the experimenter looked. The basic finding was that chimpanzees reacted similarly to the different unwilling actions by expressing frustration and impatience, and they reacted similarly to the different unable actions by being patient (possibly because they inferred that the experimenter was "trying"). This similarity of reaction across the different manifestations of the two experimental conditions suggests that the chimpanzees understood the different goals of the experimenter in the different conditions – regardless of how they were expressed behaviorally (see also Buttelmann et al., 2012, Study 1). In another interactive paradigm, Buttelmann et al. (2012, Study 2) had an experimenter feeding subjects at two feeding sites and changing sites from time to time. The subjects were free to move between sites, and the authors measured how fast the subjects left a site after the experimenter got up at this site. The manipulation was that sometimes the experimenter got up wanting to feed the subject at the other site, other times his getting up was caused by cues in the context (e.g., a walkie-talkie making noise). The apes left the feeding site slower when the experimenter had a different goal (e.g., to answer the walkie-talkie) than the goal to feed them.

Interestingly, chimpanzees also demonstrated their understanding of others' goals in other types of interaction studies previously applied to human infants, that is, interactive tasks in which the measure was more prosocial. Using a helping paradigm, Warneken and Tomasello (2006) had a human experimenter drop an object accidentally in the presence of each of three human-raised chimpanzees and then strain and reach toward it (with several different objects in several different situations). The chimpanzees retrieved it for him. Importantly, they did not retrieve it for him in various control conditions in which he threw the object away or otherwise indicated a lack of interest. The chimpanzees' different behavior in the experimental and control conditions could be interpreted as indicating an understanding of the experimenter's different goals in the two situations (see also Premack & Woodruff's, 1978, study with a single human-raised chimpanzee). Warneken et al. (2007) set up a much more novel situation in which one chimpanzee also might help a conspecific. In this study, one chimpanzee was attempting to get into an adjoining room, often shaking the door in his attempt. Another chimpanzee then quite often, from her advantageous location, pulled a chain that unlocked the door so that the first chimpanzee could have access to the room he wanted to get into. They did this more in this condition than in a control condition in which the first chimpanzee was trying to get out another door. These studies of instrumental helping suggest that chimpanzees can tell when someone needs help achieving their goal.

Finally, Tomasello and Carpenter (2005) used two imitation paradigms (from research with human infants) with the same three human-raised, juvenile chimpanzees used in the Warneken and Tomasello (2006) study. In one paradigm, based on the study by Meltzoff (1995), a human tried but failed to perform various actions on objects. The chimpanzees successfully discerned the action the human was attempting to perform and performed it themselves (as often as when they had seen her perform it successfully, and more often than when she had just manipulated the object). In the other paradigm, based on the study by Carpenter et al. (1998), a human performed two actions on a series of apparatuses, one intentional and one accidental, before it was the chimpanzees' turn. The human-raised chimpanzees copied the intentional action more often than the accidental action (see also Call et al., 2005, and Myowa-Yamakoshi & Matsuzawa, 2000, for other studies of this with less clear results).

Taken together, these studies seem to be fairly convincing that human infants and great apes, chimpanzees in particular, understand others' intentional actions in terms of their goals. For great apes, showing this ability seems boosted when observing them acting in a non-communicative manner. However, one might argue that in most of these studies, the (human) actor behaved slightly differently in the experimental and control conditions (i.e., the slightly different behavior was the cue to the different underlying goals involved). This means that any one of these studies could be given an explanation in terms of behavioral rules – an association between an antecedent and a consequent behavior of the actor – that great apes are either born with or learn. In my view, this explanation is unlikely because of the novelty and diversity of behaviors used as both cues and responses in the great number of different studies. In addition, in some of these studies (e.g., Buttelmann et al., 2012), the experimenter's observable behavior at test was identical in all conditions.

13.3 Understanding Others' Intentions

Understanding *what* state in the world an individual is trying to achieve is already helpful for explaining and interpreting the individual's behavior. However, the explanatory power of this ability is very restricted given that in most situations there are several methods of *how* to obtain a specific goal. It is thus also important to understand others' intentions. Understanding intentions in this chapter refers to an understanding of others' action in terms of both a goal – an internal representation of the desired state in the world – in combination with a rationally chosen means (Bratman, 1989). Thus, an individual that understands others' intentions has an idea of what the acting organism is trying to do and how it wants to achieve it. The chosen action is rational since for the choice of a means, the person takes into account her knowledge and skills and her mental model of the current reality (Tomasello et al., 2005). Therefore, this choice is influenced by reasons (e.g., why the organism chooses a specific means). Some reasons for such a choice can be observed, others cannot (especially if these are mental as well, such as ignorance, see next section). Whereas goals can be fulfilled in different ways, intentions are characterized by what Searle calls causal self-referentiality (Searle, 1983). Intentions have to be carried out actively as originally represented. Achieving the desired outcome in some other way does not fulfill the intention (Astington & Gopnik, 1991; Schult, 2002). When comparing intentions with desires, Bratman (1987) further argues that there is a greater commitment to action with an intention than with a desire. Unlike with desires, intentions have to be made consistent with each other due to this greater commitment. In addition, because a person commits herself to an action plan in order to form an intention, intentions are resistant to reconsideration (Bratman, 1987, p. 18).

13.3.1 Understanding of Others' Intentions in Human Infants

There is some evidence that infants understand others' intentions around their first birthdays. Gergely et al. (2002) conducted a study in which 14-month-old infants watched an adult switch on a lamp with her forehead. For half of the infants the adult was forced to use this unusual means because her hands were occupied (she was holding a blanket around her shoulders; Hands-Occupied condition). The other half of the infants saw the adult use the same unusual means even though she could have more easily used her hands, which were not occupied (Hands-Free condition). When later given the possibility to act on the lamp themselves (with no constraints), more infants reproduced the adult's unusual action when her hands had been free (69%) than when they had been occupied (21%). The most mentalistic interpretation of this result (Buttelmann et al., 2008b) is that in the Hands-Free condition, infants apparently understood that the adult must have chosen the unusual action for some reason (even if they did not know exactly what that reason was), and they copied the action in order to find out what that reason might have been. In the Hands-Occupied condition, in contrast, the adult's reason for choosing that action was clear – her hands were constrained – and, since infants were not constrained in this way, they did not copy the action. Since the model's goal was identical in both conditions (i.e., to illuminate the lamp), this study shows that infants took into account other aspects besides behavior, namely environmental variables, to identify the model's intentions.

Subsequent research has made three important extensions to the original head-touch study. First, a study including the imitation of the use or choice of a tool to obtain a reward replicated the head-touch finding conceptually (Buttelmann et al., 2008b). In this study, a model either had to use a tool because the direct access to the reward was blocked by a physical barrier or he freely decided to use the tool although direct access was available (mirroring the Hands-Occupied and the Hands-Free conditions). In a set of two studies, 14-month-old infants used the tool themselves more often in the not-blocked than in the blocked condition. In a third study, the model had to use a tool in both conditions. In the not-blocked condition, he could freely choose between a rather unusual tool for pulling (i.e., a wooden block) or a tool usually associated with pulling (i.e., a rope), while in the blocked condition, he had access to the unusual tool only. The infants imitated the use of the unusual tool more often in the not-blocked than in the blocked condition. Another study had 12-month-olds watch as an adult made a toy animal enter a toy house through the chimney instead of the door – either while access through the door was blocked or while access through the door was possible (Schwier et al., 2006). Even these younger infants made the toy animal enter the house through the chimney more often in the door-not-blocked than in the door-blocked condition. Thus, infants make use of their intention understanding not only in body-part imitation tasks but in different types of imitation tasks.

Secondly, using two types of body-part-imitation tasks (i.e., head-touch and sit-touch), Géllen and Buttelmann (2017) tested 14-month-olds in a within-subjects design. The infants flexibly alternated their imitative response in accordance with a model's changing physical constraints, demonstrating their ability to adapt their intention understanding in the light of the model's physical constraints.

Third, two very recent studies made the most important extension of the head-touch experiment given the topic of this chapter by attempting to test the mentalistic account described above. Both studies presented 14-month-olds with a model performing the exact same unusual action (e.g., a head touch) in two conditions. What differed between conditions was whether or not the model was mentally – instead of physically – constrained. More specifically, while the model knew that the unusual action was unnecessary and that there was a much more efficient action to achieve the goal (e.g., hand use) in the knowledgeable condition (mirroring the hands-free condition), in the ignorant condition (mirroring the hands-occupied condition) the model was ignorant about this fact. Thus, if infants paid attention to the model's knowledge state, they might differ in their response just as they did when being presented with physical constraints. The infants – who always knew of the efficient means either from observing an assistant or from self-experience – differed in their imitative response behavior as hypothesized in both a body-part imitation task (Géllen & Buttelmann, 2021) and in an action-on-object task (Buttelmann et al., 2021a). Thus, although all observable parameters of the model's demonstration were identical in both conditions, infants imitated the model's use of the unusual means more in the knowledgeable than in the ignorant condition. Thus, 1-year-old infants pay attention to the mental dimensions included in others' intention formation, and they use this understanding when deciding what to imitate from them.

13.3.2 Understanding Others' Intentions in Nonhuman Great Apes

Given our definition of intentions, for subjects to pass studies investigating the understanding of others' actions in terms of intentions, it does not help to focus only on the question of what the other is trying to do. Additionally, the subjects have to pay attention to the means, that is, how the actor is trying to achieve the desired result. This seems to be difficult for great apes. When being presented with a model (human or conspecific) that performs a specific action in order to achieve a certain goal, they mostly seem to focus their attention on the end result of another's action rather than the exact behavioral means that brings about the change in the world. For example, in the study by Tomasello et al. (1987), a chimpanzee was trained with a certain two-action methodology on a T-shaped tool that could be used to obtain out-of-reach food. In contrast to a control group without any model, the chimpanzees that had the possibility to observe the trained ape obtaining food with the tool also used the tool to get food that was out of their reach. Interestingly, although those subjects learned to use the tool whereas the subjects of the control did not, the successful subjects never copied the specific two-action method. They merely had learned causal relations without paying attention to the exact strategies of the demonstrator. Thus, apes mostly reproduce the end result of an action within social-learning situations (*emulation learning*, Tomasello, 1990, 1996) without copying the exact behavioral means that led to that result as human children do (e.g., Call et al., 2005; Call & Tomasello, 1994; Tennie et al., 2006). What remained unclear was whether this failure to imitate was due to an inability to focus their attention to the means used by the model. However, this might not be the case: Although the subjects did not imitate a successful means when it was their turn in a subsequent test phase, they successfully distinguished between a model trying to use a means that was successful in producing a reward in the past and a model who tried to open a reward box using a means not being demonstrated to be successful in the past (Buttelmann et al., 2013).

However, under some circumstances great apes do imitate. One such circumstance is a specific rearing environment. Indeed, human-raised or *enculturated* great apes often copy the specific actions of others (Bjorklund & Bering, 2003; Bjorklund et al., 2002; Tomasello & Carpenter, 2005; Tomasello et al., 1993). For instance, in the study of Bering et al. (2000), after a baseline period, a human demonstrator showed human-reared chimpanzees and orangutans a specific way of how to deal with several objects, e.g., use tongs bimanually to lift a cloth from a flat surface. After a delay of 10 min, the participants were then handed the objects again and scored for copying the demonstrator's actions. All six participants displayed deferred imitation in at least one trial, with each species showing deferred imitation in approximately half of the trials they were tested in. Several reasons could account for the human-raised apes' success to imitate. For example, it might be possible that those apes are exposed to tools and objects much more often than their mother-raised conspecifics, or they are notably trained to copy actions, or they actually possess a more detailed understanding of others' intentions (see Call & Tomasello, 1996). I will later come back to this issue.

There is also recent evidence that non-enculturated great apes can learn to use specific foraging techniques when observing a conspecific. This is important because it may give rise to the possibility to apply this method usually used with human infants to investigate an understanding of intentions even in mother-reared great apes. Whiten et al. (2005) trained two adult chimpanzees with different tool-use techniques on how to obtain food from an apparatus (i.e., a lifting versus a poking technique) unobserved by their group mates. When the two model chimpanzees were then re-introduced to their respective groups, most group members mastered the new technique after observing their local expert (no ape did in a control group without an expert). Most chimpanzees adopted the exact method that had been seeded in their group. In this and other studies, chimpanzees are not only shown to acquire specific techniques, but that the adopted methods are even transmitted from one group member to the other (e.g., Horner et al., 2006; Whiten et al., 2007). Further, it has been shown that the movement of the involved parts of the apparatus alone (ghost condition) does not lead to the accomplishment and the transmission of the technique (Hopper et al., 2007).

Although it is impressive that great apes do imitate others, it remains unclear whether we can actually take this as evidence for an understanding of others' intentions as rational choices of action plans. Actually, this is questionable for virtually all studies that tested mother-raised or human-raised great apes with only classical imitation tasks. Only the fact that subjects copy the means a model is performing and achieve the goal the model achieved before does not necessarily prove that successfully copying subjects understood the mental dimension behind this action (see Tomasello & Call, 1997). Still, two studies attempted to apply a rational-imitation paradigm like Gergely et al.'s (2002) head-touch task to great apes. Buttelmann et al. (2007) had enculturated chimpanzees watch a human model perform either a head touch, a foot touch, or a sit touch to illuminate a novel lamp or to play a sound from a novel sound box. The model either had to use these unusual means because of some physical constraints or he freely chose to use them without any constraint present. Like human infants, the chimpanzees imitated the model's choice of means significantly more often when they freely chose to use them than when they were forced to use them. This was the first study to demonstrate that not only do great apes imitate others, they rather do so selectively. This finding might be less surprising given that the study subjects were enculturated. A subsequent study, however, found a similar pattern of results with great apes raised by their natural mothers. The study involving the rational choice of tools described above in the infant's section (Buttelmann et al., 2008b) also tested great apes of all four species, i.e., chimpanzees, bonobos, gorillas, and orangutans, on the very same tasks as the ones applied to human infants. The interesting finding was that species differences appeared: While mother-reared chimpanzees, bonobos, and gorillas did not differentiate between conditions, the mother-reared orangutans chose/used the tool the model chose more often in the not-blocked condition (mirroring the hands-free condition) than in the blocked condition (mirroring the hands-occupied condition). Thus, while chimpanzees seem to need some enculturation to put them in a position to imitate rationally, orangutans' imitative responses suggest that they applied an understanding of the model's intentions as rational choices of action plans.

13.4 Human Infant and Nonhuman Great Ape Differences and Similarities in Their Understanding of Others' Desires, Goals, and Intentions

Summing up the previous three sections, we can thus conclude that both human infants long before their second birthdays and great apes understand at least three different mental components in others' intentional action. They can use others' emotional expressions as indicators for their desires, they can interpret what others are trying to do (their goals), and they infer why an actor has chosen a specific means for how to achieve this goal (their intentions) and imitate this actor accordingly. Infants and great apes can use this understanding when learning from others and when interpreting others' behavior. Still, given that studies on great apes' understanding of intentions focus solely on rational imitation, more studies are needed to investigate whether great apes' understanding of others' intentions is similar to that of human infants. Assuming it is, understanding others' desires, goals, and intentions does not seem to be the crucial element that differentiates infant social cognition from that of nonhuman great apes. What these three mental states have in common is that they have very strong behavioral correlates. In virtually all examples described above, subjects infer these mental states while watching a protagonist act. Thus, human infants and great apes might be able to extract mental states from protagonists' immediate actions (e.g., facial expressions, hand movements, and so on) (e.g., Gergely & Csibra, 2003). Another thing that desires, goals, and intentions have in common is that they are non-propositional, that is, they cannot be true or false. Although someone's goal might be *improper* in some moral or societal sense, it is never false regarding an objective view. The next section will investigate whether differences between human infants' and great apes' social cognition might lie in their understanding of propositional mental states, that is, beliefs.

13.5 Understanding Others' Beliefs

In the last 15 years, the investigation on understanding others' belief in preverbal children experienced a true revolution. This was because researchers found ways to present infants with language-reduced tasks. In contrast to the verbal tasks applied to toddlers and preschoolers for decades (e.g., Gopnik & Astington, 1988; Perner et al., 1987; Wimmer & Perner, 1983), these tasks on the one hand neither included long verbal instructions or stories nor did they require subjects to produce verbal responses. They thus measured subjects' social-cognition competence implicitly.[1] Different types of tasks have been developed: tasks measuring (1) gaze behavior, (2) infants' performance in interactions with others, and (3) neural activation.

13.5.1 Understanding of Others' Beliefs in Human Infants

Although the first, pioneering study applying a gaze-behavior measure to investigate belief understanding was run more than 25 years ago (Clements & Perner, 1994), the rise of implicit false-belief tasks measuring gaze behavior started in earnest with Onishi and Baillargeon's (2005) application of a violation-of-expectation paradigm. The authors presented 15-month-old infants with live theatre scenarios in which an actor either watched (true-belief condition) or did not watch (false-belief condition) an object switch locations before she reached to either the previous

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[1] I use the term "implicit" to refer to measures that do not require subjects to produce a verbal – and thus deliberate response – as well as those tasks that do not present subjects with verbal test questions.

location or the new location of the object (i.e., the test event). When the actor reached, the researchers measured infants' looking time at this event. Assuming that the actor reached because she wanted to have the object, then infants should expect her to reach for it where she knew or believed it to be (i.e., the new location in the true-belief condition and the previous location in the false-belief condition). A violation of this expectation should become visible in an enhanced looking time at the incongruent event. This is what the authors found. The interpretation was that infants considered the actor's representation of the object's current location when interpreting the actor's actions. A large body of subsequent violation-of-expectation false-belief studies added empirical evidence to this interpretation (Kovács et al., 2010; see Baillargeon et al., 2010; Scott & Baillargeon, 2017, for reviews).

Another gaze-based measure of infant false-belief understanding is the measure of anticipatory looking. For this, subjects receive a light or sound cue right before the actor re-enters the scene after a change of the target object's location. Researchers measure at which of several areas of interest (i.e., possible locations the actor might reach) infants are looking while getting this cue. This anticipatory look is considered the infants' anticipation of the actor's reach. If infants included the actor's belief about the object's location into their prediction of the actor's acting, they should look at the current location if the actor held a true belief and they should look at the previous location of the object if the actor falsely believed the object to be where it was before the switch. Eighteen-month-olds and slightly older children have been shown to expect an agent to approach the location where the agent believes the toy to be (Senju et al., 2011; Southgate et al., 2007; Thoermer et al., 2012).

Tasks measuring infants' false-belief understanding in interactive settings also put infants in situations in which they observe an actor who either holds a true believe (i.e., she knows the true location of the target object) or a false believe (i.e., she believes the object to be in a previous location). At test, infants are placed in a situation in which they can interact with the either (e.g., they can help her or communicate with her). In the first study of this kind (Buttelmann et al., 2009b), 18-month-olds needed to infer the actor's goal from the actor's behavior that was based on the actor's (true or false) belief about the location of an object. More specifically, after the actor had placed a toy in one of two boxes and left the room, an assistant relocated the toy into a second box. Thus, when the actor re-entered the scene and tried to open the now-empty box, he falsely believed the toy to be in the box he tried to open. The children then helped the actor by opening the other box (i.e., the one that actually contained the toy) because they inferred that the actor wanted to find his toy. Importantly, when the actor had witnessed the relocation and nevertheless tried to open the empty box, the infants helped him by opening the empty box rather than the one currently containing the toy. For 16-month-olds this effect was less clear: Although they differed in their choice of box between conditions in the same pattern as did the older infants, in the true-belief condition they performed at chance level (instead of choosing the empty box significantly more often than the box with object).

Several subsequent interactive studies provided converging evidence for Buttelmann et al.'s (2009b) finding with 17- and 18-month-old infants (e.g., Buttelmann et al., 2014, 2015; Knudsen & Liszkowski, 2012a, b; Southgate et al., 2010). These studies also expanded the content of the actor's beliefs about the content of a box or the identity of an object. In order to investigate whether the 18-month-olds in the Buttelmann et al. (2009b) study acted based on an understanding of beliefs (i.e., the actor believed the empty box to contain the toy) rather than an understanding of ignorance (i.e., the actor did not know where the toy was), Buttelmann et al. (2021b) presented 18-month-olds with a replication of the false-belief and a new ignorance condition, in which the actor did not know where the toy was in the first place. The infants' helping behavior differed significantly between conditions: Whereas they opened the box with the object in the false-belief condition (replicating the original finding), they performed at chance level in the ignorance condition, where it was unclear whether the actor wanted his toy or wanted the empty box open. This might suggest that 18-month-olds indeed react to where an interaction partner represents an object.

The third class of infant false-belief tasks measures infants' spontaneous neural responses to scenarios in which an actor acts while holding false or true beliefs (Hyde et al., 2015, 2018; Southgate & Vernetti, 2014). For example, in the Southgate and Vernetti (2014) study, using EEG, the authors measured 6-month-old infants' sensorimotor alpha suppression as an indicator of motor-cortex activation. The infants showed such activation when an actor faced an empty box she believed to contain a toy, but they did not show activation of the motor cortex when the actor faced a box with an object she believed to be empty. This difference in motor activation suggests that if the actor believed the box to contain a toy, she might be reaching for it, while she might not do so in case she believed the box to be empty.

Recently, the replicability of implicit infant false-belief tasks was questioned because of different levels of success in replication attempts. While some laboratories successfully replicated and broadened previous results (e.g., Fizke et al., 2017; Oktay-Gür et al., 2018; Scott et al., 2015; Träuble et al., 2010), others failed to replicate earlier findings (e.g., Grosse Wiesmann et al., 2017; Yott & Poulin-Dubois, 2016; Zmyj et al., 2015). This leads to different consequences: On the one hand, one needs to be careful when interpreting unsuccessful replication attempts because a large number of factors might influence children's performance in such tasks (see Scott & Baillargeon, 2017; Schulze & Buttelmann, 2020). Already small changes in the set-up and the procedure might lead to results that differ from that of the original studies (see Baillargeon et al., 2018; Buttelmann, 2017). On the other hand, the lack of success in some of the replications suggests that infants' understanding of others' beliefs might be relatively fragile, being subject to task demands and the specific circumstances of the testing situation.

13.5.2 Understanding of Others' Beliefs in Nonhuman Great Apes

The interesting question is how nonhuman great apes might perform in such implicit false-belief tasks. Given that these tasks do not require verbal instructions or responses, they are highly suitable candidates to be applied to species that lack language. Indeed, after a number of unsuccessful attempts to find belief tracking in chimpanzees, bonobos, and orangutans (Call & Tomasello, 1999; Kaminski et al., 2008; Krachun et al., 2009, 2010), two studies – both using modified infant false-belief tasks – indicate that great apes do track others' beliefs. In one of these studies (Krupenye et al., 2016), bonobos, chimpanzees, and orangutans as a group correctly anticipated a human actor's goal-directed actions according to his belief about the location of an object (similar to how human infants did in the studies described above). More specifically, the apes observed videos in which an actor holding a false belief about the location of an object approached two target locations. As indicated by the subjects' first look, they anticipated that the actor was likely to act on the location where he falsely believed the object to be, in contrast to the location that actually held the object (as known by the subjects). Interestingly, great apes of the same three species also correctly anticipated a human actor's searching actions in the absence of behavioral cues (Kano et al., 2019): After gaining self-experience with translucent and opaque "windows," the apes observed a human actor who saw an object being placed in one of two locations. The actor then positioned himself behind either a translucent or an opaque window (both appeared identical without self-experience), and the object was switched from the first location to the other. Then the actor positioned himself between the two locations. The subjects correctly anticipated that the actor might search for the object where he believed it to be by looking at this location (i.e., the second location after observing the switch [translucent window] or the first location after not observing [opaque window] the switch).

Like human infants, great apes also demonstrated their tracking of others' beliefs in a more active task. Buttelmann et al. (2017) adopted the change-of-location interactive helping paradigm (Buttelmann et al., 2009b) and tested chimpanzees, bonobos, and orangutans. The authors found that the apes differed in their helping behavior according to whether the human actor held a true or a false belief about the location of an object. When observing the actor trying to open the empty box, they opened the box actually containing the object more when the actor believed this pulled box to contain the object than when the actor knew the pulled box was empty.

Thus, one might conclude that human infants and great apes are highly similar in their tracking of others' beliefs, and they indeed might be. However, there might be one crucial difference, and this is the kind of actor the different species ascribe beliefs to. Human preschoolers and adults are known for their willingness to attribute mental states including goals, intentions, and beliefs not only to human actors but also to self-propelled inanimate objects (Buttelmann & Buttelmann, 2017; Heider & Simmel, 1944; Montgomery & Montgomery, 1999), and even human infants ascribe goals and beliefs to self-propelled geometric shapes (Luo & Baillargeon, 2005; Surian & Geraci, 2012). In contrast, when Krupenye et al. (2017) replaced the human actor from their 2016 study with self-propelled geometric shapes, chimpanzees, bonobos, and orangutans did not adapt their anticipatory looks to the "beliefs" of the geometric shape. Thus, great apes seem to ascribe beliefs to animate actors only. Human infants' preparedness to ascribe beliefs (and other mental states) to virtually all kinds of self-propelled objects might be a specific feature of human social cognition.

Except for this small difference, no big gap can be found in tracking others' desires, goals, intentions, and beliefs between human infants and great apes. Thus, although understanding others' mental states might provide the foundation for the emergence of human acquisitions like the creation and use of complicated tools and technologies, mathematic and graphic symbols, or the development of complex social institutions such as religions, states, or social norms, it cannot be the critical feature because much of it is shared with our closest genetic relatives who do not use mathematics or graphic symbols. But what is it then that sets human infants onto a way leading to the type of culture that outperforms virtually other species in complexity and richness?

13.6 The Crucial Difference Between Humans and Great Apes

All the sophisticated acquisitions mentioned in the paragraph above do not rely on a single individual's knowledge or ideas. They are most often products of collective cultural activities. Humans possess the motivation to take what was invented by their ancestors and accumulate and modify these inventions over generations (what Tomasello, 1999, calls the *ratchet effect*) to improve or create better artifacts. Thus, even though understanding others' intentions is a fundamental aspect of social cognition and social behavior, there seems to be another important capacity in situations that require the collaboration of several people.

In regards to this capacity, Tomasello et al. (2005) introduced a second line of human development; the human unique motivation to share psychological states with others. Human infants, at the age of only a few months, seem to have a strong interest in sharing emotions reflect by their interactions with adults in *protoconversations* – social interactions in which the adult and the infant look, touch, smile, and vocalize toward each other in turn-taking sequences. Interestingly, what most observers have noted and researchers have found is that these protoconversations are held together through the exchange of emotions (Hobson, 2002; Stern, 1985; Trevarthen, 1979). Later, at the age of around 9 months, infants begin to engage with adults in triadic activities (Ratner & Bruner, 1978; Ross & Lollis, 1987). Infants start to share goals with adults as they act together to change the state of the world in some way and to perceive the world together in acts of joint perception (*shared*, or *joint*, *attention*). The infants' motivation to share psychological states with others culminates shortly after their first birthday. At the age of 14 months, they not only understand others as intentional agents, they also have the desire to share their own intentions with others and begin to collaborate with others (Ross & Lollis, 1987; Warneken & Tomasello, 2007). At this stage of ontogeny, infants also start to use language, which in some theoretical perspectives is seen as an inherently collaborative activity by itself (see Clark, 1996).

As described before, an understanding of others' mental states allows individuals to interpret others' actions very explicitly. Being equipped with such a sophisticated understanding, an observer can make assumptions not only about the goal the observed individual is trying to achieve, but also about the particular manner with which this individual has chosen to act toward the goal. The observer can then develop some ideas about why the individual might have chosen to achieve the goal in that particular way based on the individual's beliefs. Based on these assumptions, observers are provided with a powerful system of information about the other individuals' action. This information can be used in two different contexts – competitive and cooperative. On the one hand, it can help in competitive situations, in which an individual tries to interpret a competitor's behavior or tries to predict what a competitor might do next – something apes are already quite good at (Hare et al., 2000, 2001). In situations like these, the observing individual has an egocentric goal that it wants to fulfill (e.g., to steal food from the competitor) and plans to act to fulfill its goal for its own benefit. Acting this way might help the individual to survive and might even be adaptive for a whole species by allowing only the carrier of the best genes to reproduce ("survival of the fittest," Spencer, 1864), but it averts the development of the achievements that need more skills and power than one individual alone can provide.

On the other hand, this understanding is especially helpful in more cooperative activities, such as cultural learning and collaboration, when an individual needs to decide what it should copy from another individual or how best it can help or coordinate with others (e.g., Bratman, 1992; Sebanz et al., 2006). In cooperative activities, two (or more) individuals have the same goal they want to fulfill (e.g., to build a house), and they act to fulfill their goal for their shared benefit. When using their sophisticated understanding of other's mental states in such a way, a group of conspecifics can meet challenges that one individual alone would not be able to cope with. So, although some apes apparently have the same understanding of others' intentional actions as human infants do, they do not copy others or collaborate with others to anywhere near the same extent as humans (see Tomasello, 2019; Tomasello et al., 2005, for reviews). Although an understanding of others' intentions is necessary for human-like cultural learning and collaboration, it clearly is not sufficient.

Nonhuman great apes seem to lack the puzzle piece that turns more individualistic skills of social learning and group action into their collectively based, uniquely human counterparts of cultural learning and collaboration. For suggesting what this missing piece might be, I need to reiterate Tomasello et al.' (2005) idea that what is needed for "the uniquely human aspects of social cognition" to emerge is an interaction of a sophisticated understanding of others' intentional actions and a strong motivation to share intentions and other psychological states with others. Therefore, for an action to be performed in a collaborative manner it would not be enough to have the social-cognitive skills to know what action plan the other individual has rationally chosen in order to achieve its specific goal. What is necessary for human-like collaboration are specific social-motivational skills that, in combination with the social-cognitive skills, form shared intentionality, sometimes called "we" intentionality (Tomasello, 2019). For shared intentionality, both (or more) individuals must coordinate their action plans and commit themselves to the same goal and act according to their commitment (Gilbert, 1989; Searle, 1995; Tomasello & Carpenter, 2007).

The results reviewed above suggest that great apes seem to have the social-cognitive abilities necessary for shared intentionality: they understand others' goals, intentions, and beliefs. What they might lack are the social-motivational prerequisites necessary to transform these individual social-cognitive skills into shared intentionality that then allows cultural learning and collaboration in the narrow sense of the term to take place.

However, in humans, the roots of this unique motivation to share experiences with others can already be observed in very young infants. Infants from very early in ontogeny share emotional states with others in turn-taking sequences (Trevarthen, 1979). Studies with slightly older children suggest that 24-month-olds prefer to perform an action that reveals an effect together with an adult, although they themselves could bring about the exact same effect when performing the action alone (Gräfenhain et al., 2009). Compared to this, great apes (with enculturated ones and maybe orangutans as an exception) also make use of their understanding of others' mental states to interpret and predict others' behavior (especially in competitive situations, see above) but do not copy an actor's chosen action plan for the choice of which they cannot find a plausible reason. They do not consider these means as being important or necessary and therefore insist in using their own means to find solutions to solve a problem (i.e., emulation learning versus imitative learning). Thus, even if there were a plausible reason for the actor to choose her specific action plan that would also apply to the observer (e.g., maybe because this technique is more efficient for foraging), I would not expect mother-reared great apes (in the wild) to imitate this strategy (see Tomasello et al., 1987, for experimental evidence for this statement). Interestingly, in many instances in everyday human life, it seems on the surface to be even more adaptive *not* to copy the means of an actor but to emulate, and humans still do emulate in many occasions, as great apes predominantly do when learning socially (Tomasello & Call, 1997). The question this fact raises then is why did Mother Nature "allow" the human-innate social-motivational skills necessary for imitation (and therefore human-like culture) to evolve?

13.7 Future Directions

Because my major claim is that it is not predominant differences in social-cognitive skills but in pre-humans' distinct social-motivational abilities that laid the foundation for the development of human-like culture, future studies investigating this area should compare different species' motivational levels to share psychological states with others. Now that there is evidence that under certain circumstances chimpanzees are motivated enough to help others or cooperate in a problem-solving task (Melis et al., 2006; Warneken et al., 2007; Warneken & Tomasello, 2006, 2007), studies are needed that investigate whether great apes possess some kinds of motivations but lack the specific one to share psychological states with others. However, because the chimpanzees in Melis et al.'s (2006) study did not recruit cooperating partners when they were able to solve the task on their own, apes in general might perform differently than human children in tasks like the ones used by Gräfenhain et al. (2009).

There are two more questions of importance which deserve investigation. On the one hand, there is a need for more longitudinal studies that investigate the development of the sophisticated social-cognitive skills during great apes' ontogeny (Bjorklund, & Bering, 2003; Bjorklund et al., 2000; Wobber et al., 2014) to clarify to what degree it is similar to that of human infants. On the other hand, and this poses a huge challenge for comparative research, it would be interesting to see whether great apes also attribute the mental states they seem to understand in humans to their conspecifics. This could be possible by presenting them with (trained) great ape "demonstrators" and "models." These are central questions for future research attempting to establish the evolutionary roots of human-specific social-cognitive abilities and motivations.

13.8 Conclusion

Although some groundbreaking studies enhanced our understanding of infant and nonhuman great-ape social cognition, many more studies are needed, and we need to draw conclusions carefully. However, the evidence so far helps to narrow down species differences in understanding others' mental states – insofar as at least on the level of desires (in the meaning of preferences), goals, intentions, and beliefs, the gap between humans and nonhuman primates is smaller than was previously thought (e.g., Tomasello & Call, 1997). The perfect area to look for crucial differences between humans and nonhuman primates, in my opinion, is the field of social-motivational aspects that drive individuals' behavior. Perhaps it is the lack of high motivation or interest to share psychological states with others (and less differences in social-cognitive abilities) that made the huge difference in human evolution and enabled our (*Homo*) ancestors to collaborate, to create cultures, and so to go beyond accomplishments that one individual alone could achieve.

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Chapter 14
Fear Learning in Infancy: An Evolutionary Developmental Perspective

David H. Rakison

> "There is nothing to fear but fear itself" Franklin D. Roosevelt, 1933

14.1 Introduction

This statement, made by Franklin D. Roosevelt during his inaugural address in 1933, is poetic but not necessarily accurate. Fear is a core emotion that has an evolved function: it occurs in the face of a perceived threat or anticipation of such a threat and triggers physiological and behavioral responses that, on average, were adaptive for our ancestors. Snakes, heights, strangers, and public speaking can certainly hurt an individual—albeit in different ways—and the main functions of fear are to alert us to these threats and provide options on how to overcome or avoid them. Thus, classic fear behaviors include the flight or fight response as well as hiding or freezing in the presence of potential threats. Fear is therefore a fundamental emotion that, simply put, helps to keep individuals safe and alive. In this way, there is plenty more to fear in the world than fear itself.

Typical fears—as rated by a Gallup poll in 2001—include snakes (ophidiophobia), spiders (arachnophobia), heights (acrophobia), public speaking (glossophobia), the dark (nyctophobia), enclosed spaces (claustrophobia), flying (aerophobia), and death (necrophobia). In some individuals, the fear that is experienced is extreme—or irrational—and such cases are labeled as *phobias*. In many cases, these fears and phobias develop early in life, lead to considerable distress, and can affect the day-to-day lives of those who experience them. Moreover, the incidence of fears and phobias is not trivial: for example, the most common phobias for nonhuman animals among children and adults are of snakes (5.5%) and spiders (3.5%) (Fredrikson et al., 1996), and the average incidence of fear in children across a multitude of studies is approximately 5% (Costello & Angold, 1995).

This relatively high incidence of fears and phobias in humans—and their subsequent effect on the lives who experience them—has led researchers to ask how these

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fears develop, whether the mechanisms for learning are the same for all fears, whether fears are the same in humans and nonhuman animals, and whether they are the same in human infants, children, and adults. The traditional view of fear and phobic anxiety generally relied on the concept of *fear conditioning* (e.g., the pairing of a neutral stimulus with a negative event), while others have proposed a nonassociative model that asserts that certain fears are not learned at all and are instead innate (Poulton & Menzies, 2002). However, more recent conceptualizations of fears and phobias have taken into consideration evolutionary psychology. As a result, there is now a considerable database on the existence of a specialized fear mechanism in human infants (e.g., LoBue & DeLoache, 2008, 2010; Rakison, 2005a, 2018; Rakison & Derringer, 2008), human adults (e.g., Mineka et al., 1984; Tomarken et al., 1989), and nonhuman animals (e.g., Kats et al., 1988; Kiesecker et al., 1996). In this chapter, I describe the different theories of emotions and fear acquisition and offer an evolutionary developmental approach to the study of fear acquisition, especially for recurrent threats such as snakes and spiders.

14.2 Theories of Fear Acquisition

There are three main models to explain fear learning, and each has empirical support to some extent. As the following section will demonstrate, some of these theories are not necessarily mutually exclusive. Thus, it may be possible to acquire fears for some stimuli via one mechanism and another via a different mechanism. This is largely because it has been posited that fears for evolutionarily recurrent threats—snakes, spiders, open spaces, public speaking, for example—may be acquired via specialized pathways, whereas fears for other, more modern things—clowns, guns, cars, cigarettes, for instance—may be learned via more general pathways. In the next section, I outline the three main theoretical approaches to fear learning: traditional models, nonassociative models, and prepared-learning models.

14.2.1 Traditional Models

In a seminal psychology experiment, John Watson (Watson & Rayner, 1920) demonstrated that 9-month-old "Little Albert" could be classically conditioned to fear a white rat when it was repeatedly presented with loud noise, a fear that then generalized to other furry objects including a rabbit and a fur coat. This finding, and subsequent work on the effect of classical conditioning on fear learning, underpins the oldest models of fear learning. According to these traditional models, fears are learned through *domain-general mechanisms*—often via classical conditioning—and as such these models were powerfully influenced by the work of the behaviorist movement. I use the term domain-general mechanism here to refer to those mechanisms that are not dedicated to a single function or learning context—as is often the case with adaptive specialized psychological mechanisms—but rather can underpin learning across a wide range of inputs (e.g., visual, auditory, tactile) and across a wide range of domains (e.g., math, word-learning, categorization, space).

These traditional models were later extended by Rachman (1977), who posited that there are three domain-general pathways by which individuals can learn fear. One of these pathways involves direct learning through classical conditioning, as was the case for Little Albert. The other two pathways involve indirect learning either through observation—when an individual observes fear in another person in the presence of a fear-inducing stimulus—or through verbally transmitted information when an individual is explicitly told to fear a stimulus (e.g., telling children to stay away from dark, enclosed spaces). Rachman's (1977) model has been highly influential and remains so. Few researchers question the existence of these pathways, and there is considerable evidence to support each one. For example, experience of a traumatic event—surviving the sinking of a ship or observing a lightning strike, for instance—leads to heightened fear for stimuli related to the incident (Dollinger et al., 1984; Yule et al., 1990). Not surprisingly, there are few experimental studies with humans on the effect of conditioning on fear learning because it is not ethical to teach fears to children or adults for research purposes.

There is also evidence that humans and nonhuman animals can acquire fears through the two indirect pathways, vicarious conditioning and observational learning. In one classic study, for example, monkeys that had lived only in captivity were shown video footage of other monkeys as they demonstrated a fear response to either a snake or a flower (Cook & Mineka, 1990). Following exposure to this footage, the subjects reacted fearfully to snakes but not to flowers. Related and similar findings have been reported for a variety of other nonhuman primates such as squirrel monkeys, chimpanzees, and other apes (e.g., Joslin et al., 1964; Rumbaugh, 1968; Schiller, 1952; Yerkes, 1943). Experimental work that demonstrates observational fear learning in humans is scarce, but there are a number of ingenious studies on this topic (Askew & Field, 2007, 2008). For instance, toddlers learn to avoid toy snakes, spiders, flowers, and mushrooms after observing their mothers' negative facial expressions (Dubi et al., 2008; Gerull & Rapee, 2002), and 7- to 9-year-olds more slowly approach animals—and show greater levels of fear compared to baseline—that they previously saw paired with a fearful face than those that were paired with a happy face (Askew & Field, 2007). Finally, 12- to 20-month-old children who watched their mothers model positive behaviors toward a toy snake or toy spider showed more approach behaviors toward those toys relative to a control group (Egliston & Rapee, 2007). This final study illustrates that children can acquire *positive* responses to fear-relevant stimuli through observation.

14.2.2 Nonassociative Models

According to this perspective, Rachman's 3-pathway model fails to take into account the fact that humans have experienced the same, recurrent threats over 100,000 s of years of evolution and that one-trial learning for our ancestors during this time—being bitten to find out that an animal can kill you—would not have been adaptive. The solution, according to this model, is to add one additional pathway to the Rachman model such that fears for specific recurrent threats (e.g., snakes, heights) develop early in life and are innate and present without experience (Menzies & Clarke, 1995; Poulton & Menzies, 2002). A corollary of this approach is that fear learning relies on conditioning for evolutionary neutral stimuli and a specialized mechanism for evolutionary-negative stimuli. From this perspective, children unlearn fears—rather than learn them—through multiple positive exposures to the fear-inducing evolutionary-negative stimulus.

There is considerable evidence in the literature to support the nonassociative approach, but much of it stems from research with nonhuman animals. It has been shown, for instance, that lab-reared young salamanders react to chemical cues of predatory fish by moving to shelter (Kats et al., 1988), and that toad tadpoles reared in captivity exhibit an antipredator response to three species that naturally predate on them but not to two other predators from their environment that do not find them palatable (Kiesecker et al., 1996). This suggests that toad tadpoles possess instinctual triggers to defensive responses that are activated by cues from their coevolved predators.

At the same time, there is a relative dearth of research on whether humans' fears are derived innately. What evidence exists is mostly from retrospective analyses in which parents report the root of their child's fears. Thus, a number of studies found that parents often report that their child was fearful of water, spiders, and heights during their first experience of them (Menzies & Clarke, 1993; for a review, see Poulton & Menzies, 2002). There also exist developmental data that suggest that fears are not present early in life. Thrasher and LoBue (2016), for example, demonstrated that 6- and 9-month-olds show no physiological signs of fear (e.g., accelerated heart rate or a large startle magnitude) when presented with snakes. Moreover, in two series of studies, LoBue, Deloache, and colleagues (DeLoache & LoBue, 2009; LoBue et al., 2013) found that 9-month-olds exhibit no differences in behavior toward snakes and nonsnake animals, and that 18- to 36-month-olds show no evidence of avoiding live snakes and spiders and show an equal level of interest in threatening and nonthreatening (e.g., a hamster) animals. Thus, the nonassociative model has garnered only minimal support from research with adults and young children, and the methods used to generate evidence for it have not considered how indirect pathways to fear learning may play an important role in this process (Muris et al., 2002).

14.2.3 Prepared-Learning Model

Although the general learning model can account for how many fears are acquired—Rachman's pathways account for how 94% of children and adult attribute fears (King et al., 1998)—it fails to explain why the most common fears and phobias tend to be for evolutionarily relevant stimuli such as fear of snakes and spiders, heights, enclosed and open spaces, and blood or injury (Coelho & Purkis, 2009; Marks & Nesse, 1994; Öhman & Mineka, 2001; Seligman, 1971). This observation was in part why the nonassociative model was developed. According to associative models, fears for all stimuli are acquired through domain-general learning—classical conditioning or observational learning (Mineka & Zinbarg, 2006; Rachman, 1977)—and therefore in principle it should be equally easy to acquire fears for more or less all stimuli. Indeed, this is part of the reason why the nonassociative model was developed; that is, it is evident that human's most common fears and phobias tend to be evolutionarily recurrent threats, and one potential explanation for this phenomenon was the idea that fears for these threats need not be learned (Poulton & Menzies, 2002).

According to the prepared-learning model, no fears are present without experience. Rather, because humans coevolved with a number of recurrent threats over millions of years of evolution, selection pressures would have led to the emergence of a specialized fear-learning mechanism for these recurrent threats. Thus, although most researchers concur that fear can be acquired via Rachman's three pathways, it has been suggested that there is also a class of entities, contexts, and events that humans have evolved to fear more quickly than other things—those that are privileged were recurrent threats throughout human and prehuman evolutionary history (Öhman & Mineka, 2001; Seligman, 1971). Consistent with this view is the idea that fears are on a continuum of learning such that individuals can learn fears for evolutionarily recurrent threats with only a brief exposure, whereas they learn other fears—for nonrecurrent threats particularly—through multiple negative experiences (Marks, 2002).

There is now considerable evidence with nonhuman animals to suggest that fear learning for evolutionarily recurrent threats is indeed privileged and may occur more rapidly than for nonrecurrent threats (Seligman, 1971). For example, classic work on what is now labeled the *Garcia effect* demonstrated that rats that consumed sweetened water followed by no radiation, mild radiation, or strong radiation subsequently tended to avoid the sweetened water when it was followed by strong radiation (Garcia et al., 1955), and that rats swiftly associate gastric sickness with consumption of food or liquid but do not associate sickness with stimuli such as noises or lights (Garcia & Koelling, 1966). Both of these examples illustrate that not all associations are born equal and as such support the idea that certain inputs are privileged in learning.

I described briefly earlier one study that tested the notion that fears for specific recurrent threats are privileged in learning for nonhuman mammals; that is, captive monkeys can rapidly be taught to fear snakes but not flowers through social referencing (Cook & Mineka, 1990; for a review, see Öhman & Mineka, 2001; Mineka et al., 1984). There is also evidence that snake fears are privileged in human adults. The earliest studies on this issue used classical conditioning of skin conductance responses (SCRs), in which adults were presented with snakes, spiders, mushrooms, or flowers paired with an electric shock (Öhman et al., 1976). Following exposure, adults anticipated the electric shock for all four stimuli, but this response was harder to extinguish for adults conditioned with snakes and spiders than for those conditioned with mushrooms and flowers. Similar findings have been discovered for threatening facial expressions (Öhman & Dimberg, 1978) and when the recurrent threat was presented subliminally (Esteves et al., 1994; Esteves & Öhman, 1993).

14.3 Fear Learning: An Evolutionary Developmental Approach

The theories of fear learning encompass how all fears are acquired by humans and nonhuman animals, especially if the preparedness approach is added to Rachman's 3-pathway model (see Rachman, 2002). At the same time, key aspects of fear learning—particularly within the preparedness model—cannot be addressed without adopting a developmental approach. For example, what mechanisms or processes allow for privileged processing of specific recurrent threats? This is not a trivial question, and a number of critics of evolutionary psychology are skeptical at the notion that biases for processing can be specified in the genes. In addition, at what point in developmental time do infants or children acquire fears? Until relatively recently, most of the research on fear acquisition used nonhuman animals and adult humans as participants, but this research has shed little light on the origins of fears for recurrent threats. Moreover, a prediction of the prepared-learning model is that infants and young children should initially exhibit no fear of recurrent threats—because unlike the nonassociative model, it does not assume that fears are present without experience—but should then demonstrate rapid learning of those threats in the laboratory or the real world. In the next section, I outline my theory of how infants acquire fears for recurrent threats and then present evidence to support this view as well as the prepared model more generally.

Elsewhere, I have proposed that infants possess a specialized mechanism that has two processes or components (LoBue et al., 2010; LoBue & Rakison, 2013; Rakison, 2005a, 2018; Rakison & Derringer, 2008). The first component involves a perceptual bias that leads infants to attend to recurrent threats when they are observable in the environment; a snake is more likely to grab and hold an infant's attention than a flower. I have suggested that this perceptual bias stems from innate perceptual templates of recurrent threats—such as snakes and spiders—that cause infants to detect and attend to those stimuli when they are present. The idea of a perceptual template was initially proposed to explain why newborn infants track face-like stimuli longer than scrambled versions of those stimuli (Johnson & Morton, 1991; Johnson et al., 1991; see Bjorklund & Hart, Chap. 1, this volume); that is, it was posited that infants are born with a bias for "top-heavy" stimuli that have two blobs at the top and one blob below, akin to the eyes and mouth of a human face. In a similar vein, I proposed that infants have such a bias for objects and contexts that were recurrent threats, with snakes and spiders the most likely candidates (Rakison, 2018; Rakison & Derringer, 2008). These perceptual templates comprise a basic schema of the shape of recurrent threats and are likely similar in format to the bias for top-heavy stimuli; that is, they broadly specify their shape. Thus, a spider template likely represents a central body with legs protruding outward from it, and a snake template likely represents an elongated or coiled rope-like shape.

Because these templates represent the general shape of these objects, it is possible that infants (and older children and adults) may attend to objects of that shape in the environment that are not recurrent threats. For instance, LoBue (2014; LoBue &

DeLoache, 2011) found that adult participants detect curvilinear shapes more quickly than similar rectilinear shapes and that this ability is only moderately affected by labeling the curvilinear shapes as snakes. That an evolved specialized fear mechanism may lead to “errors” in identifying threats is consistent with Nesse’s (1990) “Smoke detection principle”: it is more beneficial for smoke detectors to activate more often than they should because the cost for not activating is higher—that is, potential death—than for activating. Likewise, specialized adaptations are designed by natural selection to trigger in the direction that increases survival and reduces reproductive costs, and humans are therefore more likely to identify something as threat (e.g., a coiled rope) because the fitness cost of not identifying such a threat would be high.

The second process in the fear mechanism is an associative-learning mechanism that causes infants rapidly—perhaps in one trial—to representationally pair the threat stimulus with an emotional and behavioral response from a conspecific (i.e., social learning) or the effect it had on the self (e.g., a spider bite) (see also Clark Barrett & Broesch, 2012). As discussed earlier, this general notion is at the core of prepared-learning theory; some fears, those for recurrent threats, are learned more easily and quickly than others. Note also that the idea of rapid learning for specific stimuli is not limited to fear learning. Infants around 18–24 months of age go through the *naming explosion* during which they accelerate considerably in their ability to learn labels. Among other things, what is believed to support this sudden acceleration is the emergence of a process called *fast-mapping* whereby infants learn labels following only one exposure to the label and referent such that they are associatively represented (Carey & Bartlett, 1978). However, that dogs (Kaminski et al., 2004) can also engage in what appears to be fast-mapping for labels suggests that such privileged learning is not limited either to humans or to only one domain.

Although this perspective captures much of the preparedness model, it goes beyond that model because it applies the idea that privileged learning is underpinned by perceptual biases—that are present without experience—that cause humans to acquire fears for some threats more rapidly than others. Others have offered similar proposals that incorporate the view that humans have early perceptual biases for threatening stimuli (Field & Lester, 2010; Kindt & van den Hout, 2001). Implicit in these other perspectives is the notion that both the biases for threats and the mechanism for learning about these threats are specialized. However, although I endorse the idea that there is a domain-specific perceptual bias for threats, it remains an open question whether the process that underpins the rapid one-trial learning often observed during fear learning is domain-specific, especially given that the same basic effect is found for language learning.

Over the last 15 years, developmentalists have started to address these issues empirically, and in the sections that follow I outline the evidence that has been garnered from this research. I begin by discussing evidence for the first component of the proposed fear mechanism—a bias to attend to recurrent threats—and then assess evidence for the second component (rapid learning for fear-relevant stimuli).

14.3.1 Attention Biases for Recurrent Threats

There is evidence to suggest that human adults may possess perceptual templates—representational schematics that are present at birth—for evolutionarily recurrent dangerous taxa, including snakes and spiders, which have reliably distinctive features (see Öhman & Mineka, 2001). New and German (2015; see also Öhman et al., 2001), for example, found that adults in an inattentional-blindness paradigm detect, localize, and identify iconic spiders and are less likely to perceive stimuli with different configurations of the same features, modern threatening stimuli such as hypodermic needle, or fear-irrelevant nonhuman animals like houseflies. Because such experiments relied on human adults, it is possible that a lifetime of experience with snakes or spiders led to the observed effects. Thus, it is necessary to demonstrate that younger individuals—children and (ideally) infants—exhibit the same basic effects as adults to confirm the idea that humans are born with a bias to attend to recurrent threats.

I have conducted a number of behavioral studies to examine whether infants possess a bias to attend to recurrent threats. The studies rely on a similar paradigm to that used in classic work by Johnson and colleagues (Johnson et al., 1991) on infants' perceptual template for faces. In one experiment, Rakison and Derringer (2008) presented 5-month-old infants with three schematic images of spiders that moved horizontally back and forth across a computer screen (Fig. 14.1). One image was a schematic spider, a second was the same schematic spider except that it had reconfigured features, and a third was a linear image of the spider that was completely scrambled. Infants' total looking time to each stimulus was recorded. In line with previous work on face tracking in newborns (Johnson & Morton, 1991), it was predicted that if 5-month-olds possess a perceptual template for spiders they would look longer at the schematic spider stimulus than the other two reconfigured stimuli; this was the pattern of looking generated by infants in the experiment. Subsequent experiments with the same design revealed that infants do not show the same effect for nonthreatening stimuli such as flowers. A final experiment tested whether

Schematic Spider

Reconfigured Features

Completely Scrambled

Fig. 14.1 Schematic spider stimuli used by Rakison and Derringer (2008)

5-month-olds' perceptual template generalizes to spiders in the real world. Infants were habituated to various color photographs of real spiders and then shown the three schematic images of spiders from the first experiment. Results revealed that 5-month-old infants showed a reversal of the pattern of looking from the first experiment; that is, they looked longer at the two reconfigured images than the schematic spider, which suggests that they generalized from the real images of spiders and found the schematic image familiar.

Isbell (2006) has argued that venomous snakes—a critical predator on many nonhuman animals throughout their evolution—were a driving force in developing the vision of advanced primates. In other words, because primates were recurrently the prey of snakes, there would have been strong selection pressures to detect snakes quickly. Thus, fear of snakes may have its origins in mammalian evolution when such threats were a prevalent and recurrent threat. In line with this idea, evidence suggests the existence in human adults of neurons in the primate medial and dorsolateral pulvinar that respond selectively to visual images of snakes (He et al., 2014; Van Le et al., 2013).

To address whether infants possess a perceptual template of snakes, I conducted similar experiments to those in Rakison and Derringer (2008) with snakes instead of spiders (Rakison, 2018). Thus, 5-month-olds were shown a schematic snake, a snake with slightly reconfigured features, and a snake that was completely scrambled (see Fig. 14.2), and their looking time was measured for each one. Infants' looking behavior for these stimuli was the same as it was for spiders: they looked longer at the schematic snake than at the other two stimuli (and equally long at those other stimuli). As in Rakison and Derringer (2008), a follow-up study determined that infants treated the schematic snake as familiar after being habituated with pictures of real snakes.

This work suggests that infants attend to an image of a snake relative to scrambled versions of the same image, but it is also important to establish that infants attend to snakes when they are presented in competition with another stimulus; that is, a perceptual template for snakes should drive infants' attention toward snakes and away from other, nonthreatening stimuli. To investigate this issue, LoBue and DeLoache (2010) showed 8- to 14-month-olds a snake and a flower side by side and measured how quickly infants oriented their head to look at them. Results revealed, as predicted by the preparedness model, that infants oriented to snakes more rapidly

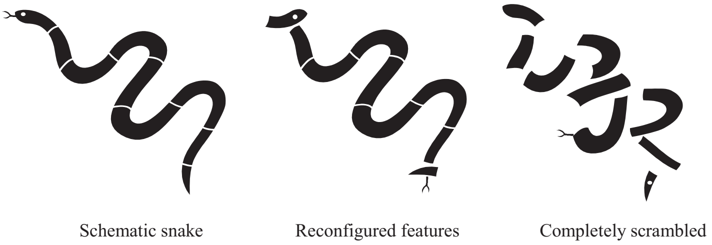

Fig. 14.2 Snake stimuli used by Rakison (2018)

than to flowers. Notably, infants also oriented more quickly to angry faces than to happy faces—an effect that holds through early childhood (LoBue, 2009), which implies that threatening stimuli more broadly may be privileged in visual attention (LoBue & DeLoache 2009).

More recently, LoBue et al. (2017) used eye-tracking to examine whether there were any developmental differences among 4- to 24-month-olds in their bias to attend to snakes. To address this question, infants were shown two images on a computer screen, one of which was threatening (e.g., snake) and one of which was not (e.g., a frog) for 1000 ms, after which the images disappeared and a probe then appeared for 500 ms in one of the two locations of the images. Results revealed not only that prior to the probe infants of all ages were more likely to look first at the snake rather than at the frog but also that infants were faster to fixate to the probe if it replaced the image of the snake than that of the frog. In a similar vein, Bertels et al. (2018) demonstrated that 7- to 11-month-olds orient more quickly to snakes than to flowers and also that detection of a snake in the visual periphery accelerates the automatic engagement of attention toward its location.

Recent electrophysiological work also suggests that the infant brain responds differently to snakes and nonsnakes (Bertels et al., 2020). The scalp electrical brain activity of 7- to 10-month-olds was measured while the infants watched sequences of flickering animal pictures (snakes vs. frogs and snakes vs. caterpillars). Results revealed that regardless of the foil (frogs or caterpillars), infants generated neural responses that were higher in amplitude and more widespread for snakes. Moreover, stronger neural activity for snakes occurred in the occipital area, which suggests that the bias to orient to snakes may be driven by their visual physical attributes. Based on these findings, the authors concluded that snake detection is underpinned by a neurobiological substrate that is functional in the first year of life, is sensitive to the physical appearance of snake, and occurs independently of prior experience with snakes.

These studies suggest that young infants may have a perceptual template for spiders and snakes. It remains an open question whether infants possess such templates for other threats. Two interesting candidates are rodents—particularly rats—and sharks because these animals typically evoke a fear reaction in humans, although they are rarely among the top 10 fears and phobias. At the same time, neither rats nor sharks predate on humans. Rats are feared not because they can physically harm humans—especially human infants—but rather because they are known to spread disease; however, because this associative link is rarely contiguous it is unlikely that selection pressures would have led to the emergence of a perceptual template for rats. Sharks, although often the center of fear-inducing media—the movies Jaws and Megalodon, for example—are responsible for relatively few human deaths each year (generally, more people die each year from falling coconuts than sharks). Thus, it is also unlikely that humans would have an evolved perceptual template for sharks. To test these predictions, 5-month-old infants were presented with schematic rodents or sharks, as well as two scrambled versions of each of those stimuli (Rakison, 2018). Consistent with the reasoning presented above, infants looked equally long at all three stimuli for both rodents and sharks. Taken together, this body of research suggests that infants may have perceptual templates for recurrent threats—snakes and spiders—but do not possess such templates for potentially dangerous animals that coevolved with humans but that rarely acted as threats to humans.

To my knowledge, the studies described above are the only ones to test whether young infants show a bias to attend to recurrent threats. An important question is whether this bias remains in place beyond infancy, because if humans possess a perceptual template for recurrent threats then this should continue to operate throughout the life span. To examine this question, LoBue and DeLoache (2008) used a *visual search paradigm*—in which participants have to find the odd-one-out in a 3 by 3 matrix of pictures—with 3-, 4-, and 5-year-old children as well as adults and with images of snakes, flowers, frogs, and caterpillars. Adults and children detected a snake among flowers more rapidly than a flower among snakes, a snake among frogs more rapidly than a frog among snakes, and even a snake among caterpillars more rapidly than a caterpillar among snakes. Follow-up studies with the same paradigm revealed that preschoolers (and adults) locate spiders more quickly among mushrooms and cockroaches than vice versa, and there is no difference in the time to find cockroaches among mushrooms and vice versa (LoBue, 2010b). Moreover, this rapid detection is accentuated if snakes are presented in a threatening pose (Masataka et al., 2010), operates for both black and white pictures of snakes (Hayakawa et al., 2011; LoBue & DeLoache, 2011; Masataka et al., 2010), and has been demonstrated in Japanese monkeys (Shibasaki & Kawai, 2009).

In sum, there is strong evidence that human infants—as well as a number of nonhuman primates—have a bias to attend to, and detect, recurrent threats such as snakes and spiders (LoBue, 2010a; LoBue & DeLoache, 2010; Rakison, 2018; Rakison & Derringer, 2008). This effect has been demonstrated in a variety of paradigms, continues through early childhood and into adulthood, and it holds, regardless of whether the recurrent threat is presented alone or in competition with a distractor stimulus. At the same time, infants do not exhibit the same bias to attend to nonthreatening inanimate stimuli such as mushrooms and flowers, or a bias to attend to nonthreatening animates such as rodents, sharks, cockroaches, or frogs. These data, especially those with infants, suggest that humans may have an evolved bias to orient to specific recurrent threats when they are in the surrounding environment. I have suggested here and elsewhere (Rakison, 2005a, 2018; LoBue & Rakison, 2013; LoBue et al., 2010) that this bias results from an innate perceptual template of those recurrent threats.

How might such templates drive attention toward threat? To address this question, LoBue and her colleagues (2014) used the visual search paradigm with adults but employed an eye-tracker to examine the factors that underpin faster fixations to threatening stimuli. They found that the effect is only present in larger matrices (3 by 3) but not in smaller matrices (2 by 2), which suggests that bottom-up factors in part drive threat detection. More importantly, they demonstrated not only that (as expected) adults fixated threatening stimuli more quickly but also that the behavioral response was faster for those threatening stimuli than nonthreatening stimuli. Thus, one way a perceptual template may cause infants (and potentially adults) to attend to threats is by not only helping them to detect the stimulus, to stay attended to it, and then to respond to it (perhaps, through a learning pathway). In this way, a perceptual template may engage the infant in both attention-getting and attention-holding (Cohen, 1972) for recurrent threats.

14.3.2 Limitations

A number of critiques have been levied at the notion that humans have a bias to detect evolutionarily relevant stimuli that were recurrent threats. For example, snakes and spiders are commonly in the top 10 fears and phobias cited by adults, and they are frequently (if not exclusively) used as the recurrent threat stimulus in psychological research on fear learning. However, although snakes likely were and currently are a threat to humans, there is little evidence that spiders are a threat to humans in modern times. Indeed, adult subjects report that spiders belong to a category of animals—along with rats and cockroaches—that are not considered dangerous to humans but are nonetheless fear-evoking (Matchett & Davey, 1991): thus, humans may fear these nonhuman animals—as well as those in a category that provokes revulsion (e.g., maggots, slugs)—due to disgust sensitivity rather than threat-relevance.

A second criticism of threat detection research relates to the fact that adults develop fears through a lifetime of experience. Thus, adults may find snakes and spiders more quickly than nonthreats in a visual search task because of their previous experience with those animals. However, although this critique cannot be addressed in research with adults, that infants and young children demonstrate the same effects as adults suggests that this bias to attend to snakes and spiders is present early in development and likely exists prior to experience with those threats.

14.4 Rapid Associative Learning for Recurrent Threats

Recall that the proposed specialized fear-learning mechanism I have outlined here has two components. Evidence for the first component—a bias to attend to recurrent threats—was outlined in the previous section. In the current section, I outline the evidence for the second component of this system whereby the recurrent threat is rapidly—potentially in one trial—associated with the appropriate response.

It is well established that infants are able to engage more broadly in paired correlation learning of two features or properties (e.g., Madole & Cohen, 1995; Rakison, 2004, 2005b, Slater et al., 1991; Younger & Cohen, 1986). This ability is present at birth, such that newborns who were familiarized to stimulus compounds—a green vertical stripe and a red diagonal stripe, for example—encoded the correlation between the two features (color and angle of the stripe) rather than each of the features independently (Slater et al., 1991). By 7–10 months of age, this ability develops—likely as a result of improving information-processing abilities—such that infants can encode correlations for features of schematic animals (Younger & Cohen, 1986). There is also evidence that for infants, at least, some correlations are privileged in a learning context. In a number of studies, I have demonstrated that infants in a variety of learning contexts will encode some of the available correlations and ignore others (Rakison, 2004, 2005b, Rakison & Poulin-Dubois, 2002; see also Madole & Cohen, 1995); at 14 months of age, infants encode relations between dynamic cues (i.e., a moving part and an object's motion trajectory) but not relations involving static cues (i.e., those involving the body of the object) (Rakison & Poulin-Dubois, 2002); at 16 months of age, infants encode relations when an agent of a causal action has a moving feature but not when a recipient does (Rakison, 2005b). This phenomenon has been attributed in part to attentional biases, such that infants are born with a preference to attend to, for example, large, moving features and objects (Rakison & Lupyan, 2008). The question of interest in this section is whether human infants demonstrate a similar capacity for learning about recurrent threats; that is, whether infants are more likely to learn some correlations—those involving recurrent threats—than others (those that do not). To date, only a small handful of studies have investigated this issue.

In one of the first studies to examine this question, DeLoache and LoBue (2009; Experiment 2) used the audiovisual matching paradigm to test whether infants would look at a snake rather than a nonthreat when they heard a fearful voice. This paradigm relies on the finding that infants tend to look at images or videos that match; for example, 5- to 7-month-olds look at a happy face longer than at an angry face when they hear a happy voice (Walker-Andrews, 1986; see also Golinkoff et al., 1987). To investigate whether infants would show the same pattern for threatening stimuli, DeLoache and LoBue (2009) showed 7- to 16-month-olds pairs of videos (Experiment 2) or still color photographs (Experiment 3) in parallel with one stimulus (a snake) and the other an exotic nonsnake (e.g., elephant, giraffe). As the stimuli were presented, a central speaker played either a fearful voice or a happy voice speaking a nonsense phrase. As predicted by the prepared-learning model, infants at both 8 and 16 months of age looked at the snakes longer when they heard a fearful voice than when they heard a happy voice, but this effect held only for the videos and not the still images. Moreover, in both studies, infants oriented to the snakes more quickly than to the other animals. Thus, even though the participants in the study likely had minimal or no experience of snakes, in the presence of a fearful sounding voice the infants oriented to the snake, suggesting that snakes may constitute privileged stimuli for fear learning.

The previous study demonstrated a bias to attend to snakes in the presence of a fearful voice, but it included no measure of learning. Thus, an important question is whether infants preferentially associate snakes and spiders with a fearful response when given an opportunity to learn. To examine this issue, I habituated 11-month-old infants to an event in which a snake or spider appeared on a screen paired with either a happy or a fearful face (Rakison, 2009, Experiment 1). During the test phase, infants were presented with a novel snake or spider—depending on which they were habituated to—paired with a different face from that seen during habituation (e.g., happy if fearful). They also saw a novel stimulus (mushroom or flower) paired with a different face from that seen during habituation. The rationale for this design was that if infants learned the pairing between face (happy or fearful) and snake or spider, they should look longer at a violation of this pairing than at a novel face with novel nonthreatening stimuli (following habituation, infants typically prefer to look at novel stimuli rather than familiar ones, Hunter and Ames 1988). The results of this experiment revealed the infants—but only female infants—looked longer at the violation of the snake or spider when they had observed it paired with a fearful face during habituation. Female or male infants demonstrated no such effect for spiders or snakes that had been paired with a happy face, and a second experiment revealed that neither female nor male infants demonstrated this effect when habituated to flowers and mushrooms paired with a fearful face (Rakison, 2009, Experiment 2).

These data suggest that female 11-month-olds, but not their male counterparts, readily associate snakes and spiders with a fearful stimulus. Why should such a sex difference exist? First, it is worth noting that adult women are four times more likely than men to experience fears and phobias for snakes and spiders, but this effect does not hold for other stimuli (e.g., injections, heights, flying) (Fredrikson et al., 1996). That infant girls are more likely than boys to associate snakes and spiders with fearful faces suggests that this difference has its foundation in an evolved specialized fear-learning mechanism. This difference would have emerged as a result of the different selection pressures on ancestral men and women: the fitness costs on women for being bitten by a snake or spider would have been greater than for men because infants and young children are less likely to survive if a mother dies than if a father dies. A competing selection pressure would have been the higher reproductive variance for men: males who are fearful would likely have taken fewer risks, would have been less effective at hunting and fighting, and would be seen as less attractive long-term mates for these reasons. Thus, fear may have been selected against in males. Of course, it is also impossible to rule out cultural influences to explain this difference. In other words, it is possible that social transmission of fears and phobias is more common or promoted among girls than boys, such that caregivers are more likely to display fear in the presence of female infants and are more likely to encourage fears of snakes and spiders in female infants (Fredrikson et al., 1997).

More recently, Hoehl and Pauen (2017) tested whether 9-month-olds preferentially associate fearful faces with recurrent threats, but in contrast to Rakison (2009) they used photographs of real faces and used brain measures rather than looking times. In the studies, infants saw a fearful or neutral face looking toward a spider or flower (Experiment 1) or a snake or fish (Experiment 2), and then they saw the spider, flower, snake, or fish alone, and their brain response was measured using event-related potentials (ERPs). Hoehl and Pauen (2017) found that 9-month-old infants attended to objects longer—as indicated by the negative central (Nc) amplitude—when paired with a fearful face, but this effect was larger for spiders than for flowers. They also found that regardless of the facial emotion of the adults, snakes generated greater Nc amplitude than fish. According to the authors, the finding for spiders supports the prepared-learning account—preferentially learning for spiders relative to fish—and the finding for snakes supports the nonassociative account. However, infants in the study showed no evidence of fear—as implied by the nonassociative account—and it may be that snakes were (and continue to be) a powerful recurrent threat such that they elicit a greater response, regardless of the facial expression with which they are paired.

14.5 Limitations

The studies reported in this section suggest that infants may preferentially associate snakes and spiders with the emotional response of a conspecific (typically fear). Thus, infants orient to spiders in the presence of a fearful voice (DeLoache & LoBue, 2008), infant girls associate snakes and spiders with fearful faces (Rakison, 2009), and 9-month-olds direct increased attention in the presence of a fearful face to spiders and to snakes more broadly. A first limitation is that, to date, there are only three studies that have assessed whether learned associations between recurrent threats and an emotion expression are privileged. Although these studies demonstrate consistent findings, more research on this issue is needed to establish the robustness of this effect as well as to ascertain to what extent this learning is privileged.

A second criticism relates to real-world application. It is assumed that early learned associations between recurrent threats and fearful expression in some cases lead to the development of fear for those threats. However, none of the cited studies with infants (or adults) actually tested fear learning itself, partly because it is not ethical to teach individuals to fear things. (Thankfully, things have changed considerably since Watson's seminal work with Little Albert.) This issue is important because there is evidence to suggest a causal relation between an individual's attention bias to threat and the development of anxiety in adults and children (Bar-Haim, 2010; Fox et al., 2007). Anxiety disorders affect up to 20% of the population (Bosquet & Egeland, 2006; Gross & Hen, 2004), and therefore this issue is far from trivial. Indeed, increased bias to threat—and subsequent learning that occurs as a result of this bias—can shape how individuals view the world and is linked not only to anxiety but to social withdrawal. Thus, it is important to establish how a bias for recurrent threats and early learning about those threats can have long-term effects on individual's mental health.

14.6 Concluding Remarks

In this chapter, I outlined the three main theories of fear acquisition. According to the traditional model, fear is learned through conditioning alone; according to the nonassociative model, fear is present without experience; and according to the prepared-learning model, fear is learned through conditioning for nonevolutionary stimuli but is learned via a different, specialized pathway for recurrent threats such as snakes and spiders. I then presented my approach to fear learning in infancy. According to this perspective, infants' fear learning for recurrent threats is underpinned by an evolved specialized mechanism that has two components. The first component—a perceptual template—orients infants to recurrent threats when they are in the environment. To support this view, I outlined a large database of evidence drawn from a wide range of methodologies that reveal that infants (as well as children, adults, and monkeys) demonstrate a bias to detect recurrent threats. The second component is theorized to be an associative mechanism that offers privileged and rapid learning to link threats with an emotional (and perhaps, behavioral) response. To support this view, I outlined a smaller series of studies but that nonetheless offer a consistent and robust set of findings.

In conjunction, the evidence presented in this chapter supports the idea that all fear learning—for recurrent and nonrecurrent threats—can be explained by Rachman's 3-pathway model combined with the prepared-learning model. The added value for the perspective presented in this chapter is that it goes some way to explain how infants—and children, adults, and nonhuman animals—have privileged processing for recurrent threats. In other words, the prepared-learning model predicts that learning is privileged for a certain category of things—namely, recurrent threats—but it does not explain how those things are privileged in processing. The theory I have offered here and elsewhere (LoBue & Rakison, 2013; Rakison 2005a, 2018: Rakison & Derringer, 2008) suggests that recurrent threats are privileged by virtue of a perceptual template that causes rapid detection of those threats, and perhaps to respond behaviorally more quickly to them (LoBue et al., 2014, 2017).

Because fear learning often occurs early in life, perhaps the only way to gain insight into this process is by adopting a developmental—and evolutionary—approach to studying this process. The evidence presented in this chapter not only supports this notion but also raises many other questions. For example, it remains to be seen to what extent learning about recurrent threats is privileged early in life because only a small handful of studies have investigated this issue. In a related vein, many of the studies outlined here used snakes and spiders as threatening stimuli, but many other recurrent threats—some of which are not animals such as open spaces, enclosed spaces, and public speaking—remain unexamined. Moreover, it is as yet unknown whether there is a causal relationship between a bias for threat and the actual development of fear or anxiety, especially in nonclinical populations. Given the sensitivity of the topic—parents are not keen to have researchers teach their infants or children to fear things—research on this question must adopt a long-term longitudinal approach to gain traction on the real-world aspect of fear learning. However, given that research on fear learning in infants is relatively novel, it is only a matter of time before the pathways for fear learning for all threats—whether they be recurrent or not—are clearly elucidated.

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Chapter 15
Jealousy and the Terrible Twos

Sybil L. Hart

Jealousy has long been recognized as a cause of intra- and interpersonal conflict. Yet, the twentieth century saw changes in the way it was construed. In parallel with western trends toward regarding it as a sign of psychopathology when manifested in adults (Buss, 2000; Buss & Haselton, 2005), jealousy came to be seen as a sign of maladjustment in children (Stearns, 1989, 2010). The transition is thought to have stemmed from demographic influences involving decreases in family size. As relationships among family members became less numerous they tended to grow more intense, resulting in a reconfiguration of family dynamics that is thought to have encouraged greater parental investment in children, which was increasingly manifested by concerns with mental health that included apprehension over jealousy (Stearns, 1989, 2010). To some extent, these concerns were outgrowths of psychoanalytic tradition in which personality is seen as being shaped during childhood through processes that involve the resolution of intrafamilial rivalry; specifically competition with a same-sex parent (Klein, 1957, 2002; Oberndorf, 1929; Sokoloff, 1947; Winnicott, 1977, 2002). Over time, the focus of attention shifted to concern over rivalry in which the competitor was a sibling rather than a parent (Adler, 1928, 1931; Foster, 1927; Levy, 1934, 1937; McFarland, 1937; Ross, 1931; Sewall, 1930). Eventually, these concerns spawned literature that included ominous depictions of acute jealousy in the context of a newborn sibling's arrival. In line with pronouncements, such as "the coming of a new baby creates a crisis, which affects all of the child's relationships – with the family and the world at large" (Levy, 1934, p. 233), jealousy in children came to be linked with psychopathology.

This notion was reinforced by Bowlby in his seminal work on infant-caregiver attachment. His volume, *Attachment and Loss: Separation Anxiety and Anger* (Bowlby, 1973), opened by discussing material that had been written by Sigmund

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Freud's daughter, Anna Freud, and Sophie Dann (Freud & Dann, 1951), in which they described six Jewish orphans' rehabilitation at the conclusion of World War II following their liberation from harrowing conditions at Tereszin concentration camp. In addition to being described as highly disturbed, the children were depicted as "strongly possessive" and "acutely jealous" (Bowlby, 1973, p. 4). Hence, the linkage between psychopathology and jealousy that had been gaining prominence in clinical literature in the fields of social work and psychiatry eventually spread to mainstream developmental psychology. There it was explained in terms of contextual influences and widely distilled as problem behavior that could be prevented or corrected by proper parenting.

The pathologized view of jealousy and views of it as the outcome of exogenous influences were preceded by a much longer tradition in which jealousy was accepted as an integral feature of human nature. Its presentation in young children was seen as a natural, if not inevitable, sort of human failing (Stearns, 1989, 2010). This charitable interpretation was expressed by Darwin (1877) in a biographical sketch of his son, Doddy; in which Darwin observed that "jealousy was plainly exhibited when I fondled a large doll, and when I weighed his infant sister, he being then 15 ½ months old" (p. 289). Interestingly, unlike other examples of Doddy's negativity that Darwin treated in a section on the emotion of *anger,* jealousy was discussed in a section on the emotion of *affection*. Nor was Doddy described as being in any way flawed or disadvantaged. To the contrary, he was portrayed as a child who was "truthful, open, and tender, as anyone could desire" (Darwin, 1877, p. 292). Thus, in contrast with subsequent work that linked jealousy with maladjustment and exogenously organized risk factors, Doddy's presentation of jealousy was interpreted as an expression of love and linked with psychological well-being and the protective influences of a privileged environment and doting caregivers.

This interpretation underlines jealousy as a phenomenon that comes in a range of forms, even in children, and the one that is omnipresent (Cicirelli, 1995), perhaps more like that displayed by Doddy, has received scant attention. This commonplace form is the focus of this chapter, and we approach it with the primary aim of ascertaining the potential influence of an endogenously organized element. The chapter starts by identifying and defining a form that can be construed as normative. Toward that end, we examine evidence that has emerged from laboratory research using infants. The normative form is then addressed toward insight into the possibility of an inherited foundation. This issue is approached by considering how it could have originated in ancestral infants under conditions that existed 200,000 to 300,000 years ago, when modern humans lived in clans of nomadic hunters and gatherers (Galway-Witham & Stringer, 2018). In a final section, we discuss jealousy's emergence as a function of ancestral infants' psychosocial, cognitive, and motor development, and we conclude with suggestions for future research. Note that throughout this chapter, infants in the 12- to 36-month age range are referred to as *toddlers.*

15.1 Jealousy Protest in Infants

Our quest for evidence of an evolved foundation of jealousy in infants begins with efforts to identify and define a form that unfolds through a normative process of development. Gesell (1906) described screaming, crying, destructiveness, and physical aggression as evidence of "violent outbreaks of jealousy" (Gesell, 1906, p. 453) in infants as young as 6 months. In his account of institutionalized infants, Renee Spitz observed that "jealousy appears in the ninth and tenth months" (Spitz, 1949, p. 146). These reports were precedents for an operational definition of *jealousy* as the infant's presentations of negatively valenced behavior in response to an eliciting event in which a beloved individual, such as a parent or caregiver, directs attention preferentially toward a third party, such as a child (Hart, 2010, 2015; Hart & Carrington, 2002). This type of definition aligns with notions of jealousy in adults (Parrott, 1991; Pfeiffer & Wong, 1989) in that its key component, that is, the feature by which it is distinguished from other negatively valenced emotions that arise from feelings of loss, is that in the case of jealousy the loss, or perceived loss, occurs at the hands of a rival.

This operational definition formed the basis of laboratory procedures and experimental methodology that sought to rule out the possibility that an infant's negatively valenced response was due to a confounding stressor, and had indeed been precipitated by a rival. This was achieved through use of a differential treatment paradigm that included control conditions which manipulated the object of the adult's preferential attention and/or the nature of the adult. In the experimental jealousy-inducement condition, the infant's mother held a lifelike baby doll while she and a stranger directed attention preferentially toward the baby doll as if it were a real infant. In the control conditions, the mother directed preferential attention toward a musical story book or the stranger directed preferential attention toward the baby doll. The validity of the eliciting condition has been upheld by evidence of continuity in infants' responses across the laboratory and home setting where jealousy has been induced by parents using a real infant (Chapman & Hart, 2017; Chapman et al., 2018; Szabo et al., 2014); perhaps not unlike the description of jealousy in Doddy, which did not seem to depend on whether Darwin had induced it by attending preferentially to a large doll or Doddy's newborn sister.

Using these procedures, laboratory studies have consistently found that infants demonstrate greater negativity in the experimental condition. In 6-month-olds, it was characterized by facial affect of sadness and interest, suggesting desire, accompanied by mother-directed gaze and forward-leaning motor agitation (See Fig. 15.1). Facial affect of fear/wariness was fleeting; when it appeared it was more prominent in females (Hart & Carrington, 2002; Hart et al., 2004).

Mobile 9- to 14-month-olds' responses in the experimental condition were characterized by decreases in play, coupled with sharp increases in efforts to retain exclusive proximal contact with mother. These efforts consisted of negatively charged bids for recouping maternal attention, such as loud vocalizations, vigorous gesturing, swiping at the baby doll, and guarding or physical intrusion between

Fig. 15.1 A 6-month-old male exhibits facial affect of sadness and mother-directed visual attention, approach posture, and motor agitation as his mother directs attention preferentially toward a lifelike baby doll as if it were a real infant. (Photo by Kenny Braun, courtesy of Sybil L. Hart, Texas Tech University)

mother and baby doll (See Fig. 15.2). These bids were interspersed with self-comforting behaviors, such as sucking fingers and clinging, to help attenuate stress-induced dysregulation (See Fig. 15.3). This type of coping mechanism was greater among infants who had older siblings, and is the only known report of a distinction between infants who do and those who do *not* have siblings (Hart, 2015; Hart & Behrens, 2013a; Hart et al., 1998a; Mize & Jones, 2012; Mize et al., 2014).

Work with 9-month-olds that examined neurophysiological substrates of jealousy found that negativity being displayed during the experimental condition was associated with approach-style anterior EEG activity (Mize & Jones, 2012; Mize et al., 2014), which is a pattern that has been associated with the emotion of anger in infants (He et al., 2010). Interestingly, this EEG pattern has also been linked with jealousy in adults (Harmon-Jones et al., 2009). Another finding that seems parallel with jealousy in adults was evidence that in the experimental condition (when the object of maternal attention was a lifelike baby doll) *versus* the control condition (when the object of maternal attention was a children's story book), increases in mothers' positive affect were associated with decreases in infants' positive affect (Hart, 2010; Hart et al., 1998a). This instance of *inversed affect sharing* seems consistent with findings on jealousy in adults where, for example, a woman's smile evokes jealousy in her husband if he perceives that the object of her smile is a rival (DeSteno et al., 2006; Sheets et al., 1997).

The experimental condition also elicited atypical patterns of response. Suggesting acute distress and reminiscent of descriptions of "violent outbreaks of jealousy" (Gesell, 1906, p. 453); some infants displayed disinhibited negativity, such as full-blown temper tantrums and hostile acts against their mothers, the baby doll, and/or

Fig. 15.2 A 10-month-old female demonstrates jealousy protests during an experimental condition in which her mother directs attention preferential toward a lifelike baby doll as if it were a real infant. (Photo courtesy of Sybil L. Hart, Texas Tech University)

Fig. 15.3 A 10-month-old male exhibits regulatory behaviors, including averted gaze, sucking fingers, and proximal contact with mother, while maternal attention is directed preferentially toward a lifelike baby doll as if it were a real infant. (Photo courtesy of Sybil L. Hart, Texas Tech University)

themselves (which is one reason why a live infant was not used as the stimulus in these studies). Other responses were characterized by a contrasting pattern marked by suppressed emotionality and behavioral inhibition. Some infants recoiled, as if in fear, while others simply remained stuck in place, as if frozen with panic. Still other atypical responses were characterized by disorganization. In some of these cases, infants displayed negativity, but not until the baby doll had been removed from the room, which was the exact opposite of the typical pattern where the rival's removal and the resumption of exclusive contact with mother were usually met by a decrease, rather than an increase, in negativity. In rare instances, an infant would approach and seek succor from an unfamiliar and impassive adult (a researcher whose presence nearby was required in case an infant's behavior could cause harm to her mother or herself) rather than her mother, which is a behavior that suggests indiscriminate friendliness and is a marker of severe emotional disturbance in infants (Chisholm et al., 1995; Zeanah et al., 2002).

Taken together, laboratory studies discovered that the prototypic response to the experimental condition is the infant's presentation of mother-directed demands for exclusive proximal contact, which occurs with stunning regularity. Such contact is accompanied by various attention-seeking behaviors for protecting exclusive access to mother, emotionality suggesting sadness, anger, and desire, and self-comforting responses for moderating levels of stress. Due to evidence that this pattern of response is triggered specifically by an infant's encounter with a rival for mother's exclusive attention, and in line with common usage of the label *jealousy* in anecdotal accounts (Gesell, 1906; Spitz, 1949) and in similarly designed laboratory research using toddlers- and preschool-aged children (Bauminger et al., 2008; Szabo et al., 2014; Teti & Ablard, 1989; Volling et al., 2002), we refer to it as *jealousy protest* (Hart, 2015; Hart et al., 1998a).

The regularity of jealousy protest's typical pattern of response establishes it as being statistically normative. Further support for this conclusion arose from evidence that it was found linked with the protective influences of secure infant-maternal attachment and maternal sensitivity. In stark contrast, atypical patterns were found associated with risk factors, including insecure quality of infant-maternal attachment, maternal depression, and maternal parenting behavior characterized by disengagement, insensitivity, and hostility (Hart, 2015; Hart et al., 1998b, 2003; Hart & Behrens, 2013a, b). Consistent with a central tenet of developmental psychopathology that knowledge of normative development is informed by knowledge of atypical development (Cicchetti & Toth, 2006) – evidence that the pattern which is statistically typical is also positively associated with protective influences *and* negatively associated with risk factors – establishes that it is the outcome of a normative process of development.

In sum, the findings on individual differences as a function of birth order, quality of attachment security, and variation in the quality of maternal socialization practices showcase learning as a mechanism that plays a role in determining *how* jealousy protest unfolds. However, these influences do not determine *if* it unfolds. This observation led us to attribute jealousy protest to an innately based temperamental characteristic that we refer to as *nascent jealousy* (Hart, 2010, 2015; Hart & Carrington, 2002).

15.2 The Psychological Weapon

Like other early and easily acquired motivational states (Nesse, 1990; Ohman & Mineka, 2003), nascent jealousy is construed as an outcome of psychological preparedness that was shaped by events that took place as modern humans arose. As for other evolved features of personality, it is likely to have been sculpted over deep time by selection pressures (Panksepp, 2010). The nature of these pressures has been recognized in light of thought in evolutionary developmental psychology (Bjorklund, 2021; Bjorklund & Yunger, 2001; Bjorklund, Chap. 2, this volume) that, as an evolved behavior, jealousy protest can be unpacked by examining ancestral habitats for life-threatening events that would have been encountered routinely by ancestral infants, and by then asking how these infants' presentations of jealousy protest would have been adaptive toward managing that particular threat. These notions have called attention to the fact that jealousy protest unfolds in infants just as the 9-month period of human gestation concludes. Dovetailing between the conclusion of the human gestational period and the onset of jealousy protest has led us to interpret jealousy protest as a mechanism that was compelled by the life-threatening consequences of usurpation by a newborn sibling which could have been met by infants following interbirth intervals (IBIs) as brief as 9 months (Hart, 2016a).

Of course, mortal threats were likely to have been precipitated by events other than usurpation. Migration exposed humans to a wide range of conditions that entailed any number of mortal dangers (Simpson, 1999; Simpson & Jaeger, Chap. 11, this volume). In addition to environmental dangers involving predation and accidents (Bowlby, 1969/1984), humans would have encountered extreme climate conditions that resulted in floods, drought, and famine, as well as natural disasters, such as epidemics and infestation, in addition to social conditions that posed threat of conflict and displacement. However, it seems unlikely that any of these sorts of dangers could have been responsible for nascent jealousy. As consequential as any might have been, none could have been encountered as regularly by ancestral toddlers as the birth of a sibling.

Insight into this type of recurrent threat can be approached by appreciating the scale of its impact on toddlers' vulnerability to morbidity and mortality. In extant traditional societies, where individuals live in bands of nomadic hunter-gatherers that resemble those of our evolutionary ancestors, almost one half of children do not survive. Mortality rates among children are highest among those under 5 years of age (Christian, 2008; Volk & Atkinson, 2008, 2013), and over half of those deaths involve toddlers in the 12- to 23-month age range. In fact, the probability of dying during the second year can match or even exceed the probability of dying in the first year (Dyson, 1977), which can be as great as 40% (McDowell & Volk, Chapter, 5, this volume). In such settings, the leading cause of death is infectious disease, and since malnutrition adds to the burden of disease, malnourished children are especially susceptible to disease, which can account for mortality rates that are 7 times greater than those of well-nourished children.

Due to their immature digestive and immune systems, and the fact that these systems are strained further by malnourishment, toddlers are exceptionally vulnerable to malnutrition (Alberda et al., 2006; Christian, 2008; Dyson, 1977; Khoshed et al., 2000; Worthman, 2010). Malnutrition in toddlers is often attributable to a sequence of events that starts with close birth spacing. In regions where food scarcity is prevalent, suboptimal outcomes have frequently been observed in neonates and young infants as consequences of prenatal conditions *in utero* during preceding IBIs (Conde-Agudelo et al., 2006; Dadi, 2014; Kozuki & Walker, 2013; Whitworth & Stephenson, 2002). Importantly, some have also discovered suboptimal outcomes as consequences of *subsequent* IBIs that start at parturition. These intervals culminate upon a subsequent birth, and so they vary in duration. Those which are short in duration, and result in close birth spacing, are especially hazardous for toddlers (Bøhler & Bergström, 1995, 1996; Bøhler et al., 1995; Hailemariam & Tesfaye, 1997; Koenig et al., 1990; St. George et al., 2000). For example, mortality rates of toddlers in Kenya were found doubled among those who had encountered a sibling's birth by the age of 20 months (Fotso et al., 2013). Work in Senegal reported a fourfold increase in mortality rates among 2-year-olds if their mothers had already given birth to a sibling (Ronsmans, 1996). Research conducted in Bangladesh found that malnutrition was increased among toddlers who had encountered the birth of a sibling by their second birthday (Khoshed, et al., 2000).

Dire outcomes of short subsequent IBIs are most prevalent in environments marked by acute food insecurity where it is customary for toddlers to be weaned prior to a sibling's birth. Deprived of the nutritional and immunological benefits of breast milk in settings where healthy substitutes for breast milk and effective health systems are scarce, prematurely weaned toddlers succumb to morbidity and mortality (Christian, 2008; de Onis, 2008; Jakobsen et al., 2003; Konner, 2010; Nath et al., 1994; Thapa et al., 1988). These tragic outcomes occur with such regularity that the life-threatening severe acute malnutrition disease, *Kwashiorkor*, takes its name from language spoken in Ghana that literally means, "the disease the deposed baby gets when the next one is born" (Williams et al., 1935, pg. 1151). In a similar vein, it seems likely that ancestral toddlers were not fully weaned until a subsequent IBI had ended or was near conclusion. At that juncture, substitutes for mothers' milk were limited or entirely nonexistent (Dettwyler, 1995; Ellison, 1995). It would take hundreds of millennia for even substandard substitutes to become available in large scale through the advent of agriculture and animal husbandry during the Neolithic era (Bocquet-Appel, 2011; Davis, 1986).

Until that era, allomaternal breastfeeding would have been an option, but only on a limited basis. The hunter-gatherer clans where modern humans lived were thinly populated (Eibl-Eibesfeldt, 1989; Narvaez et al., 2014), and so lactating mothers could not have been numerous. Moreover, allomaternal caregiving was rarely provided to the detriment of biological offspring (Hrdy, 2007). Thus, as in harsh contemporary settings (Gray et al., 2002; Lancy, 2015), the few lactating mothers who may have been present would have been reluctant to share their precious breast milk with nonbiological offspring. Indeed, given the metabolic demands of breastfeeding two children at the same time, many contemporary traditional societies prohibit suckling more than one infant at a time. In some, giving birth to twins or the existence of an unweaned toddler has been linked to infanticide. In these cases, an undernourished mother can feel compelled to sacrifice one of her offspring in order to keep from placing both at risk of malnutrition (Daly & Wilson, 1988; Lancy, 2015; Scrimshaw, 1984). It seems likely that similar perils and prohibitions were in effect in ancestral societies. Given that these customs would have kept an ancestral mother from suckling an additional biological child, it seems even less likely that she would agree to breastfeed an additional *non*biological child. Overall, it must have been unusual for ancestral women to divide their breast milk among biological or nonbiological offspring (Hart, 2016a; Chap. 7, this volume).

This had implications for ancestral infants' relationships with their mothers who were sources of a constellation of salient proximate stimuli associated with breastfeeding (Hart, Chap. 7, this volume). In addition to pleasure of satiety and physical well-being, the constellation included enjoyment of breast milk's sweet taste, intimacy of skin-to-skin contact, as well as comfort of heat transfer and feelings of safety due to the common practice of breastfeeding while co-sleeping during night time hours when heat loss and feelings of vulnerability would have been exacerbated by darkness and cold. Because bed sharing was practiced universally by breastfeeding dyads, and because physical contact is an inherent feature of lactation, ancestral infants must have experienced proximal contact with their mothers for substantial amounts of time each day. Given the importance of proximal contact to attachment formation, affectional ties between mother and infant (Ainsworth et al., 1978; Bowlby, 1969/1984) would have been guaranteed by lactation, thereby ensuring that mothers were sources not only of breast milk but also of affection. Furthermore, by also being an exclusive relationship, the bond of affection could have endowed infants with feelings of "specialness" (Cohen, 1974, p. 207). This construct has been viewed as a core feature of the construct of attachment (Cohen, 1974) that is thought to characterize nurslings' experiences of the breastfeeding relationship (Bottorf, 1990) since it is still the case that women usually breastfeed only one infant at a time (Hart, 2016a; Chap. 7, this volume).

Conceivably, history of exclusive access to a steady source of physically and psychologically pleasurable care endowed infants with expectations of continuing to have exclusive access to their mothers for breast milk that, over deep time, co-evolved with expectations of continuing to have unrivaled access to mother herself along with exquisite sensitivity to violations of those expectations. Support for this suggestion can be derived from evidence that ancestral infants were endowed with cognitive capacities that enabled the formation of expectations with regard to the nature of upcoming events (Buttelmann, Chap. 13, this volume). Indeed, infants form expectations about upcoming desirable events, and when these are violated, as in situations that involve goal blockage, they display anger or sadness (Lewis & Ramsay, 2005; Lewis et al., 1990). They also form expectations regarding the nature of social exchanges. Drawing on history of interactions with caregivers, they form expectations with respect to the nature of upcoming care. By the age of 9 months, infants are able to process triadic social exchanges (Buttelmann, Chap. 13, this volume; Tomasello, 2019), and so they are able to form expectations about the nature of upcoming care that is to be directed toward infants other than themselves (Fivaz-Depeursinge et al., 2005; Hamlin et al., 2007; Jin et al., 2018). Interestingly, violations of such expectations precipitate disturbances (Gekoski et al., 1983; Mcquaid et al., 2009; Mesman et al., 2009) that are especially pronounced in infants with history of skin-to-skin contact with their mothers (Bigelow & Power, 2012).

Consequently, it seems tenable that by the age of 9 months, ancestral infants' cognitive capacities allowed them to process history of maternal caregiving so as to have formed expectations of exclusivity in the infant-maternal relationship. These capacities would have also supported the ability to process triadic social exchanges involving mother and another infant, and to interpret maternal caregiving toward another infant as a violation of those expectations. Hence, we have proposed that ancestral infants' expectations of exclusive access to their mothers represents the ultimate foundation of nascent jealousy, and violations of those expectations, typically upon the birth of a sibling, compelled adaptations resulting in jealousy protest, a behavioral mechanism, also known as a "psychological weapon" (Trivers, 1974, p. 249), for protecting exclusivity in the infant-maternal relationship (Hart, 2016a, b).

15.3 Jealousy Protest and the Attachment System

Jealousy protest was not the only mechanism for managing the consequences of usurpation. It has been construed as part of an arsenal of mother-directed protests that unfolded in tandem (Hart, 2018; Chap. 7, this volume). The arsenal would have included weaning distress, defined as protest behavior that is deployed by nurslings to impede breastfeeding discontinuation. Weaning distress by 12-month-olds was observed in Uganda by Ainsworth and Tracy (1972) who found it "as great a trauma as traditional psychoanalysts have always claimed weaning to be… They behaved like children after a traumatic institutional separation" (pp. 7–8). In modern Western settings where breast milk substitutes, such as commercially available formulas and easily digestible complementary foods, are readily available and can be delivered to infants by caregivers other than mothers, weaning distress is rarely as intense. This reality informed Ainsworth's practical decision to turn attention from weaning distress to separation distress, a caregiver-directed presentation of protest behavior that was more accessible at the time and place of her writing (Bowlby, 1973; Heinicke & Westheimer, 1966; Robertson & Robertson, 1971). Through attention to individual differences in infants' responses to mothers' departure, Ainsworth identified a normative pattern, which came to be recognized as secure attachment, and two atypical patterns, insecure-avoidant and insecure-resistant attachment (Ainsworth et al., 1978).

Separation protest is presented in a manner that is remarkably similar to jealousy protest. Both patterns of protest are caregiver directed. They also match in terms of their affective tone, the timing of their unfolding, and the ways in which typical and atypical variations are organized and patterned in relation to risk and protective influences. Such commonality has led to conceptualizing jealousy protest, like separation protest, as a member of a class of caregiver-directed behaviors, known as the attachment system. The system is theorized as having been compelled by altricial infants' dependence on caregivers' resources for survival due to infant vulnerability to mortal threat (Bowbly, 1969/1984), which is a concept that has been interpreted in light of attention to the timing of its unfolding. Its onset in accord with the 9-month period of human gestation points to the possibility that the mortal threat responsible for the system's unfolding was the birth of a sibling (Hart, 2016a, 2018; Chap. 7, this volume).

Oddly, the overlaps between jealousy protest and separation protest have led some to overlook distinctions. For example, in a volume on attachment and bonding in which Thompson and associates (2005) listed several scenarios involving behavior problems that are common among young children, the list ends with a description of protest behavior provoked by favoritism. To explain it, the authors state, "we might colloquially call the latter 'jealousy,' the activation of attention-seeking behaviors" (Thompson et al., 2005, p. 355, quotes in the original). In our view, narrow focus on jealousy protest's outward appearance, that is, discounting it as simply another example of "attention-seeking behavior," dismisses critical distinctions that pertain to factors that underlie its function and adaptiveness (Campos et al., 2010; Frijda, 2004, 2016). Whereas the function of an attachment behavior other than jealousy protest is to access a primary caregiver's resources by maintaining proximal contact with the caregiver (Bowlby, 1969/1984), jealousy protest aims to retain *exclusive* proximal contact with the caregiver. The difference between exclusive *versus* nonexclusive contact with mother was not lost on ancestral toddlers. As we have shown, proximal contact with mother could still have life-threatening consequences for toddlers – if it was shared with a newborn sibling.

15.4 The 9-Month Revolution

The infant's capacity to form expectations of exclusivity arises among a number of skills in social cognition that account for a transformation by the end of the first year (Moore & Dunham, 1995; Saarni et al., 2006) that is considered to be of such magnitude that it is known as the 9-month social-cognitive revolution (Tomasello, 1999, 2019). A key development involves the capacity for *joint attention*. This requires that an infant is able to look where an adult is looking by focusing on the adult's eyes, to attend to movement of the adult's gaze, and to follow it toward the object of the adult's visual attention. At this point, shared attention has been achieved, which facilitates the infant's capacity to process triadic exchanges. It also enables *social referencing*, which requires not only the ability to be directed to the object of an adult's gaze but also the ability to be informed by the cues that the adult directs toward that object. For example, Boccia and Campos (1989) found that 8.5-month-olds' reactions to a stranger depended on their mothers' facial affect expressions when the stranger entered the room, suggesting congruence between maternal and infant behavior as a consequence of the infant's ability to learn from the adult simply by observing social signals, such as smiling or frowning.

Reciprocally, infants of this age have the ability to draw an adult's attention to objects that are of their own interest. Toward this end, they establish eye contact with the adult and then lead the adult's gaze toward the object they find of interest. They also exhibit communicative gestures, such as pointing to an object, and pantomime, such as reaching toward an adult with outstretched arms, raised as if to say, "pick me up" (Boccia & Campos, 1989; Moore & Dunham, 1995; Tomasello, 1999).

These skills in social cognition enable the infant's presentation of jealousy protest, which begins by tapping the capacity for joint attention so that an infant's attention can be directed correctly to a third party, and can recognize that the third party is a baby. Infants must then be able to process the cues that the adult directs toward the baby. In order to arrive at jealousy protest, infants do not simply mirror adult affect, as in affect sharing, nor present congruent behavior as in social referencing. Rather, they must process the adult's affect cues in light of their own expectations. This requires that they take into account the fact that the cues are being expressed by someone who is a primary caregiver and are being directed toward a baby, at which point the cues are interpreted as representing a violation of infants' expectations of exclusivity. This, in turn, enables *inversed affect sharing*, which is illustrated in Fig. 15.4, where a mother's expression of delight coincides with her infant's expression of displeasure.

Jealousy protest also requires that an infant's experience of displeasure can be communicated to an adult. Drawing on his skill in the use of gaze, the infant in Fig. 15.4 looked directly toward his mother's eyes in an attempt to establish distal contact. At the same time, he communicated through gesture by reaching toward his

Fig. 15.4 A 10-month-old male exhibits inversed affect matching whereby he expresses displeasure as his mother expresses delight over a lifelike baby doll. (Photo courtesy of Sybil L. Hart, Texas Tech University)

mother with one outstretched arm, waving it as if to say, "hey, look at *me*!" while placing the other hand on her knee, using touch to establish proximal contact as if to say, "we're still connected." Compared with unregulated presentations of jealousy protest, including melt downs colorfully depicted in clinical accounts (and also documented in laboratory research), jealousy protest's normative form is sophisticated and by incorporating skills in emotion regulation, as illustrated in Fig. 15.3, it is also measured.

The skills involved in the social-cognitive revolution are associated with another monumental transition, one that involves independent locomotion (Anderson et al., 2013; Campos et al., 2000). By the age of 9 months, most infants are able to crawl. With new ways to explore and engage the world, infants are exposed to an expanded range of experiences that precipitate developmental cascades. In addition to facilitating advances in spatial cognition and memory, independent locomotion leads to experiences that stimulate social and emotional development (Anderson, 2018; Campos et al., 2000; Clearfield, 2011). Indeed, they enable both exclusive and non-exclusive forms of proximal contact with mother, behaviors that are central to jealousy protest and separation protest and to formulation of the attachment system (Bowlby, 1969/1984; Hart, 2018).

Paradoxically, experience that is enabled by independent locomotion has also been implicated in a reconfiguration of the infant-maternal relationship, a transformation that has been described as "a major transition toward independence from caregivers" (Anderson et al., 2013, p. 14). Inquiries into upright locomotion found that the onset of the ability to walk is associated with increases in infant-initiated encounters, including increases in interaction time with mother (Biringen et al., 1995; Clearfield, 2011; Karasik et al., 2011) that are characterized by a rise in behavior described as "testing of wills" (Biringen et al., 1995, p. 511). These findings call to mind early clinical reports (Gesell & Ilg, 1943; Levy, 1953) of toddlers' noncompliant and oppositional behavior that Gesell and Ilg (1943) famously characterized as the "terrible twos." Their reports were later substantiated by Kopp (1992), who observed that maternal requests for cooperation were met by 15- to 48-month-olds demonstrating temper tantrums and resistant behaviors in the form of refusals and off-task negotiations, as well as crying that peaked in the second year.

Reports of this nature spawned decades of investigative attention. In addition to treatment in clinical literatures, where problematic aspects of toddler behavior are seen as maladaptive, a growing body of research has been conducted by developmental psychologists who find that some aspects of toddlers' troublesome behaviors are not maladaptive (Calkins & Williford, 2009; Hughes et al., 2020; Kochanska et al., 2015; Nucci et al., 1996; Roberts et al., 2018). Following theorists, such as Erikson (1963) and Mahler (1979), and with increasing insight into bidirectional influences in the infant-maternal relationship (Kochanska & Aksan, 2004; Lewis & Rosenblum, 1974), troublesome behaviors that reflect agency and autonomy vis-à-vis the infant-maternal relationship reflect the idea that as they enter the second year, infants are not merely passive recipients of adult directives. As Baillargeon and associates point out, "one of the most important developmental issues facing the toddler in the second year of life is to maintain 'connectedness' with the caregiver while carrying his or her own inner aims and goals. Hence, toddlers' deliberate noncompliance to parental requests, directives, and prohibitions is not, in and of itself, necessarily maladaptive, and many authors have stressed its adaptive nature" (Baillargeon et al., 2011, p. 429).

In line with this formulation, the stance shown by the infants in Figs. 15.2 and 15.4 illustrates jealousy protest as behavior that requires that infants have acquired the ability to operate as autonomous agents who are able to act assertively as sources of influence during bidirectional exchanges with their mothers, including those that are confrontational. Emboldened by being equipped with these capacities, infants as young as these 10-month-olds are able to "stand up" for themselves, both literally and figuratively.

The origin of the 9-month revolution in social cognition has been attributed to an adaptation that was compelled by children's ongoing need for care once weaning came to conclusion (Tomasello, 2020), at which point these skills would come into play toward enabling sociability that would be applied toward soliciting care from caregivers other than mother (Hrdy & Burkart, Chap. 8, this volume). Indeed, the increases in social interactions that emerge with infants' growing mobility and autonomy also include exchanges that are positive in tone (Biringen et al., 1995; Brownell & Kopp, 2007; Clearfield, 2011; Karasik et al., 2011). Yet, ancestral 9-month-olds would not be fully weaned before the age of approximately 36 months, which was several years in the future, and so the abrupt onset and earliness of the 9-month revolution in social cognition is perplexing. A possible explanation can be approached by noting that the timing of its onset coincides not only with a milestone in socioemotional development that involves the unfolding of infant-caregiver attachment (Bowlby, 1969/1984) but also with a milestone in motor development marked by the onset of independent locomotion (Campos et al., 2000). A parsimonious explanation for convergence in timing during the final quarter of the first year would highlight a selection pressure that unifies these milestones in socioemotional, sociocognitive, and motor development.

As we have shown, advances in each of these areas are requisite to the 9-month-old's ability to address usurpation. Socioemotional development is responsible for the formation of a valued relationship, namely infant-maternal attachment, at which point indiscriminate sociability gives way to specific preferences for attachment figures (Bowlby, 1969/1984), much as jealousy protest is found greater when mother, rather than a stranger, directs preferential attention toward a lifelike baby doll (Hart et al., 1998a). Jealousy protest also requires skills in social cognition. These underlie the infant's ability to form expectations with respect to the nature and direction of maternal caregiving and insight into violations of such expectations, as well as joint attention, communicative gesture, and the ability to grapple with a triadic social context so as to arrive at inversed affect sharing. Finally, it calls on skills in self-produced locomotion. These enable efforts to regain exclusive proximal contact with mother, which is essential to infants' efforts to defend against usurpation, and toward enhanced sense of agency and assertiveness by which such efforts are invigorated.

The fact that each of these milestones in socio-emotional, socio-cognitive, and motor development enables jealousy protest may not be coincidental. Nor is it likely to be coincidental that each does so by an infant's 9th month, just as the 9-month period of human gestation concludes along with guarantee of exclusive access to mother. We propose that these milestones in development came about in tandem as *ontogenetic adaptations* (Bjorklund, 1997, 2015; Chap. 2, this volume) to threat posed by the birth of a sibling. Each of the skills involved would have served adaptively by enabling jealousy protest's functionality as a mechanism for defending against the life-threatening consequences of usurpation, and did so following IBIs as brief as 9 months so as to prepare infants for managing a source of threat that would became increasingly imminent as the second year of life approached. Presumably, infants in whom these skills failed to unfold in time were among the one half of children who did not survive (McDowell & Volk, Chap. 5, this volume; Volk & Atkinson, 2008, 2013).

15.5 Future Research: Beyond the Terrible Twos

By the age of 36 months, ancestral infants would have encountered monumental changes in psychosocial functioning that were precipitated by physical maturation. These involved a manner of development that was observable – the eruption of molar teeth – and growth that was *not* observable – maturation of infants' digestive and immune systems, which lessened their reliance on breast milk for nutrition and passive immunity to disease (Hart, Chap. 7, this volume). The appearance of full dentition would have been interpreted by ancestral mothers as a sign that their infants' metabolic requirements could be satisfied without breastfeeding, which prompted them to bring weaning to conclusion. The nonobservable developments would have allowed mothers to do so without causing serious harm to their children's chances of survival (Dettwyler, 1995; Humphrey, 2010; Kennedy, 2005; Locke & Bogin, Chap. 6, this volume; Stuart-Macadam, 1995; Tsutaya & Yoneda, 2015). At this juncture, vulnerability to malnutrition and morbidity would have been diminished – along with weanlings' dependence on maternal caregiving – and so exclusive access to mother was less likely to be a matter of life or death (Hart, Chap. 7, this volume). Thus, it is unclear whether jealousy protest continued to play a role in 36-month-olds as it had since they reached the age of 9 months, when guaranteed access to mothers' milk expired.

Some insight into nascent jealousy's continuing role has come to light through longitudinal research on continuity in children's responses to differential treatment. Studies that explored presentations of jealousy protest in toddlers and preschoolers following a sibling's birth found that their responses did not differ from those that they had exhibited prior to the sibling's arrival in a laboratory procedure which took place during their mothers' final trimester of pregnancy (Chapman & Hart, 2017; Chapman et al., 2018; Szabo et al., 2014). Such evidence of stability seems to suggest that nascent jealousy continues to exert influence beyond infancy.

It is also notable that evidence of jealousy protest has been documented in laboratory studies where it was induced in infants, toddlers, and preschoolers by mothers directing attention preferentially toward siblings (Teti & Ablard, 1989; Volling et al., 2002); twins (Gewirtz & Pelaez-Nogueras, 1999); younger, older, and same-aged peers (Bauminger, 2010; Bauminger et al., 2008; Draghi-Lorenz et al., 2001; Masciuch & Kienapple, 1993); and spouses (Cummings et al., 1981). It has also been observed in settings where differential treatment was exhibited by fathers (Miller et al., 2000; Szabo et al., 2014; Volling et al., 2002). These studies were conducted in the United States, the Netherlands, the United Kingdom, and Israel, by different teams of researchers, using samples from different social classes. The unequivocal results uphold the idea that jealousy is an omnipresent phenomenon among siblings (Cicirelli, 1995), and that exclusivity is a feature of valued relationships that extend beyond the infant-maternal relationship and reaches across cultures and social classes, which suggests that it is a robust phenomenon. Such robustness lends weight to thought that children's sensitivity to differential treatment by a parent is to some degree innately based. We believe that future research on children's responses to differential treatment that incorporate longitudinal approaches stands to yield insight into nascent jealousy as a mechanism that continues to function across age and valued relationships among children past the age of 36 months.

Of course, such approaches will find that presentations of jealousy protest differ with child age. Evidence suggests that it also differs with marker variables, such as gender and birth order (Hart & Behrens, 2013a; Hart et al., 2004), and depends on whether it is elicited by mother *versus* father (Miller et al., 2000; Szabo et al., 2014; Volling et al., 2002), and with experiences related to qualities of maternal caregiving (Hart et al., 1998b, 2003). These findings point to the contributions of child characteristics involving maturation of socioemotional, cognitive, and motor functioning, as well as contextual influences, such as parenting practices. Continued investigative attention to the exceptionally wide range of individual differences that result stands to help isolate endogenous influences from those which are organized by exogenous influences.

Efforts to address individual differences also stand to establish an empirical basis for defining a form of jealousy in children which can be upheld as normative. In addition to illuminating a feature of infants and children that is ubiquitous, yet poorly understood, doing so opens possibilities for addressing innately based aspects of jealousy that help account for its enduringness beyond its roots in ancestral settings. We believe that work along these lines will shed light on nascent jealousy's origin within the context of exclusive infant-maternal relationships, as well as the pathways along which it unfolded in an adaptive fashion in children in ancestral settings, where they navigated complex social environments, marked by multiple supradyadic relationships that called upon skills in both cooperation (Hrdy, 2005; Hrdy & Burkart, Chap. 8, this volume; Tomasello, 2020) and competition (Bjorklund & Pellegrini, 2002; Myers & Bjorklund, 2018; Trivers, 1974).

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Chapter 16
Caring for Others: The Early Emergence of Sympathy and Guilt

Amrisha Vaish and Tobias Grossmann

Humans have evolved to be highly social and cooperative beings. Our survival and success depend on living and cooperating with one another, such as by helping people in need, working together to build shelters and find food, assisting each other with childcare, and so forth. This interdependence is argued to have come about in our evolutionary history in response to environmental pressures that required humans to band together, collaborate, and cooperate to achieve the most fundamental tasks (Tomasello, 2016). Our reliance on others meant, in turn, the need to ensure the well-being of those with whom we were – or could potentially be – interdependent.

Although this account explains human prosociality at the *ultimate level* (i.e., why prosociality emerged), it does not do so as the *proximate level* (i.e., what causes an individual to behave prosocially). After all, *prosocial behavior* involves a greater loss for the actor, who typically invests resources such as time, energy, or material resources, than for the receiver, who gains benefits without having invested their own resources. This raises a vital question: If individuals who act prosocially stand to lose more than the individuals whom they benefit, how can prosocial behavior be maintained? Why would an individual ever put aside their selfish interests to benefit others?

One part of the answer is that natural selection has favored a wide range of psychological adaptations that help us solve this dilemma at the proximate level. In particular, we have evolved emotional mechanisms that help us detect and respond prosocially toward those who need help or are suffering, thereby protecting the well-being of those whom we (might) rely on (Fessler & Haley, 2003; Frank, 1988). This view aligns with the functional approach to emotions more generally, wherein emotions are seen as adaptations that motivate us to behave in ways that help us solve challenges of adaptive and social import (Campos et al., 1989; Darwin, 1872;

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Keltner & Haidt, 1999; Nesse, 1990). We further propose that these emotional mechanisms appear early in ontogeny and, thus, allow even the youngest members of our species to promote others' welfare and thereby foster cooperation (Bjorklund, 2018; Vaish & Hepach, 2020).

Our focus in this chapter is on two emotional mechanisms that we argue are essential for this purpose: sympathy and guilt. *Sympathy* involves feeling concern for those in need or distress, and it motivates us to alleviate the need or distress of those individuals (Eisenberg et al., 2006). Thus, sympathy moves us to promote the welfare of those with whom we are or could be interdependent. We review recent evidence demonstrating that, in contrast to what has long been believed, infants experience sympathy for others from the very first postnatal year, and this sympathy motivates their prosocial behavior by the second year. Moreover, by the second year, children respond with sympathy that is flexible and appropriate to the situation, rendering sympathy a reliable and powerful prosocial mechanism from early on.

Guilt is prototypically experienced when one has *caused* another's need or distress and promotes reparative and prosocial behavior toward that individual (Hoffman, 2000; Vaish, 2018). Thus, guilt not only promotes others' welfare but additionally repairs ruptures in our cooperative relationships. We review evidence that guilt serves these critical functions by the third year of life, thereby enabling even young children to safeguard valuable relationships. We end the chapter with caveats to our account and open questions and predictions that emerge from the evolutionary account of early sympathy and guilt.

16.1 Sympathy

Perhaps the most foundational affective mechanism underlying prosocial behavior is empathic responding, which includes *empathy* (an affective response to another's emotional state and congruent with the other's emotional state) and sympathy (the feeling of concern about the welfare of another person in need or distress) (Batson, 1991; Eisenberg et al., 2006; Hoffman, 2000; Marsh, 2015). Though empathy and sympathy are related processes, they are separable, and it is sympathy rather than empathy that is linked to prosocial action (Bloom, 2017; Jordan et al., 2016).

One major proponent of empathic responding as an evolved altruistic motive is Martin Hoffman, who argued that such responding is a species-wide phenomenon that gives observers quick and direct access to the suffering of others and motivates prosocial behavior to alleviate that suffering (Hoffman, 2000, 2007). Hoffman further laid out an influential developmental account in which he proposed that empathic responding is rooted in the emotional contagion seen soon after birth, wherein infants automatically cry in response to other infants' cries (e.g., Sagi & Hoffman, 1976; Simner, 1971). Around 12–14 months of age, infants show "egocentric empathic distress," in which they respond to another's distress as if they themselves were in distress. This is argued to occur because, although infants at this age can feel empathic distress, they still lack a clear differentiation between self and other (Hoffman, 2000). Hoffman proposed that true empathy emerges in the second half of the second year, when children more fully differentiate between self and other and thereby understand that others are separate beings (as evident in their capacity to recognize themselves in the mirror; Lewis et al., 1991). With this important cognitive development, toddlers realize that others have independent inner states, and they now begin to show not only empathy but also sympathy. Thus, toddlers often respond to those in distress with facial and verbal expressions of sympathy and prosocial actions such as helping and comforting, and their expressions of sympathy predict how prosocial they are (Bischof-Köhler, 1991; Eisenberg & Fabes, 1998; Svetlova et al., 2011; Zahn-Waxler et al., 1992).

Moreover, this early sympathy is genuinely prosocial: Young children's primary motivation appears to be to see the person in need be helped. For instance, a series of studies has used *pupillometry* to tap into toddlers' internal arousal upon seeing someone in need. Pupillometry is the measure of the dilation of the eyes' pupils. Systematic changes in pupil size reflect activation of the sympathetic branch of the autonomous nervous system and are indicative of experienced internal arousal (Bradley et al., 2008; Hepach & Westermann, 2016; Loewenfeld, 1993), and have recently been shown to index children's motivation to help. Specifically, by 1.5–2 years of age, children's pupils dilate in response to seeing others in need of help, and the greater the increase, the likelier and faster children are to subsequently provide help to that person (Hepach et al., 2012a, 2016, 2019). The striking finding relevant to children's prosocial motivation is that children's pupil dilation returns to baseline both when they are able to provide help and when they simply watch someone else provide help, indicating that their motivation is not to be the ones to help and, thus, receive credit for helping but rather to see the person receive help (Hepach et al., 2012a, 2017a). This is in line with the finding that toddlers help others anonymously and thus without any social recognition for helping (Hepach et al., 2017).

Toddlers' primary motivation is also not simply to see the physical order of things be restored. Recent findings showed that toddlers' pupillary arousal was only reduced in a social condition, in which a person received the object they needed to complete a task, but not in a nonsocial condition, in which the identical physical event occurred but without anyone present (Hepach et al., 2016). Moreover, both toddlers and preschoolers are more likely to hand a person the object they actually need rather than an irrelevant object or the object the person is reaching for but, unbeknownst to that person, is in fact broken and would thus not serve their purpose (Hepach et al., 2016, 2020; Martin et al., 2016; Martin & Olson, 2013).

Finally, there is evidence that acting prosocially is emotionally rewarding, even for very young children. For instance, cross-cultural research indicates that giving away treats makes toddlers happier than receiving treats, and, strikingly, costly giving makes them happier than noncostly giving (Aknin et al., 2015; Aknin et al., 2012). Further, toddlers' body posture is elevated as much after helping another person to achieve a goal as when toddlers achieve a goal themselves (Hepach et al., 2017b). This suggests that helping another person results in a positive and potentially rewarding emotional state in young children, which likely serves as a potent motivator for future prosocial actions (see Aknin et al., 2018). All in all, there is now substantial evidence that by age 2 years, children are genuinely invested in and motivated to improve the welfare of others.

16.1.1 Sympathy in Infancy

Until recently, Hoffman's proposal that infants could not respond with true sympathy for others until about 1.5 years of age due to limitations in their self-other differentiation was widely accepted. As such, younger infants' responding to emotional expressions in others has generally been dismissed as "immature" emotional contagion. However, this pervasive view has recently been put into question, for a few reasons. First, cross-cultural work has not supported the universality of the association between mirror self-recognition and empathic responding (Kärtner et al., 2010). Second, although a conceptual, reflective self-awareness may not emerge until late in the second year, there is now substantial evidence that an implicit sense of self as distinct from others is present even in newborns (see Davidov et al., 2013). And finally, newer empirical work shows that sympathy for distressed others does not first appear during the second year; rather it is evident within the first few months after birth and increases only modestly with age, whereas prosocial behavior first appears only during the second year (Davidov et al., 2013, 2020; Roth-Hanania et al., 2011). Importantly, infants' sympathy in the first year predicts their prosocial behavior in the second year, suggesting that early sympathy does indeed signal a prosocial motivation, even if infants in their first year do not yet have the knowhow or skills to alleviate others' distress (Davidov et al., 2020; Roth-Hanania et al., 2011).

Researchers have also recently begun to explore other affective mechanisms beyond emotional contagion that may serve as foundations for early sympathy. In particular, the rich and growing body of research on emotion processing during infancy has proved fruitful. This research shows that infants competently detect, discriminate, and integrate emotional expressions from others' faces, voices, and bodies (Grossmann, 2012, 2015; Missana et al., 2015; Rajhans et al., 2016b). One emotional expression that is of particular interest with respect to sympathy and prosocial behavior is fear (Marsh, 2015). Facial fear displays are commonly classified and used as threat stimuli (Vuilleumier, 2006). However, research on the psychology of prosociality has shown that, in adulthood, the capacity to help and benefit others is intimately tied to processes that make us recognize and care about others' emotional displays of distress as exemplified in fearful faces (Marsh & Ambady, 2007; Marsh & Blair, 2008; Marsh et al., 2007; Marsh et al., 2014). In fact, there is evidence that extremely antisocial psychopaths and extremely prosocial individuals show substantial differences in fear processing and may thus represent opposite ends of a caring continuum (Marsh, 2015). Specifically, when compared to a control group, anonymous kidney donors show increased neural and behavioral sensitivity to seeing others in distress (fearful faces) (Marsh et al., 2014). In contrast, psychopaths exhibit decreased sensitivity to fearful faces when compared to control individuals (Marsh & Blair, 2008). Moreover, research with a typical population of adults shows that better recognition of fear from faces is associated with higher levels of prosocial behavior (Marsh & Ambady, 2007; Marsh et al., 2007). Taken together, this line of research with adults strongly suggests that variability in responding to fearful faces is linked to variability in prosocial behavior, raising the question of when this link emerges in development.

One recent study demonstrated that heightened sensitivity to fearful faces is linked to enhanced prosocial behavior among 5-year-old children in two different cultures (Rajhans et al., 2016a). In this study, children in both India and Germany who were quicker to orient to fearful faces displayed greater prosocial behavior in a dictator game. Thus, the fundamental link between variability in responding to fear in others and prosocial behavior already exists in preschool-age children. Note, however, that the ability to detect and sensitively respond to various emotional facial expressions including fear emerges during the first year of life (Grossmann, 2012). Specifically, by around 7 months of age, human infants begin to show increased neural and behavioral (attentional) responses to fearful faces and distinguish them from other positive and negative facial expressions (Grossmann & Jessen, 2017; Jessen & Grossmann, 2014, 2016; Krol et al., 2015; Peltola et al., 2009). Given this evidence from behavioral and neuroscience research, infancy can be considered a sensitive developmental period during which fear processing skills come online. The question thus arises: Can understanding individual differences in responsiveness to fearful faces during this sensitive period in ontogeny provide insights into the foundations of sympathy and prosocial behavior in human development?

Recent research suggests it can. In one recent study, variability in neural responses (measured by functional near-infrared spectroscopy) and attentional responses (measured by eye tracking) to fearful faces at age 7 months predicted prosocial behavior at 14 months (Grossmann et al., 2018). Importantly, this association was selective: Only responsiveness to fearful faces – not to happy or angry faces – predicted prosocial behavior. This finding is noteworthy because it establishes a clear link to existing work with adults (Marsh, 2015), showing that fear processing is selectively linked to prosocial responding from early in ontogeny. More generally, this and the other recent findings on infants' fear processing critically extend the existing work on emotional contagion by supporting the idea that responsiveness to fear in others can be seen as a key marker and ontogenetic predictor of prosocial action among humans.

Taken together, the research with young infants described above shows that not just the precursors to empathic responding but also true sympathy for others is evident very soon after birth. Of note, although these findings contradict the specific developmental model proposed by Hoffman, they do support his broader and key argument that human infants come to the world prepared to care about the welfare of others and to become affectively involved in others' suffering (Hoffman, 1981, 2000, 2007).

16.1.2 Flexible Sympathy

A further crucial aspect of Hoffman's proposal was the idea that "natural selection requires an altruistic response system that is reliable and yet also flexible" (Hoffman, 1981, p. 127). In other words, the most effective and reliable prosocial motive from an evolutionary standpoint would be one that had a deep biological basis but was also flexible rather than automatic and fixed, and was amenable to cognitive control so as to differentiate when concern and prosocial behavior are feasible and warranted and when they are not. Research over the past several years bolsters this proposal, demonstrating that empathic responding is indeed flexible and amenable to control, even in early childhood (see Vaish, 2016).

First, empathy-related responses have been found to be multidetermined, that is, elicited in response to whatever cues are available, even in the absence of perceptible distress. Some early experiments tackled this question using assessments of pictures and stories (Iannotti, 1985). Preschool-aged children heard about protagonists in emotion-eliciting situations but were not given information about the protagonists' feelings. Because many of the children reported emotions that matched the protagonists' presumed emotions, they were believed to have empathized by taking the protagonists' perspective. However, children participating in these tasks may instead provide what they believe are the correct responses, or responses they believe the experimenter wants to hear (Eisenberg et al., 2006). Furthermore, because they require sophisticated cognitive and linguistic skills, they limit the ages that researchers can test.

More recent research addresses these problems. In one study, 1.5- and 2-year-olds saw one adult either harming another adult (e.g., tearing the other adult's picture) or behaving neutrally (e.g., tearing a blank paper). In both cases, the second adult observed the event neutrally, without displaying emotion. Nevertheless, children showed greater sympathy for the adult if her picture was torn (i.e., she was harmed), and subsequently behaved more prosocially toward her. Furthermore, individual children's sympathy correlated with their later prosocial behavior (Vaish et al., 2009; procedure adapted from Hobson et al., 2009). Children's sympathy could not have been elicited by affective resonance with the victim's distress because the victim showed no overt distress. Rather, children must have relied on a different, more top-down cognitive process such as affective perspective taking.

Extending this work, another study (Chiarella & Poulin-Dubois, 2015) examined 18-month-olds' responses to a victim displaying a neutral or sad expression. As in the work described earlier (Vaish et al., 2009), infants in this study showed sympathy for the neutral victim; however, they showed more sympathy for the sad victim, suggesting that although situational cues alone can generate sympathy, overt cues of distress intensify that sympathy. Although this is likely true, the critical point for our purposes is that 1.5-year-olds sympathized with a victim even in the absence of conspicuous distress. Whether this is true at younger ages remains unanswered.

Vaish et al. (2009) did also test 14-month-olds using the same procedure, but these younger infants did not fully grasp the situations presented. With simpler events, perhaps even younger infants could demonstrate multidetermined sympathy. However, current research suggests that this ability emerges around 18 months.

Second, research demonstrates that early empathic responding can be controlled based upon contextual information. In one study, 3-year-olds showed greater sympathy for an adult displaying justified distress (his hand was caught in a box) than unjustified distress (his sleeve was caught) (Hepach et al., 2012b). Children also helped the justifiably distressed adult more quickly, and the more sympathy children expressed, the more quickly they helped the adult. In more recent work, 18-month-olds also showed more sympathy for an adult who was justifiably distressed than for one who was unjustifiably distressed, whereas 15-month-olds did not react in this way (Chiarella & Poulin-Dubois, 2013). The 15-month-olds also did not look longer at the situations in which the adult displayed unjustified distress, suggesting that infants of this age do not yet engage in contextual appraisal. Alternatively, they may not have enough experience with the kinds of situations used in the study to appraise them relative to the emotional response. As with multidetermined sympathy, context-dependent sympathy based on appraising context may also emerge around 18 months.

In summary, humans appear to enter the world ready to be drawn into others' suffering and, as recent work shows, to feel concern for others' suffering. This concern has a genuinely prosocial flavor, as is evident in the emergence of prosocial behavior as soon as infants are motorically and sociocognitively capable of such behavior and in the satisfaction that toddlers seem to derive from seeing others receive the help they need. Furthermore, early sympathy meets the requirements that Hoffman argued natural selection would have for an altruistic response system: It is multidetermined and therefore reliable, yet also amenable to cognitive control and therefore flexible (Hoffman, 1981; Vaish, 2016). From very early in life, then, sympathy serves as a foundational and powerful proximate mechanism to promote humans' prosocial tendencies.

16.2 Guilt

Sympathy for another's distress can occur both when one is an uninvolved bystander who witnesses the other's distress (i.e., in a third-party interaction) or when one has caused the other's distress (i.e., in a dyadic context). In the latter case, sympathy for the person in distress combined with the awareness of being the cause of that distress can lead to the aversive emotion of guilt (Hoffman, 1976). Guilt focuses attention on the action and the harm done (or help not given) to the other, inflicts subjective discomfort on the actor due to its unpleasant valence, and crucially, motivates the actor to make amends by aiding or otherwise compensating the victim.

Thus, guilt is tuned to identifying and reversing the damage done to a cooperative relationship (Baumeister et al., 1994).[1]

Guilt has long been shown to serve these functions among adults (e.g., Brock & Becker, 1966; Cunningham et al., 1980; Ketelaar & Au, 2003; Regan et al., 1972). For instance, college students who believed they had caused someone great harm (and, thus, presumably felt guilty) were later more likely to help that individual than students who believed they had caused only minor harm (Brock & Becker, 1966). Similarly, individuals in another study who were made to feel guilty after behaving uncooperatively in a decision-making game were more likely to behave cooperatively on subsequent rounds of the game than people who did not feel guilty (Ketelaar & Au, 2003). Guilt, thus, goes beyond the general prosocial motivation created by sympathy; it specifically increases the motivation to make amends or to otherwise compensate the person one has harmed, thereby helping to repair and sustain one's valuable cooperative relationships.

16.2.1 Feelings of Guilt

Guilt begins to serve these vital prosocial functions from remarkably early in ontogeny. Some work indicates that following minor transgressions (e.g., accidentally breaking someone's favorite doll), children as young as 2 years show signs of guilt such as accepting responsibility and attempting to repair the damage (Drummond et al., 2017; Kochanska et al., 1995; Zahn-Waxler & Kochanska, 1990). Though suggestive, these studies are inconclusive because it is unclear whether they tapped into guilt specifically or into related but distinct processes. In particular, guilt is composed of two critical components: sympathy for a victim of harm and the awareness that one has caused that harm (Hoffman, 1982). Neither component is by itself sufficient for guilt, yet each component separately can motivate repair. For instance, when children harm someone, their reparative behavior could either arise from sympathy alone – without any recognition that they caused the harm, or from the recognition that they caused the outcome and the desire to fix it – without any sympathy. Thus, to study the prosocial effects of guilt specifically, we must use controlled experiments that can tease these processes apart.

Toward this end, we recently compared 2-year-old and 3-year-old children's reparative behavior after they caused a harmful outcome (guilt condition), someone

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[1] Guilt is often confused with the related social emotions of shame and embarrassment. However, though all three emotions are elicited by transgressions, they are distinct in critical ways. Guilt pertains to one's harmful actions and motivates reparative behavior, which benefits one's relationships. On the other hand, shame involves feelings that the whole self is a failure and thus leads one to withdraw from social contact rather than to repair, and embarrassment generally follows transgressions of social conventions rather than moral transgressions (Keltner & Buswell, 1996). Guilt is thus considered the quintessential moral emotion – one that plays a critical role in restoring and maintaining cooperation (though see Sznycer, 2019).

else caused the harmful outcome (sympathy condition), or children or someone else caused the same outcome but in a nonharmful context (Vaish et al., 2016). Three-year-olds (but not 2-year-olds) showed greater verbal and physical reparative behavior in the guilt condition than in the other conditions. This design enabled us to isolate the effects of guilt from its component processes and to show that the reparative motivation created by guilt is greater than that created only by sympathy or only by the desire to undo an unwanted but nonharmful outcome. We thus demonstrated that early in development, guilt distinctly serves to motivate children's reparative behavior.

In a different approach to this question, we examined whether after harming someone, children are especially motivated to repair the harm themselves – because they recognize that they need to fix the relationship that they damaged. Using pupil dilation to measure internal arousal, we found that 3-year-olds' (and more weakly, 2-year-olds') arousal decreased when they were able to repair damage that they had caused, but remained high if someone else repaired damage that the children had caused (Hepach et al., 2017a). However, if children had not caused the damage, then their arousal was similarly reduced when they or someone else repaired it. Thus, as bystanders, children are primarily motivated to see a person in need be helped regardless of who provides the help (see also Hepach et al., 2012a). Guilt alters this motivation such that children not only want the harmed individual to be helped but also want to be the helpers – as a way of repairing and showing commitment to the disrupted relationship.

All in all, by 3 (perhaps even 2) years of age, children recognize when they have caused harm and are motivated to repair that harm and restore their ruptured relationships. Thus, there seems to be an early preparation to experience guilt after causing harm, which helps even young children maintain cooperation from early in development.

16.2.2 Displays of Guilt

Interestingly, guilt is also thought to serve crucial social functions when it is *displayed* by a transgressor (see Keltner & Haidt, 1999). A prevailing view is that guilt displays serve appeasement functions by communicating vital information to victims and bystanders. They communicate that the transgressor is also suffering (Keltner & Anderson, 2000; Leary et al., 1996), the transgressor did not mean harm and is not generally the kind of person that means harm (McGraw, 1987), and the transgressor intends to make amends and behave more appropriately in the future (Castelfranchi & Poggi, 1990). A remorseful transgressor is, thus, seen as self-policing, dependable, and cooperative, and elicits forgiveness, affiliation, and cooperation from victims and bystanders (Darby & Schlenker, 1982, 1989; Goffman, 1967). Among adults, guilt displays do serve these functions. For instance, victims positively evaluate and show reduced aggression toward an apologetic transgressor

(Ohbuchi et al., 1989), and bystanders state that remorseful transgressors need not make as many restitutions as unremorseful ones (O'Malley & Greenberg, 1983).

A sizable body of work shows that guilt displays also serve these functions in childhood. Some work has explored children's responses to apologies, which are admissions of blameworthiness and regret and, thus, a stand-in for guilt. When 4- to 8-year-olds hear stories about transgressions, they blame and punish the transgressor less, and forgive and like her more if she apologized than if she did not apologize (Darby & Schlenker, 1982, 1989; Smith et al., 2010). They also judge situations in which a transgressor apologized as more just and attribute improved feelings to a victim who received an apology (Irwin & Moore, 1971; Smith et al., 2010; Wellman et al., 1979). A similar pattern emerges when children are themselves the victims. For instance, 4- to 7-year-olds who suffered minor transgressions reported feeling better, rated the transgressor as being nicer, and were more prosocial toward the transgressor if she apologized (Drell & Jaswal, 2016; Smith & Harris, 2012). Apologies are, thus, effective elicitors of preschool-aged children's forgiveness and prosociality.

Note, however, that from an early age, children are heavily prompted to apologize, even when they might not feel sorry (Smith et al., 2017). Children's positive evaluations of apologetic transgressors may, thus, be based on hearing key words they expect to hear ("sorry") rather than on the remorse as such. To account for this, recent work has examined children's responses to transgressors' remorse in the absence of explicit apologies. In one study, 4- and 5-year-olds watched two videos of third-party transgressions. One transgressor was remorseful without explicitly apologizing ("I did not mean to do that. It's my fault."), whereas the other was neutral and unremorseful (Vaish et al., 2011). Five-year-olds preferred and distributed more resources to the remorseful than the unremorseful transgressor, whereas 4-year-olds showed no systematic preference or distribution pattern. In a follow-up study, when the transgressor apologized explicitly ("sorry"), 4-year-olds did prefer and distribute more resources to her. Very similar results emerged in a more recent study in which children were themselves the victims (Oostenbroek & Vaish, 2019). Thus, by age 5, children respond positively and with greater cooperation toward remorseful transgressors; a year earlier, children show a similar appreciation when transgressors provide conventional cues of remorse such as explicit apologies.

In sum, guilt serves vital prosocial functions from early in ontogeny. By 2–3 years, children experience guilt about causing harm: they show nonverbal and verbal signs of guilt and are motivated to repair the damage. By 4–5 years, children respond favorably to transgressors' displays of guilt: they positively evaluate and are more prosocial toward remorseful transgressors. At age 4, these responses hinge on the transgressor using conventional phrases such as "sorry," but by age 5, even remorse without such phrases elicits these responses.

Why might the experience of guilt motivate prosociality earlier than guilt displays? In part, this discrepancy might be a methodological byproduct. Since studies on children's responses to guilt displays involve asking children interview questions (which very young children find challenging), these studies have not generally assessed children younger than age 4. However, one study that included 3-year-olds found that they did not evaluate apologetic transgressors more positively than non-apologetic ones (Wellman et al., 1979). Children's appreciation of guilt displays may thus only emerge around 4 years. Why might this be the case? One proposal is that as guilt has no single facial expression and is instead expressed through actions such as confessions, apologies, and repair (Keltner & Buswell, 1996; Zahn-Waxler & Kochanska, 1990), young children might have a hard time identifying it in others. By age 4, they have the capacity and sufficient experience to identify and respond to the most common sign of remorse (apologies), and by age 5, to other, less-common signs of remorse as well. Be that as it may, it is interesting to consider that the earlier emergence of children's own expressions of guilt may serve children well by appeasing others and lessening the negative consequences that children might otherwise receive for their transgressions. Thus, children might benefit from displaying their own guilt substantially earlier than they respond positively to such displays in others.

16.3 Conclusions, Caveats, and Future Directions

Human survival and success depends on banding together, collaborating, and cooperating with one another (Tomasello, 2016). This interdependence has meant, in turn, the need to ensure the well-being of our (potential) cooperation partners. We argue that natural selection has favored emotional mechanisms that, at the proximate level, help us detect and respond prosocially toward those who need help or are suffering. Moreover, these emotional mechanisms appear early in ontogeny and, thus, allow even the youngest members of our species to promote others' welfare and thereby foster cooperation (Bjorklund, 2018; Vaish & Hepach, 2020).

We focused in this chapter on two such mechanisms that are essential for this purpose: sympathy and guilt. Both mechanisms are evident remarkably early in development. Sympathy is seen as early as 3 months of age and seems to rest on multiple emotional processes including affective contagion and fear processing. Furthermore, early sympathy is both reliable and flexible, meeting Hoffman's requirements for an evolved altruistic response system (Hoffman, 1981). Building on this foundation of sympathy and a basic sense of causality or agency, a nascent guilt emerges between 2 and 3 years of age. Critically, both mechanisms serve the proposed prosocial functions, with sympathy predicting prosocial behavior (both concurrently and longitudinally) by 12–14 months of age and guilt motivating reparative behavior by age 3 years. Somewhat later in development, others' displays of guilt also serve important reparative functions by appeasing victims and observers and eliciting cooperation. Together, these early-emerging emotional mechanisms highlight the ways in which humans are prepared to be drawn into others' suffering, to act on others' behalf, to repair their valuable social relationships, and to identify who is or is not likely to be a good cooperative partner.

There are, of course, important caveats and supplements to this account, as well as important questions that remain open. We consider some of these in the remainder of this chapter.

16.3.1 Biases in Sympathy and Guilt

First, despite being early-emerging, reliable, and flexible, empathic responding does not necessarily work as an optimal moral guide. This is certainly true by school age, when children show more sympathy for peers of their gender than peers of the other gender (Feshbach & Roe, 1968) and for those in their "minimal" in-group (i.e., assigned arbitrarily by the experimenter) than their minimal out-group (Masten et al., 2010). Some evidence suggests that even infants can be selectively prosocial, such as by directing more help toward mothers than strangers (Davidov et al., 2020; Young et al., 1999). As such, empathic responding and the prosocial behavior it motivates is not foolproof and may even lead us astray from our presumed goal of transcending biases and behaving in more "rationally" prosocial ways (see Bloom, 2016; Wynn et al., 2018).

Important and compelling as these considerations are, they do not, to our minds, detract from the account of empathic responding as a naturally selected and early-emerging mechanism to link an observer's affective state with another person's and thereby create a vested interest in the observer to act on the other's behalf. Indeed, the biases evident in empathic responding are precisely the kinds of biases one would expect for an evolved system whose purpose is not to create impartial "moral" beings but rather beings who behave in ways that ultimately benefit themselves (and/or their genes). This is entirely consistent with the proposal that social forces and rationality may capitalize on – or even work against – this foundational affective mechanism in order to shape prosocial behaviors and decisions according to the moral values of the particular group or culture (Bloom, 2016).

With that in mind, we can use the evolutionary framework to propose further hypotheses about the forms that early sympathy and guilt should take. First, if these mechanisms evolved to motivate prosocial behaviors toward those with whom we are likely to be interdependent, then they should, from early on, be biased in favor of such individuals. As reviewed above, such biases do exist in school-age children's sympathy, but little research has examined whether this holds true among infants and toddlers. We do know that even within the first year, infants show a preference for familiar faces, the faces of those who belong to the race they encounter most often, and those who speak their native language rather than a foreign language or with a foreign accent (Bar-Haim et al., 2006; Bushnell, 2001; Kinzler et al., 2010). Further, by 9 months of age, infants' processing of important social cues such as faces, voices, emotions, and pupil size primarily occurs in the context of own-race faces, not other-race faces (Kelsey et al., 2019; Vogel et al., 2012). Given the importance of attending to, parsing, and processing social stimuli for empathic responding, we may predict that these early-emerging biases should result in biased sympathy even in infancy and early toddlerhood. Yet beyond the few studies that suggest greater prosocial behavior toward mothers than strangers (Davidov et al., 2020; Young et al., 1999), researchers have not seriously examined biases in infants' and toddlers' sympathy.

This applies to young children's guilt as well. If guilt has evolved, first and foremost, to repair our valuable relationships, then we may expect that from early in development children should feel more guilty after causing harm to - and should be more forgiving of - those who are like them or are in their group (see Vaish & Oostenbroek, in press). This will be an exciting direction for future work on early guilt and its reparative functions.

Equally, we can consider other, more complex functions of guilt beyond the repair of interpersonal, dyadic relationships. In particular, "collective guilt," that is, guilt about the transgressions of close others such as in-group members, motivates individuals to accept responsibility and compensate for the negative actions of in-group members, thereby reducing intergroup conflict and regulating group life (Doosje et al., 1998; Lickel et al., 2004). Though it seems unlikely that guilt evolved primarily to serve this intergroup function, it is nonetheless possible that as humans became more group minded a couple of hundred thousand years ago (due to competition from other groups), natural selection exapted the existing interpersonal guilt to serve intergroup reparative functions as well. Yet the developmental foundations of collective guilt remain largely unexplored. In one recent study, 5-year-olds reported greater willingness to accept responsibility for harm caused by an in-group than an out-group member (Over et al., 2016). However, children did not attempt to repair the damage caused by the in-group more than the out-group member, leaving open whether children's acceptance of collective responsibility translates into reparative behavior. Moreover, no research has examined collective guilt in children younger than 5 years. This is an important direction for future work.

16.3.2 Other Prosocial Motives

A second important caveat is that although humans are clearly prepared from early on to care about and for others, we also simultaneously harbor self-serving motives (see Eisenberg et al., 2016). We are less likely to help others when it would mean a large cost to ourselves, and we may behave selfishly if we believe no one will find out, to name just a few examples. Moreover, in addition to acting prosocially out of a genuine concern for others' welfare, we may also do so for *selfish* reasons, such as to enhance our reputations (Wedekind & Milinski, 2000). Recent work shows that reputational concerns motivate prosocial behavior as early as the preschool years, such that children act more prosocially when they are being watched – or are simply in the presence of an image of eyes – than when they are unobserved (Engelmann et al., 2012; Kelsey et al., 2018; Leimgruber et al., 2012). Moreover, as reviewed above, when they have caused someone harm, even 2-year-old children seem to want to be the ones to repair that harm, hinting that even toddlers may care about being recognized for their prosocial actions under some circumstances (Hepach, Vaish, et al., 2017a).

It is worth noting that these more self-centered motivations do not seem to be the primary drivers of prosocial behavior in the first 2–3 years (Hepach et al., 2016), and perhaps even later in development. More critically, however, the presence of self-serving prosocial motives does not preclude the possibility of genuine regard for others' welfare; the two kinds of motives can coexist and even work in conjunction to promote prosociality. If we keep in mind that the "goal" of natural selection is to bring about behaviors of adaptive import, then it seems entirely reasonable to allow for multiple motivational forces that lead us to those adaptive behaviors (see Vaish & Tomasello, 2014).

Indeed, prosocial behavior can also be motivated by positive affective states. As reviewed above, acting prosocially increases happiness, even among very young children, and this happiness likely motivates further prosociality (Aknin et al., 2018; Hepach et al., 2017b). Beyond this, however, children recognize and respond positively to others' prosocial behaviors. Infants in their first year already differentiate helpful from harmful characters and prefer to interact with helpful ones (Hamlin, 2013; Krol & Grossmann, 2020), and toddlers and preschoolers selectively help prosocial over antisocial individuals (Dahl et al., 2013; Vaish et al., 2010).

Recent evidence also reveals the role of more complex positive emotions in motivating prosocial behavior (Vaish & Hepach, 2020). Specifically, receiving help elicits a nascent sense of gratitude among young children, which motivates them to act prosocially – seen both in their reciprocity toward the individual who provided help and, strikingly, in their "paying it forward" to new individuals (Beeler-Duden & Vaish, 2020; Hepach et al., 2019; Vaish et al., 2018). We may also expect that, like displays of guilt, displays of gratitude might serve important social and cooperative functions. Specifically, gratitude displays are thought to indicate that one appreciates the kindness and is likely to reciprocate, thus communicating one's commitment to the norms of reciprocity and to one's relationships (Keltner et al., 2006; McCullough et al., 2008). Gratitude displays should, thus, elicit affiliation and cooperation from benefactors and bystanders, perhaps even fairly early in development. One recent study provides initial evidence for this proposal (Vaish & Savell, 2018), but far more research is needed to fully understand the role of positive social emotions in early prosociality.

16.3.3 Uniquely Human?

Finally, we end with some speculative thoughts about the degree to which the emotional mechanisms we have focused on here are unique to humans versus shared with other species, particularly our closest living primate relatives, the Great Apes. There is now a great deal of evidence that chimpanzees (and bonobos, to the extent they have been studied) are sensitive to others' immediate needs and requests for help and respond by doing such things as supporting their allies, removing barriers to provide conspecifics with access to food, providing conspecifics with tools that will help them fulfill their need, and so forth (e.g., de Waal & Suchak, 2010; Warneken et al., 2007; Yamamoto et al., 2012). Yet the motivations underlying their prosocial behavior remain contested – and challenging to study experimentally. Still, the evidence we do have to date suggests that chimpanzees' helping may not be motivated by a genuine concern for others' welfare. Thus, chimpanzees (and the other Great Apes) do not help a conspecific more after they have seen the conspecific being harmed (Liebal et al., 2014); this stands in contrast to toddlers, who show sympathy for and subsequently act more prosocially toward individuals who are harmed (Hepach et al., 2012b; Vaish et al., 2009). Further, whereas chimpanzees reliably help a conspecific by providing a tool that the conspecific is requesting, they do not help paternalistically. That is, if the tool being requested will not in fact fulfill the conspecific's need, chimpanzees do not correct the request and hand the tool that *would* fulfill the need (Hepach et al., 2020). This is again in contrast to toddlers and preschoolers, who consider what the other person needs rather than only what the other person is requesting (Hepach et al., 2020; Martin et al., 2016; Martin & Olson, 2013). Together, the existing evidence presents us with a picture in which prosocial behaviors are shared among humans and other Great Apes, but the undergirding other-oriented affective motivators are unique to humans. This further underscores the importance of studying the affective processes focused on in this chapter in order to arrive at a better understanding of the proximate mechanisms that enable and promote human cooperation. Moreover, it hints at the possibility that during human evolution, interdependence among group members may have indeed served as the breeding ground for the emergence of these affective processes.

In conclusion, based on the empirical evidence reviewed here, we suggest that human prosocial behaviors are rooted in other-oriented affective processes – sympathy and guilt – that emerge early in human ontogeny. These insights are based upon novel tasks that tap into infants' and young children's responses to others in need or distress, which have identified the affective predictors, motivators, and consequences of various forms of early prosocial behavior. These advances have not only opened the door to fostering a more mechanistic understanding of cooperative tendencies in early development but are also beginning to change how we view infants' and young children's abilities to engage with and care about others. Specifically, in recent years, the field has come a long way toward dismantling the long-held view of infants as immature social beings simply infected by another person's displays of need and distress. This view is being replaced by empirical evidence attesting to infants' and young children's competent navigation of their social environment and their genuine, affect-guided prosocial orientation toward social partners. Yet there is much to be learned about the early origins of human prosocial behavior and its affective bases. In our view, a promising path forward is to adopt an evolutionary perspective based on the interdependence hypothesis (Tomasello, 2016) and take an interdisciplinary approach combining psychophysiological and behavioral methods with the aim of uncovering the foundational affective mechanisms of early cooperative behaviors.

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Glossary

Adaptations (1) in evolutionary theory, universal and reliably developing inherited features that arose as a result of natural selection and helped to solve some problem of survival. (Bjorklund and Hart, Chap. 1)

Adaptations (2) evolutionary and ecological shifts in biology or behavior that arise as a result of natural selection (ultimately) and local ontogenetic and proximate processes that help to solve time and energetic problems of efficiency and survival. May or may not include intergenerational change. (Ivey Henry and Morell, Chap. 10)

Allocare time or energetic investment in the protection and nurturing of infants by individuals other than mother. (Ivey Henry and Morell, Chap. 10)

Allomother term used to refer to a female or male caretaker other than the mother. Note that when paternity is unknown, the term may be applied to the father. (Hrdy and Burkart, Chap. 8)

Alloparent (allocaregiver) caretaker other than a genetic parent. (Locke and Bogin, Chap. 6; Hrdy and Burkart, Chap. 8; Ivey Henry and Morelli, Chap. 10)

Altricial a term used to characterize animals born in a helpless state, often with eyes closed, fur or feathers absent, and with no ability to locomote on their own. (DeSilva, Chap. 4; Ivey Henry and Morell, Chap. 10)

Angelman syndrome a complex genetic disorder that primarily affects the nervous system. Characteristic features of this condition include delayed development, intellectual disability, severe speech impairment, and problems with movement and balance. Children with Angelman syndrome typically present as happy and excitable, interacting a great deal with caregivers. (Salmon and Hehman, Chap. 9)

Apoptosis programmed cell death. (Wilder and Semendeferi, Chap. 3)

Ardipithecus an early hominin genus from Eastern Africa known from fossils discovered in 4.4–5.8 million-year-old sediments. (DeSilva, Chap. 4)

Attachment behavioral system the system of evolved psychological and behavioral mechanisms that promote proximity-seeking and relationship maintenance with attachment figures, promoting survival (Simpson and Jaeger, Chap. 11) that

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has been interpreted according to an evolutionary developmental psychology model of attachment as a mechanism that arose for advancing ancestral infants' survival by promoting *exclusive* proximal contact specifically with mothers. (Hart, Chap. 7)

Attachment theory a middle-level evolutionary theory that explains social and personality development in response to the significant environmental and interpersonal experiences across life. (Simpson and Jaeger, Chap. 11)

Attachment-based caregiving construct that refers to an evolutionary developmental psychology model of a psychological mechanism for upholding maternal caregiving of weanlings that took over for biobehavioral features of lactation at the juncture when an ancestral mother transitioned from caring for a nursling to caring for a weanling. (Hart, Chap. 7)

Australopithecus a Plio-Pleistocene hominin genus from Africa known from fossils discovered in 4.2–1.0 million-year-old deposits and likely to be the ancestral genus to our own *Homo*. (DeSilva, Chap. 4)

Axons nerve fibers that conduct electrical impulses away from the nerve cell body. (Wilder and Semendeferi, Chap. 3)

Beat repetitive pulse that underlies music. People often make tapping movements in synchrony with beat. (Doi and Masataka, Chap. 9)

Beckwith–Wiedemann syndrome a genetic disorder commonly characterized by overgrowth. It occurs in approximately 1 in 11,000 births, with about equal incidence in boys and girl. One feature is macrosomia, or large birth weight and length. (Salmon and Hehman, Chap. 9)

Biased threat detection faster orienting and detection of certain stimuli, often for recurrent threats. (Rakison, Chap. 14) See also **Recurrent threats**.

Biocultural reproduction (BCR) the human style of hyper-cooperation by alloparents in the extra-maternal production of food and other material and emotional resources for the feeding and care of offspring. BCR is based on culturally defined rules for marriage and kinship and the obligations these entail toward cooperation in reproduction and care of offspring. (Locke and Bogin, Chap. 6)

Cephalopelvic index the ratio between linear or area measurements of the neonatal skull and dimensions of the female pelvis. (DeSilva, Chap. 4)

Child-to-mother attachment term that refers to an evolutionary developmental psychology model of the bond of affection that connected ancestral weanlings to their mothers. It is theorized as a psychological mechanism, born of proximal contact anchored in 3 years of breastfeeding as practiced in ancestral settings. (Hart, Chap. 7)

Chord multiple notes that are perceived to sound simultaneously. (Doi and Masataka, Chap. 9)

Collective intentionality in Tomasello's theory, the ability to establish a *group-minded "we"* with other people beginning around the age of 3. (Bjorklund and Hart, Chap. 1)

Cooperative breeding refers to species in which alloparents in addition to parents help care for and provision offspring. (Hrdy and Burkart, Chap. 8; Ivey Henry and Morelli, Chap. 10) See also **Cooperative reproduction**.

Cooperative development refers to reciprocal processes in development that are directly and indirectly influenced by the contributions of persons other than parents that increase a child's capacity to successfully adapt to their environment. This includes features that are directly influenced by allocaregivers, as well as community behaviors and norms that shape a child's experience and future success. Examples are social agency, reciprocity, and cultural competencies exhibited by hunter-gatherer children. (Ivey Henry and Morelli, Chap. 10)

Cooperative reproduction refers to the reproductive dependence of parents on the time and energetic contributions of others to successfully rear young. It represents diverse processes, including allocare, provisioning, teaching, and cultural contributions to child survivorship and successful future reproduction. (Ivey Henry and Morelli, Chap. 10) See also **Cooperative breeding**.

Deferred adaptations aspects of childhood that serve as preparations for adulthood and were selected over the course of evolution. (Bjorklund and Hart, Chap. 1)

Dentate gyrus region of the hippocampal formation. (Wilder and Semendeferi, Chap. 3)

Developmental niche construction a special form of niche construction during ontogeny. It describes ecological feedbacks embedded in developmental processes (e.g., maturation) that bias phenotypic outcomes. It characterizes adaptive processes without inferring trait selection at an evolutionary scale, although they may be related. (Ivey Henry and Morelli, Chap. 10)

Developmental plasticity phenotypic variability across biological and behavioral systems that is produced via developmental processes. (Ivey Henry and Morelli, Chap. 10) See also **Plasticity**.

Differential treatment procedure a laboratory procedure designed to elicit jealousy protest in an infant or young child by exposing the child to a situation in which his or her parent directs affectionate or playful attention preferentially toward another child or toward a representation of another child, such as a lifelike baby-doll. (Hart, Chap. 15) See also **Jealousy protest**.

DHA (Docosahexaenoic acid) an essential fatty acid found in breast milk that is considered to be of importance to neurodevelopment in infants. (Hart, Chap. 7)

Disorganized attachment an infant attachment pattern that results from abusive or neglectful caregiving. (Simpson and Jaeger, Chap. 11)

EEA See **Environment of evolutionary adaptedness**.

Empathy an affective response to another's emotional state and congruent with the other's emotional state. (Vaish and Grossmann, Chap. 16)

Endocast internal cast of the cranium. (Wilder and Semendeferi, Chap. 3)

Environment of evolutionary adaptedness (EEA) the physical and social environments in which humans evolved. The EEA is not a single environment, but rather the amalgamation of all the times and places under which humans faced evolutionary pressures. (McDowell and Volk, Chap. 5; Simpson and Jaeger, Chap. 11)

Epigenetics refers narrowly to changes in the expression of gene code as a result of methylation (methyl groups attached to DNA) or histone modification (changes in the coiling of DNA). Broadly defined, it describes any heritable phenotype changes that do not involve alterations in the DNA sequence. (Ivey Henry and Morelli, Chap. 10)

Epigenetic signal Evidence of epigenetic modifications (e.g., DNA methylation, upregulation) to specific regions or sets of genes or proteins associated with variation in biological functions. (Ivey Henry and Morelli, Chap. 10)

Event related potential (ERP) electrophysiological responses recorded on the scalp surface that reflect mental processing of external stimulation. (Doi and Masataka, Chap. 9)

Evo devo (Evolutionary developmental biology) a discipline in biology that looks mostly at the embryonic development of different animals to infer their evolutionary relationship and how different developmental mechanisms affect species change. (Bjorklund, Chap. 2)

Evolutionary developmental psychology the study of the genetic and ecological mechanisms that govern the development of social and cognitive competencies common to all human beings and the epigenetic (gene-environment interactions) processes that adapt these competencies to local conditions. (Bjorklund and Hart, Chap. 1)

Evolutionary level of explanation refers to causal processes of trait selection over evolutionary time, that is, adaptive and phylogenetic changes across generations. (Ivey Henry and Morelli, Chap. 10)

False-belief understanding the ability to track an individual's representations of reality that, in the case of false beliefs, differ from the "objective" reality. For example, a toy might be in location A but the individual believes the toy is in location B. (Buttelmann, Chap. 13)

Fear a core emotion that occurs for a perceived threat or in anticipation of such a threat, and triggers physiological and behavioral responses that, on average, were adaptive for our ancestors. (Rakison, Chap. 14)

Fetal microchimerism occurs when a low number of fetal cells are transferred across the placental barrier during pregnancy and are found to persist in the mother's system for decades after she gives birth. (Salmon and Hehman, Chap. 9)

Formant spectral peaks in voice that define a perceived vowel. (Doi and Masataka, Chap. 9)

Fundamental frequency (f_0) lowest frequency contained in sound waveform. (Doi and Masataka, Chap. 9)

Glial cells non-neuronal cells of the central nervous system and peripheral nervous system. (Wilder and Semendeferi, Chap. 3)

Gliogenesis production of glial cells. (Wilder and Semendeferi, Chap. 3)

Globularization developmental changes that result in a more rounded, globular braincase. (Wilder and Semendeferi, Chap. 3)

Goal a mental state, a representation of a desired end state or result of an action. (Buttelmann, Chap. 13)

Guilt an aversive, self-conscious, social emotion experienced, most fundamentally, when one has harmed someone or violated a moral norm. Over development, guilt can take on far more complex forms and be elicited in more complex ways; for example, anticipatory guilt, collective guilt, survivor guilt. (Vaish and Grossmann, Chap. 16)

Harshness the extent to which resources are limited in an environment, with environments containing less abundant resources being harsher. (Simpson and Jaeger, Chap. 11)

Heterochrony differences in timing or duration of developmental processes. (Bjorklund, Chap. 2; Wilder and Semendeferi, Chap. 3)

Hominin group consisting of modern humans and their bipedal ancestors. (Bjorklund, Chap. 2; Hrdy and Burkart, Chap. 8; Wilder and Semendeferi, Chap. 3)

Human placental lactogen (hPL) a hormone that is released by the placenta during pregnancy, with maternal serum levels rising in relation to the growth of the fetus and placenta. (Salmon and Hehman, Chap. 9)

IBI See **Interbirth interval**.

Imprinted genes genes expressed differently as a function of whether they were inherited from the mother versus the father. (Salmon and Hehman, Chap. 9)

IMR See **Infant mortality rate**.

Individual differences in attachment variations from normative features of the attachment behavioral system. (Simpson and Jaeger, Chap. 11)

Infant care hypothesis attributes expansions in the brain and social cognition to intense socialization associated with evolutionary changes in human infancy. Unlike the Social Brain Hypothesis, the Infant Care Hypothesis is concerned with sociality itself, especially the need to be around and to interact with others, and to enjoy the feeling of belonging. (Locke and Bogin, Chap. 6)

Infant mortality rate (IMR) the probability of an infant dying before it is 366 days old, typically expressed as a percentage or as a number of deaths per hundred. (McDowell and Volk, Chap. 5)

Insecure-anxious attachment an infant attachment pattern characterized by high levels of anger and clingy behavior when distressed. (Simpson and Jaeger, Chap. 11)

Insecure-avoidant attachment an infant attachment pattern characterized by high levels of self-reliance and behavioral autonomy when distressed. (Simpson and Jaeger, Chap. 11)

Intention understanding the ability to track and understand others' intentions. Intentions comprise both a goal (what the other is doing) and a means chosen to achieve that goal (how the other is doing it), along with the rational dimensions of this choice (why the other has chosen to do it in that particular way). This is not to be confused with an understanding of intentionality (i.e., understanding that something or someone *is* an intentional agent). (Buttelmann, Chap. 13)

Intentional agents beings whose behaviors are based on what they know and what they want, and who act deliberately to achieve their goals. (Bjorklund and Hart, Chap. 1)

Interbirth interval (IBI) term refers to the number of months between two subsequent births. Child outcomes are often discussed in terms of *preceding IBIs,* which point to prenatal exposure to influences in utero, such as maternal nutrition, and *subsequent IBIs,* which implicate postnatal exposure to influences, such as infant nutrition. (Hart, Chaps. 7 and 15)

Internal working models (of attachment) general expectations about how caregivers and relationship partners will respond based on prior relational experiences. (Simpson and Jaeger, Chap. 11)

Inversed affect sharing joint attention, in which two people attend to the same object or event, but do *not* share experience. In broad terms, one of the individuals experiences/expresses positively valenced affect while the other experiences/expresses negatively valenced affect. (Hart, Chap. 15)

Jealousy protest an evolved behavioral mechanism for protecting exclusivity in the infant-caregiver relationship. (Hart, Chap. 15)

Joint attention See **Shared attention**.

Kindchenschema (baby schema) a suite in facial features possessed by infants that promote feelings of affection and caregiving in adults. (Bjorklund, Chap. 2)

Kwashiorkor a malnutrition-related disease that takes its name from a word in the Ga language that literally means *the disease the deposed baby gets when the next one is born*. (Hart, Chap. 7)

Lactation-based caregiving maternal caregiving of nurslings that is characterized by voluntary and involuntary presentations of responsiveness to infant cues that are underpinned by neuroendocrine features of lactation. (Hart, Chap. 7)

Lactation-based cohesion term that refers to the nursling-mother relationship as a biobehavioral bond marked by cycles of bidirectional involvement that connect nurslings to their mothers much as they connect mothers to their nurslings. (Hart, Chap. 7)

Lexical stress salience and emphasis placed on a syllable, word, or phrase. Stress is often characterized by pitch change, loudness, or long duration. (Doi and Masataka, Chap. 9)

Life history theory an overarching evolutionary framework that describes how individuals navigate various tradeoffs regarding the allocation of time, energy, and resources across the lifespan. (Ivey Henry and Morell, Chap. 10; Simpson and Jaeger, Chap. 11)

Metopic suture fibrous joint that divides the two halves of the frontal bone of the skull. (Wilder and Semendeferi, Chap. 3)

Mismatch negativity (MMN) event-related potential component with negative polarity elicited by a deviant sound. (Doi and Masataka, Chap. 9)

Mother-to-child attachment construct that refers to an evolutionary developmental psychology model of the bond of affection that bound ancestral mothers to their former nurslings. It is theorized as a psychological mechanism that was forged during 3 years of lactation-based caregiving and cohesion. (Hart, Chap. 7)

Myelin insulating layer that forms around axons to aid in the transmission of electrical signals. (Wilder and Semendeferi, Chap. 3)

Nascent jealousy construct theorized as a psychological adaptation to threat of usurpation by a newborn sibling that arose in ancestral infants by the age of 9 months. (Hart, Chap. 15)

Niche construction evolutionary ecological feedback processes of phenotype-environmental interactions, whereby organisms directly and indirectly influence the parameters of their own environmental experience, and, therefore, the subsequent ecological conditions they encounter from the proximate, adaptive, and evolutionary scale. (Ivey Henry and Morelli, Chap. 10)

Neonatal imitation the ability of newborns to reproduce some behavior, such as a facial expression, that they have seen in others. (Bjorklund and Hart, Chap. 1)

Neonaticide the act of a parent deliberately murdering an infant during the first 24 hours of life. (Salmon and Hehman, Chap. 9)

Neonatal learning literally, learning in the month after birth; of significance here because much of this learning involves cues that identify the mother. Since the human infant is born into a state of extreme helplessness, and the mother supplies much of its nourishment and protection, it is desirable that her offspring form a strong emotional bond with her, which is facilitated by the neonate's response to – and preference for – maternal cues. (Locke and Bogin, Chap. 6)

Neoteny retention of ancestral infantile or juvenile traits. (Bjorklund, Chap. 2)

Neural neoteny the extension of plasticity at the neuronal level into adulthood. (Bjorklund, Chap. 2)

Neural progenitor cells cells that can differentiate into different types of neuron and glial cells. (Wilder and Semendeferi, Chap. 3)

Neurogenesis production of neurons. (Wilder and Semendeferi, Chap. 3)

Neuropil area of the central nervous system composed of unmyelinated axons, dendrites, and glia cell processes. (Wilder and Semendeferi, Chap. 3)

Non-associative models of fear the theory that fears for recurrent threats are innate. (Rakison, Chap. 14) See also **Recurrent threats**.

Normative attachment species-typical features of the attachment behavioral system. (Simpson and Jaeger, Chap. 11)

Obstetrical dilemma hypothesis proposed by Sherwood Washburn in which bipedal adaptations in the pelvis led to the birth of helpless human infants. (Bjorklund, Chap. 2; DeSilva, Chap. 4)

Ontogenetic adaptations behaviors that play a specific role in survival for an individual at one time only, and then disappear when they are no longer needed. (Bjorklund and Hart, Chap. 1; Hart, Chap. 15)

Ontogeny development of an individual organism. (Wilder and Semendeferi, Chap. 3)

Pan genus including chimpanzees and bonobos. (Wilder and Semendeferi, Chap. 3)

Parent-infant synchronization matching of parental behaviors to an infant's unique development stage, which facilitates and maintains social and emotional bonding. (Simpson and Jaeger, Chap. 11) See also **Synchrony**.

Perceptual narrowing a process by which infants become "tuned" to sociocultural relevant information as a result of experiences during the first year of life. Infants' ability to make discriminations among frequently experienced stimuli, such as faces of individuals of their own race, which increase, whereas infants become relatively less effective discriminating among infrequently experienced stimuli, such as faces of individuals of other races. (Bjorklund and Hart, Chap. 1)

Perceptual template an innately specified representation of evolutionarily relevant stimuli, such as snakes, spiders, and faces. (Rakison, Chap. 14)

Pitch perceived height of sound determined primarily by its fundamental frequency. (Doi and Masataka, Chap. 9)

Pitch Contour curve that tracks the rise and fall pattern of changes in pitch. (Doi and Masataka, Chap. 9)

Plasticity the extent to which behavior or brain functioning can be changed. (Bjorklund and Hart, Chap. 1). See also **Developmental plasticity**.

Platypelloid a term used to characterize a female pelvis that is wide from side to side. (DeSilva, Chap. 4)

Pluripotent stem cells cells that can replicate indefinitely and differentiate into various types of cells. (Wilder and Semendeferi, Chap. 3)

Prader–Willi syndrome a genetic disorder caused by a loss of function of specific genes on chromosome 15. Symptoms in newborns include weak muscles, poor feeding, and slow development. Beginning in childhood, those affected become constantly hungry which can lead to obesity and/or type 2 diabetes. (Salmon and Hehman, Chap. 9)

Precocial a term used to characterize animals born alert, with their eyes open, body covering (e.g., fur or feathers) present, and able to independently locomote. (DeSilva, Chap. 4)

Prefrontal cortex portion of the cerebral cortex covering the front part of the frontal lobe, involved in complex cognitive and social behaviors. (Wilder and Semendeferi, Chap. 3)

Preparedness, or prepared fear the theory that some associations are learned more readily than others, most notably for recurrent threats, via a specialized learning mechanism. (Rakison, Chap. 14)

Primates order of Mammals that includes humans, apes, monkeys, lemurs, tarsiers, and a few other species. They are distinguished by having, in general, grasping hands and feet, forward-facing eyes, large brains relative to body size, slow rates of growth and development, and complex social life. The living non-human primates are each successful species in their own right and none is the ancestor of humans. However, study of the non-human primates can provide indications of earlier stages in the evolution of humans and the possible origin of some human behaviors. (Locke and Bogin, Chap. 6)

Prosocial behavior behavior that benefits another individual or group of individuals; for example, helping, sharing, comforting. (Vaish and Grossmann, Chap. 16)

Proximate level of explanation concerned with the immediate mechanisms that underpin a trait or behavior; what causes the trait or motivates the behavior in an individual. (Ivey Henry and Morell, Chap. 10; Vaish and Grossmann, Chap. 16)

Pupillometry measure of the dilation of the eyes' pupils, which indexes activity of the sympathetic branch of the autonomous nervous system and is indicative of experienced internal arousal (e.g., the arousal induced by listening to emotionally charged stimuli) or mental effort. (Vaish and Grossmann, Chap. 16)

Pyramidal neuron primary excitatory neuron of the prefrontal cortex. (Wilder and Semendeferi, Chap. 3)

Recurrent threats Environmental stimuli that were potentially dangerous to humans and their pre-hominid ancestors over 100,000 s or millions of years. (Rakison, Chap. 14)

Reproductive fitness behaviors that facilitate survival and lead to genetic reproduction of offspring. (Simpson and Jaeger, Chap. 11)

Reproductive strategies how individuals allocate time, energy, and resources between current and future reproduction, often characterized as fast (i.e., prioritizing current reproduction) or slow (i.e., prioritizing future reproduction). (Simpson and Jaeger, Chap. 11)

Rotational birth a characteristic of most human births in which the neonate corkscrews through the birth canal and is born facing posteriorly, with the occipital region of the head presenting anteriorly. (DeSilva, Chap. 4)

Secure attachment an infant attachment pattern characterized by high levels of relying on caregivers for support when distressed. (Simpson and Jaeger, Chap. 11)

Selection pressures environmental and social factors that have shaped the way in which individuals behave to increase their survival and reproductive fitness. (Simpson and Jaeger, Chap. 11)

Shared (or joint) attention two people both attending to the same thing or event and sharing that experience. (Bjorklund and Hart, Chap. 1; Buttelmann, Chap. 13; Hart, Chap. 15)

Silver–Russel syndrome a growth disorder characterized by slow growth before and after birth. Newborns with this condition have low birth weight and often fail to grow and gain weight at the expected rate, sometimes referred to as failure to thrive. (Salmon and Hehman, Chap. 9)

Social agency a social process by which a child initiates or directs experience related to learning and development. (Ivey Henry and Morelli, Chap. 10)

Social brain hypothesis the theory that increased social cognition was a driving force in human evolution and necessitated a large brain to handle the variety and complexity of human communities. (Bjorklund, Chap. 2; Locke and Bogin, Chap. 6)

Social referencing an infant's use of another person's emotional cues to interpret an ambiguous or uncertain event. (Bjorklund and Hart, Chap. 1; Hart, Chap. 15)

Sympathy an affective response to another's emotional state that involves feelings of concern for the other. (Vaish and Grossmann, Chap. 16)

Synaptogenesis formation of synapses. (Bjorklund, Chap. 2; Wilder and Semendeferi, Chap. 3)

Synchrony biobehavioral and microsocial processes that attune individuals to each other's rhythms and responses, and which facilitate and maintain social and emotional bonding. It implies mutual adaptations of physiology and behavior in relationships over time, increasing the efficiency of communication and provisioning of needs. (Ivey Henry and Morelli, Chap. 10). See also **Parent-infant synchronization.**

Temple syndrome a short stature disorder of imprinting. It is characterized by low birth weight, hypotonia and motor delay, feeding problems early in life, and significantly reduced final height. (Salmon and Hehman, Chap. 9)

The strange situation procedure a laboratory procedure in which caregiver-infant pairs experience two separations, each followed by a caregiver-infant reunion, designed to assess different patterns of attachment in infants and young children. (Simpson and Jaeger, Chap. 11)

Theory of mind an ability to attribute mental states such as goals, intentions, desires and beliefs to others (and oneself) and to understand that mental states determine behavior. (Buttelmann, Chap. 13)

Traditional models of fear theories that hold that all fears are learned through domain-general mechanisms such as conditioning, observation, and through verbally transmitted information. (Rakison, Chap. 14)

Ultimate level of explanation concerned with the fitness consequences of a trait or behavior; why did the trait or behavior evolve and how does it contribute to a species' survival and reproduction? (Vaish and Grossmann, Chap. 16)

Unpredictability how consistent or foreseeable future events are in an environment, with environments that are less consistent being more unpredictable. (Simpson and Jaeger, Chap. 11)

Vocal learning Ability to modify one's vocal sounds by mimicking others' vocalizations and environmental sounds. (Doi and Masataka, Chap. 9)

Word segmentation process of figuring out word boundaries in linguistic sound. (Doi and Masataka, Chap. 9)

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