Chapter 5
The Phylogenesis of Human Personality: Identifying the Precursors of Cooperation, Altruism, and Well-Being

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Introduction

Human beings have a natural potential for love and altruism that is expressed when they are functioning in a healthy way. Prosocial behavior is a prominent aspect of health and happiness in human beings, which is characteristic of integrated states of physical, mental, social, and spiritual well-being (Cloninger and Zohar, 2010). From a neuropsychiatric perspective, selfish and uncooperative behaviors are signs of mental dysfunction because they are strongly associated with life dissatisfaction and ill health (Cloninger, 2004). From an evolutionary perspective, antisocial behavior in human beings is the unregulated expression of primitive impulses because it is a consequence of the failure of the human capacity for apperception of unity (Cloninger, 2009).

Because humans retain both primitive and higher cognitive functions, people are capable of either terrifying violence and cruelty (Virkkunen et al., 2007) or peaceful kindness and altruism (Moll et al., 2006). Cooperation or violence may be expressed by different people in the same situation or by the same person in different situations (Fleeson, 2004). Whether people act violently or kindly depends on complex influences on their past personality development, their immediate situation, and their values and aspirations for the future (Cloninger and Svrakic, 1997; Fleeson, 2004).

In order to understand the development and regulation of prosocial and antisocial behavior in individuals, it is essential to understand the complex evolutionary development of cooperation in human beings. A rigorous understanding of personality, like everything else in biology, makes no sense except in the light of evolution (Dobzhansky, 1973). The unity of personality within a person and its diversity among people can only be understood when considered from the perspectives of both ontogeny (Cloninger, 2003) and phylogeny (Cloninger and Gilligan, 1987; Cloninger, 1994).

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Personality is defined as the way people learn, but as simple as that sounds, the processes by which living organisms learn involve complex adaptive systems. The self-organizing unity of an individual's personality must ultimately be understood in its full context, which includes awareness of its sexual, material, emotional, intellectual, and spiritual aspects (Cloninger, 2004). There is widespread agreement among cognitive scientists and psychobiologists that personality is (i) a complex set of abilities or adaptive functions, and (ii) the functions crucial for information processing involve multiple steps including the initial perception of sensory inputs, conceptual processing of percepts, and intuitive synthesis of perceptual and conceptual phenomena in self-aware consciousness, and (iii) that apperception (i.e., the contextual spatio-temporal processing of perceptions in self-awareness) is episodic, intuitive, preverbal, and synthetic. Most neuroscience assumes that there is a universal structure of human brain functions that has a distinct evolutionary history. However, much uncertainty remains about how to specify the complex set of functions that comprise human adaptation, but, as I will describe here, accumulating evidence about human phylogeny may finally fill that gap (Cloninger, 2009).

Abilities that emerge at one point in phylogeny are often co-opted later for more general functions that expand awareness within this hierarchy. For example, complex functional abilities like language have many precursors that emerge before the syntactical functions of modern human language—among them the ability to communicate through expressive gestures, emotional vocalizations, and meaningful signs (Christiansen and Kirby, 2003; Hauser et al., 2002; Pollick and de Waal, 2007; Weiss and Newport, 2006). Hence, modern language is like "a new machine built out of old parts" (Bates and MacWhinney, 1989). Similarly, many animals can cooperate in diverse ways, but there are diverse physical, emotional, intellectual, and transcendental abilities that are needed before altruism (i.e., the intentional practice of disinterested and selfless concern for the well-being of others) is possible.

The Triune Human Brain

From the evolutionary perspective of comparative neuroanatomy, the human brain is "triune," that is, one whole with three distinct components. MacLean distinguished these components as the "reptilian" brain, the old mammalian brain, and the new mammalian brain of primates (MacLean, 1985). A closely related, but not identical, distinction is between the components of the human brain that regulate the three major systems of learning and memory: behavioral conditioning, semantic learning, and episodic or self-aware learning (Cloninger, 2004, 2009; Tulving, 1987). These perspectives are based on recognition of fully developed brain systems for behavioral conditioning in reptiles and birds, followed by more complex mental processing with differentiation of the neocortex in the forebrain of mammals, and self-awareness in human beings (Cloninger, 2009). These three major systems of learning and memory have distinct properties and can be dissociated experimentally by specific brain lesions (Tulving, 1987, 2001, 2002).

Self-aware consciousness has an objective biological basis and produces observable phenomena, such as autobiographical memories, about which predictions can be made and tested (Levine, 2004; Tulving, 1987, 2002). Self-aware memory matures at about 4 years of age in human children, and it is only after this that human children show much cognitive advantage in development when compared to chimps (Povinelli, 2000; Povinelli and Giambrone, 2001; Tulving, 2001).

What Evolutionary Transitions Led to Humans?

Elsewhere I have described in detail the timeline of major transitions in brain system structure and function in human evolution (Cloninger, 2009). Here I will only briefly review this and summarize key information in Table 5.1.

All life forms share DNA and its associated cellular apparatus as the mechanism of genetic inheritance going back to the emergence of the first life forms on earth 4 billion years ago. The ancestral lineage leading to humans includes the first eukaryotes, craniates, and amniotes, thereby leading to the common ancestor shared by squamates and mammals. Among mammals, the line probably continues from the earliest non-placental mammals to ancestral tree shrews and then to the proto-primates called plesiadapiforms (see Table 5.1).

Mating behavior is the first brain function to come under neocortical control in mammals, as is colorfully displayed by Echidnas (Rismiller, 1999). During the mating season, echidnas form a train of three to four males (sometimes 2–11) following a single female. The female produces a pheromone that attracts the males. They walk nose to tail in queue for up to 6 weeks before mating. Males may lose up to 25% of their body mass while pursuing the female. Echidnas are highly versatile in mating either above or below ground, indicating intentional regulation of a strong sex drive by the somatosensory (touch) neocortex (Proske et al., 1998; Proske and Gregory, 2003; Kaas, 2008).

The tree shrews are small placental mammals that are known from around 125–65 mya during the Cretaceous when flowering plants were beginning to diversify and dinosaurs were still the dominant land animals. The common ancestor of tree shrews, colugos, and primates diverged before 65 mya from other orders of placental mammals (Murphy et al., 2001; Springer et al., 2003). Modern tree shrews are solitary foragers in pair territories marked by scent (Kawamichi and Kawamichi, 1979; Emmons, 2000). Tree shrews must spend most of their time foraging in order to consume enough arboreal insects to survive (Emmons, 2000). Their young develop rapidly to begin their own solitary foraging. Understanding the behavior of tree shrews is important because, as remote ancestors of all primates, the behavior of ancestral tree shrews can serve as homologues of the functions common to all placental mammals, such as the basic drives for sex and food. In particular, tree shrews provide a model of the common neurobiological mechanisms that produce anxiety, aggression, craving and sensitization to drugs of abuse when confronted by intruders who would compete in foraging for the limited nutrients in their territory

Table 5.1 Overview of the evolution of major brain functions in human evolution

Clade 0: Craniates (ancestor of hagfish—505 mya)

Emergent Functions: Animals with skulls, all associated with emergence of the neural crest for development of central nervous system. Also all have ectodermal placodes for development of paired organs for smell, hearing, and vision in the head.

Emergent Structures: Neural crest derivatives—skull, brain with five components, and cranial nerves 1–10 (except for eye muscle nerves 3,4,6 which may have been secondarily lost by hagfish). All have peripheral nervous systems, endocrine tissues, in addition to paired organs for smell, hearing, and vision in head. Neuropeptides have important regulatory functions in all craniates (Holmgren and Jensen, 2001) as well as in early invertebrates (Strand, 1999).

Clade 1a: Early Vertebrates (ancestor of fish, amphibia—480 mya)

Emergent Functions: Fish and amphibia show well-developed associative conditioning. Whole genome duplicated. Amphibia still reproduce in water.

Emergent Structures: Fish have a bony vertebral column, fins for locomotion in water, scales, and a two-chambered heart. Fins are adapted for walking on land in lung fish and amphibia. Cranial nerves for eyes (3,4,6) are present typically (Janvier, 1997). Unlike higher vertebrates, the earliest vertebrates (i.e., lampreys) have no myelin sheaths around nerves, so neural responses are slow. In fish and amphibia, cerebral hemispheres are small and mostly concerned with smell. Amphibians were the first vertebrates to develop vocalization, making sounds with their mouth closed. The midbrain is the dominant association center that regulates both sensory input and motor output in fish and amphibians. Midbrain receives nervous input from throughout the body and sends extensive output to other parts of the brain and spinal cord. Midbrain has two large optic lobes for processing visual information. Cerebrum and thalamus in the small forebrain receive sensory input but have no feedback to or control of midbrain.

Clade 1b: Early Amniotes (ancestor of reptiles and birds—315 mya)

Emergent Functions: Adaptations for tetrapods to live and reproduce on land, breathing oxygen, and amnion to protect developing fetus.

Emergent Structures: The hypothalamus in the basal forebrain is enlarged in amniotes compared to anamniotes. The brain of squamates is centrally regulated by the hypothalamus without thalamo-cortical feedback to or control of hypothalamus. The dorsal cortex of squamates is a single layer of pyramidal neurons with connections with the thalamus (Bruce and Neary, 1995; Nieuwenhuys, 1994). The thalamus receives much sensory input and is larger than the midbrain in amniotes. In birds, forebrain control of vision becomes important and smell unimportant, much as it does in primates.

Table 5.1 (continued)

Clade 2a: Early Mammals (ancestor of non-placental mammals—220 mya) *Emergent Functions*: All mammals are warm-blooded, have skin with hair and glands, including milk-producing glands to feed young. The behavior of early mammals is concerned with intentional control of basic impulses of life preservation, such as mating and eating. *Emergent Structures*: Neocortex emerges with five to six layers as the dominant association center for sensory input and motor output, allowing cortical control of bodily functions integrated by the midbrain of fish and amphibians, including sex, diet, and movement, in a way directed primarily for life preservation. All special senses are represented neocortically, but most of neocortex processes touch with no separate motor areas. Neocortex is the dominant association center for control of sensory input and motor output in all mammals but is not differentiated into sensory and motor regions in non-placental mammals. Hence intention and action are not well-differentiated in non-placental mammals.
Clade 2b: Placental Mammals (ancestor of tree shrews—125–65 mya) *Emergent Functions*: Specialized genital openings and placenta so tree shrews can bear live young. Young develop quickly and require little maternal care, so they can spend most of their time foraging for insects in trees. They have well-developed distance senses and skill in grasping insects but limited ability to digest fruits. They have greater ability to regulate cravings, such as desire for sex or food, than monotremes, and do not reproduce when there is inadequate supply of nutrients for childbearing (Emmons, 2000). Anxiety and impulsive aggression may result when frustrated or threatened by intruders into their territory, which threatens their source of food and self-preservation. *Emergent Structures*: Somatosensory, motor, and pre-motor areas are differentiated in neocortex of tree shrews. About 20 distinct cortical regions have been identified compared to over 200 in human beings (Kaas, 2008).
Clade 3a: Proto-primates (ancestor of plesiadapiforms—65–55 mya) *Emergent Functions*: Enhanced physical agility to grasp food and digest fruit, and provide extended maternal care of young compared to tree shrews. Eyes still laterally directed. *Emergent Structures*: Only fossils are extant, but fossils and functions suggest similarity to strepsirhines except eyes are not forward-directed.

Table 5.1 (continued)

Clade 3b: Strepsirhines (ancestor of lemurs, lorises, bushbabies—47 mya) *Emergent Functions*: Nocturnal solitary foragers with skill in finding and selecting food. Brain size varies with foraging complexity, flexibility of diet and activity patterns, not social variables. Extensive maternal care provided to young. Teeth are distinctive for highly variable diets of primates. *Emergent Structures*: Taste is processed in primary gustatory cortex prior to hypothalamus and amygdala (frontal operculum and insula) (Verhagen et al., 2004). Eye–hand coordination facilitated by greater topical ordering of inputs to nuclei for hand and foot and expansion of parietal association cortex. Ventromedial hypothalamus has many oxytocin receptors, allowing regulation of feeding behavior in favor of reproductive role. Social bonding and maternal care are regulated by olfactory cues, mediated by oxytocin binding in amygdala, nucleus accumbens, and the olfactory bulb that facilitate preference bonds and scent recognition (Broad et al., 2006). Differentiation of dorsal posterior insular cortex (DPIC) supports awareness of the affective aspects of sensation (Craig, 2005).
Clade 4a: Haplorhines (ancestor of tarsiers and monkeys—40 mya) *Emergent Functions*: Modern tarsiers are nocturnal or crepuscular in activity but have specializations for day-time activity (fovea and absence of light-reflecting tapetum lucidum in their eyes). Monkeys are diurnal and social with increased metabolic rate able to support larger body and brain. In order to take advantage of warmth and light of day-time activity in a cooling climate, there was increased reliance on visual information accessible at a distance, rather than chemosensory input, even in simians of small size (Broad et al., 2006; Ross, 2000; Ross and Kirk, 2007). Anthropoids have enhanced emotional awareness from adaptation to diurnality, which fostered development of enduring social relationships. Much time in social activities of large groups provides protection from visual predation. Monkeys show cooperative behaviors such as prosocial giving (de Waal et al., 2008) and noncooperation with inequity (Brosnan and De Waal, 2003; Brosnan et al., 2006). *Emergent Structures*: Prefrontal cortex (mainly orbital and medial PFC) expands and projects directly to hypothalamus, thalamus, septum, basal amygdala, and striatum, allowing neocortical control of functions regulated by hypothalamus in basal forebrain of squamates. Olfactory links to social reward centers in amygdala and nucleus accumbens are largely, but not entirely, replaced by PFC inputs concerned with multisensory integration, emotion regulation, and motor sequence planning (Broad et al., 2006). Central integration of sensory and motor functions in the limbic forebrain (hypothalamus and interconnected portions of prefrontal cortex) allows affective regulation of behavior and social interactions. Mirror neuron system appears in monkeys, allowing mirroring of observed behaviors by neurons in speech motor area (BA 44, posterior inferior frontal gyrus), ventral premotor area (VPA), and IPL (BA 40) (Rizzolatti and Craighero, 2004). The VPA supports action understanding and imitation, a precursor to language. In monkeys, multi-modal affective information is also relayed to the middle insular cortex, which has extensive reciprocal connections with the amygdala and hypothalamus, so it is well-positioned for the regulation of sensuality.

Table 5.1 (continued)

Clade 4b: Apes (ancestor of lesser and greater apes—16–4 mya)
Emergent Functions: Highly social, warm emotional expression and affectivity, flexible dominance hierarchies, imitation learning, and proto-cultural transmission of traditions and local conventions (Bonnie et al., 2007; Whiten et al., 2007). Australopithecines emerged about 4 mya and developed skilled bipedal walking (Agnew et al., 1996).
Emergent Structures: Somatosensory processing becomes serial and less parallel for greater depth of processing. Differentiation of parietal association cortex for integration of visual, auditory, and somatosensory information. Great apes and humans, and not other primates, have Von Economo Neurons that allow reciprocal connections of AIC and ACC. Mirror neurons are also present in great apes in Broca's area (BA 44) and IPL. Also in great apes there is differentiation of the anterior insular cortex (AIC) for enhanced emotional awareness, which supports the communication of social emotions in great apes (Craig, 2009).
Clade 5a: Hominids (ancestor of *H. ergaster*, 1.9–0.8 mya)
Emergent Functions: Precision grip for making stone tools, omnivorous with reduced size of post-canine teeth, group-living gatherers with some planning, and/or hunting in social groups to obtain essential nutrients for increasing brain size. This is described as early "mimetic" or "intellectual" culture in which there are executive skills for non-emotional problem-solving and long-term planning according to a mental template (Donald, 1991; Cloninger, 2009). *H. habilis* had enlarged brain of about 640 cc (about half of modern *H. sapiens* 1350 average) (Conroy et al., 1998), smaller back teeth and jaw muscles for chewing (Rak, 1985; Rak et al., 2007), and hemispheric asymmetry like later hominids (Corballis, 2003), but postcranial skeleton similar to australopithecines (Wood and Collard, 1999). *H. ergaster* had an enlarged brain (about 800 cc), reduced arm length with arm/leg proportions like modern humans, forward projection of external nose, narrow pelvis, barrel chest, and reduced sexual dimorphism compared to australopiths and possibly *H. habilis* (Klein, 2009). They were able to emigrate out of Africa and were ancestors of all later species of *Homo*, so they are likely to have been the first largely hairless hominids and developed dark skin replacing the pale skin under the fur of apes and earlier hominids. The external nose and naked dark skin provided adaptation to hot arid climate and seasonal rainfall that occurred at the time of their emergence (Klein, 2009).
Emergent Structures: Hemispheric asymmetry is observed in *Homo* and some australopithecines, particularly around the lateral sulcus in regions related to language in modern humans (Corballis, 2003, 2009b; Deacon, 1997; Eccles, 1989). Fossils only but enlarged frontal opercular area and IPL, suggesting emergence of executive planning and representation based on cross-modal transformation of tactile, auditory, and visual information. PFC inputs to brain reward centers allow meaning and purposeful planning to organize social relationships and solve physical problems using a non-syntactical protolanguage of mime, vocalization, and metaphoric understanding (Broad et al., 2006; Bickerton, 2010; Pinker, 2010) and/or segmentation of loud calls (Geissmann, 2002). The frontal opercular and ventral premotor area support action understanding and imitation, which are characteristic of an early "mimetic" culture with a longer working memory than observed in great apes (Corballis, 2009a; Deacon, 1997).

Table 5.1 (continued)

Clade 5b/6: Pre-modern hominids of Middle Pleistocene (780–126 kya)

Emergent Functions: Development of gatherer–hunter culture of middle Pleistocene with evidence of executive intellectual abilities (i.e., objective/non-emotional problem-solving and long-term planning), such as refined tools with local stylistic traditions, domestication of fire, organized group hunting, cooperative division of labor, sharing, trade, prolonged care for young and disabled, and possibly taboo, as well as construction of temporary shelters and widespread migration in social groups (McBrearty and Brooks, 2000; Goren-Inbar et al., 2000; Tattersall, 2008a). There was a cooperative social structure with cultural transmission of skills and traditions in hunting and tool-making, but communication was probably by gesture and meaningful sounds involving observation of body language, action understanding, and imitation without a syntactical language involving conceptual shifts in time and viewpoint. There is no direct evidence for or against modern language or self-awareness in pre-modern hominids except that no pre-modern hominids competed successfully for survival with modern *Homo sapiens*, who are the only primates who do have the capacity for autobiographical narrative and flexible viewpoint shifting as observed in modern syntactical language. The only known advantage of modern humans over Neandertals and other pre-modern hominids of the Middle Pleistocene is their self-awareness, which is necessary for the syntactical functions of modern language and music, such as perception of harmony and temporal viewpoint. Because of lack of detail about brain networks and lack of certainty about the functional capacities of particular hominids, it is unclear whether all hominids existing during the Middle Pleistocene should be grouped together or if Neandertals or possibly other pre-modern hominids should represent a sixth clade.

Emergent Structures: Only fossils are extant, but findings indicate cross-modal symbolic ability with prominent development of IPL (BA 39/40) and emergence of brain default network that supports daydreaming, holistic attention, and subconscious problem-solving. Default brain network includes neo-neocortical regions as subsystems in the ventral medial PFC, dorsal medial PFC, IPL, posterior cingulate/retrosplenial cortex, and hippocampal formation and related entorhinal and parahippocampal cortex (Buckner et al., 2008; Raichle et al., 2001).

Clade 7: Modern *Homo sapiens* (about 150 kya to present)

Emergent Functions: Early "mythic" culture (7a) of *H. sapiens* involves evidence of self-awareness suggested by ritual burials with grave-goods and ornamentation and probably spoken syntactical language suggested by prehistoric oral traditions in cosmogenic and heroic myths. By 35 kya, there is strong evidence of a "theoretic" culture (7b) with self-aware consciousness allowing uniquely human development of art, science, and spirituality, including symbolic representation of lunar cycles. There was still a hunter–gatherer culture until near the end of the Ice Age about 11–10 kya when there were founding of permanent cities with agriculture of domesticated grains and domestication of animals.

Emergent Structures: The face of *H. sapiens* is distinguished from earlier hominids by absence of thick brow and by presence of a chin due to small size of structures for mastication (Rak et al., 2002). Auto-noetic awareness depends on a distributed fronto-temporo-parietal network with encoding via hippocampus (Levine, 2004). The same brain regions are most recently differentiated in evolution and are late to myelinate. The whole neocortex becomes a functional whole by linking all association areas through projections of visual system, Once developed in children after 4 years of age, anterior and medial prefrontal cortex is activated in support of egalitarianism (Fehr et al., 2008), charitable donation (Moll et al., 2006), spontaneous musical improvisation (Limb and Braun, 2008), and syntactical functions for shifting viewpoints in dialog and perception of harmony in musical sequences (Schellenberg et al., 2005).

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(McEwen, 2000; Toates, 2001) (see Table 5.1). Hence tree shrews are a model for the root causes of aggression in human beings when there is failure of the regulatory mechanisms that evolved later to promote cooperation in primates.

Only one arboreal species of tree shrew can survive in the same area because of the limited number of arboreal insects, so they are aggressive for sake of self-preservation in craving to obtain what they need for survival. They develop anxiety with impaired spatial memory when stressed by a dominant intruder to their territory (Kawamichi and Kawamichi, 1979; Magarinos et al., 1996; McEwen, 2000). Consequently, adaptive radiation from the primitive tree shrew involved expansion to diurnal and terrestrial niches in more derived tree shrews (*Tupai*) (Emmons, 2000).

The common ancestor of tree shrews and primate-like mammals are thought to be like the pentail tree shrew in being strictly nocturnal, arboreal, and having only rudimentary capacity for obtaining and digesting fruits. To be able to exploit the availability of fruits in flowering trees more fully, ancestors of primates needed hands for grasping fruit in terminal branches, teeth adapted for eating fruit, and a more complex digestive system with a slower transit time compared to ancestral tree shrews and pentails (Emmons, 2000).

The primate-like mammals called Plesiadapiforms, like *Carpolestes simpsoni*, are known from 65 to 55 mya in the Paleocene epoch of North America and Eurasia. They had a grasping foot like primates, including an opposable toe and a nail rather than a claw. It could probably grasp with its hands as well. As a result, it was well-adapted to move in the terminal branches of fruit-bearing trees that flourished at that time (Sussman, 1991; Sargis, 2002; Bloch et al., 2007). Other proto-primates, like *Purgatorius ceratops*, were also small, arboreal, and nocturnal, like ancestral tree shrews, but were better adapted for consuming fruit and nuts, as indicated by their primate-like teeth, shorter snouts, and adaptations for grasping. Unlike ancestral tree shrews, proto-primates were omnivorous, consuming fruits, nuts, seeds, leaf buds, insects, and small vertebrates (Biknevicius, 1986). Visually guided reaching and grabbing with the forelimb tended to replace grasping with the mouth, requiring eye–hand coordination, as observed in true primates.

Among primates, the line to human beings continues through ancestors in common with lower primates (i.e., suborder *Strepsirhini*, characterized by their wet noses, including lemurs, lorises, and bushbabies) and later with higher primates (i.e., suborder *Haplorhini* with simple dry noses, including tarsiers, monkeys, and apes) (Fleagle, 1999; Springer et al., 2003). The members of the primate suborder Strepsirhini are remarkably varied in their characteristics. The ancestral Strepsirhini (i.e., ancestral adapiform or earliest lemur) was the earliest true primate, which is known from fossils dated to the early Eocene (56–50 mya) or perhaps slightly earlier based on phylogenetic analyses (Kay et al., 1997, 2004). Like ancestral tree shrews and plesiadapiforms, they were nocturnal and arboreal with wet noses (Fleagle, 1999; Kay et al., 1997). A prominent behavioral breakthrough from plesiadapiforms to strepsirhines is superior adaptation for grasping and leaping for feeding and locomotion in trees (Szalay and Delson, 2001). The superior grasping and leaping abilities were accompanied by only minor skeletal changes, such as a grasping pollex and hallux (probably already present in plesiadapiforms) and changes in the articulation of bones in the arm. However, the superior grasping–leaping ability coevolved with great dietary flexibility in ancestral primates (Chivers and Hladik, 1980; Chivers, 1998).

Despite the benefits of their improved physical agility and their ability to digest fruits and seeds well, strepsirhines are still constrained by the need for energy conservation. For example, many of the traits of lemurs in Madagascar are either adaptations to conserve energy (e.g., low basal metabolic rate, torpor, sperm competition, small group size, and seasonal breeding) or to maximize the efficiency of use of scarce resources in a harsh and unpredictable environment (e.g., the ability to alternate activity between day and night, territoriality, female dominance, fibrous diet, weaning synchrony) (Wright, 1999). Gestation and lactation are periods of high expenditure of energy, so they are limited to seasons when nutrients like fruits are relatively abundant (Meyers and Wright, 1993).

Strepsirhine characteristics were originally associated with solitary activity at night in trees, but are often still retained in strepsirhine lines that successfully adapted to other habitats and social organizations. For example, lemurs include species that are solitary, pair-living, or group-living (Kappeler, 1997). The nocturnal strepsirhines are usually solitary, and the pair-living strepsirhines are usually at least partly active at night. Diurnal species, like the ring-tailed lemur, are group-living (Kappeler, 1997; Sussman, 2003). Despite this variability in habitat and social organization, all strepsirhines are typified by characteristics that distinguish them from anthropoid primates. The typical strepsirhine features include a highly developed sense of smell, specialized scent glands for non-visual communication, protruding snout, prominent whiskers, a dental comb from lower incisors and canines, large and mobile external ears, a postorbital bar, and forward-directed eyes with binocular vision and tapetum lucidum (which reflects light back toward the pupil and makes eyes visible in the dark). Strepsirhines have a simple (epitheliochorial) placenta, and they lack the capacity for year-round reproduction conferred by the menstrual cycle of haplorhines (Chivers, 1998). Their upper lip is attached to their gums by a membrane, thereby limiting facial expression. The regulation of social and parental relationships in strepsirhines depends on individual recognition by olfactory cues (Broad et al., 2006).

The ancestral strepsirhines were nocturnal and solitary (Kappeler, 1997; Overdorff, 1998; Jolly, 1998; Hilgartner et al., 2008), presumably because of the continued reliance of social organization on close contact for olfactory cues and hormonal regulation by the hypothalamus in strepsirhines, rather than emotional processing of visual information and integration of multisensory information at a distance in the prefrontal cortex in anthropoids (Broad et al., 2006). With no competition with anthropoid primates on Madagascar, lemurs were able to diversify in many ecological niches, including gregarious species that are active during the day (i.e., either diurnal or cathemeral). Gregarious lemurs differ from anthropoid primates in several social, demographic, morphological and ecological features (van Schaik and Kappeler, 2010). They lack sexual dimorphism in canine and body size. They live in groups with equal adult sex ratios (pairs or larger groups). In most species of lemurs, females dominate males and have brief and often synchronized estruses. Gregarious lemurs illustrate a pathway to social organization in which the strepsirhine social groups are based on pair-bonding with breeding pairs of adults at the core of the social structure and additional individuals serving to bolster an essentially pair-bonded relationship that facilitates reproductive success (Shultz and Dunbar, 2007; van Schaik and Kappeler, 2010). Social interactions between male and female lemurs help to initiate ovarian cycles and behavioral estrus (Whitten and Brockman, 2001). However, gregarious lemurs differ clearly from gregarious anthropoid primates: most species of pair-living lemurs are at least partly nocturnal and do not provide direct paternal care for young dependents (Kappeler, 1997). A qualitatively distinct second pathway to bonded social systems involves extending the maternal-infant attachment into adulthood and to other members of a social group as conciliatory caretakers of one another for protection from predators, as typically occurs in anthropoid primates (Broad et al., 2006; Dunbar and Shultz, 2007; Shultz and Dunbar, 2007). The human nuclear family emerges much later along with reduced sexual dimorphism, pair-bonding, and specialized roles for both parents in child care in *Homo ergaster* and its descendents (Klein, 2009).

Tarsiers have mixed features of both strepsirhines and anthropoids (see Table 5.1). They are classified with anthropoids on the basis of their dry nose, cranial morphology, and specialization for day-time activity, but behaviorally they are closer to strepsirhines in their nocturnality, solitary foraging, seasonal breeding, and reliance on scent marking for social communication. Like nocturnal strepsirhines (i.e., lorises, bushbabies, pottos, and some lemurs), the solitary activity of tarsiers suggests that they do not form emotional attachments like those of anthropoid primates (Mineka and Suomi, 1978; Suomi, 1984; Weaver and de Waal, 2002).

By the end of the Eocene, there was a climatic upheaval with temperatures cooling during which the early anthropoids emerged and many strepsirhine species became extinct. Tarsiers survive only on several islands in Southeast Asia. The transition from nocturnality to diurnality has been considered to be the key adaptive shift that occurred at the base of the tarsier-anthropoid transition (Kay et al., 1997). The early anthropoids were small, diurnal, arboreal insectivore–frugivores with unfused mandibular symphyses, small brains, and either dichromatic or trichromatic vision (Kay et al., 1997). The early anthropoids adopted locomotor patterns with more arboreal quadrupedalism and less leaping. The fundamental importance of diurnality during the cooling temperatures of the Eocene-Oligocene transition is shown by the extensive anthropoid adaptations for diurnal visual acuity in comparison to their nocturnal ancestors who became extinct except in isolated island habitats (Ross, 2000; Ross and Kirk, 2007). Distinctive adaptations of the anthropoid visual system for diurnality include highly convergent orbits, small corneal diameter and posterior nodal distance, high concentration of cones and ganglion cells, and extreme magnification of foveal regions of the visual field in the visual cortex (Ross, 2000; Ross and Kirk, 2007).

Monkeys and apes are typically diurnal and active in social groups most of the time (Sussman, 2003; Sussman and Chapman, 2004). Like tarsiers, monkeys have non-reflective eyes and binocular vision. In contrast to prosimians (i.e., strepsirhines and tarsiers), monkeys have a reduced snout and less reliance on smell for communication, a free upper lip allowing for more expressive faces, usually one offspring with extended maternal care, delayed sexual maturity and an extended life span. The olfactory input to limbic areas concerned with social reward, such as amygdala and nucleus accumbens, is replaced in monkeys and apes by prefrontal neocortical inputs concerned with multimodal sensory integration, emotional regulation, and planning (Broad et al., 2006). These changes allow greater social regulation of aggression and conflict in anthropoids than in prosimians. Compared to prosimians, the social interactions of anthropoids became less dependent on olfaction as a result of the combination of enhanced diurnal visual acuity, facial mobility, and related sensory changes facilitating emotional intimacy and attachment (Broad et al., 2006). The evolution of larger brains, symphyseal fusion, and definitive trichromacy occurred later in anthropoid evolution (Ross, 2000).

Mentally, chimps show learning abilities comparable to a 2- or 3-year-old modern human child (Suddendorf and Whiten, 2001) but not the capacity for self-aware recollection that develops in 3–4-year-old human children (Povinelli, 2000; Povinelli and Dunphy-Lelii, 2001; Povinelli and Giambrone, 2001). For example, chimpanzees have excellent visual-motor hand coordination and learn to make stick tools from opportune plants to fish out termites from their mounds for eating, and their status in social groups varies according to which of their friends and family are present (Donald, 1991; Preston and De Waal, 2002; van Lawick-Goodall, 1967). They can identify themselves in a mirror and can plan how to obtain food that is out of reach by using what is in their environment instrumentally, as demonstrated in the early "insight" experiments of Wolfgang Kohler (Donald, 1991). Chimps have also been taught to communicate with gestures like sign language. They can be trained to produce two- to four-word sentences, but they do not spontaneously develop symbolic language or have a capacity for syntactic functions beyond simple two-word order rules or to fully describe what they evidently know about the environment (Donald, 1991; Povinelli, 2000). Chimps can be trained to use signs for dozens of things to obtain food rewards but they do not display evidence of any recollection of internal memories in self-aware consciousness, such as shifts in viewpoint about things that are out of sight (Suddendorf et al., 2009).

The great apes can show warm emotional expressions and affectivity, including ventral hugging, but do not do not spontaneously provide food to other group members, which suggests that they lack a capacity for perception of unity needed for a concept of fairness or egalitarianism. Prosocial giving is well-documented in monkeys, particularly when there is social affiliation and the distribution of rewards are equitable (Brosnan and De Waal, 2003; Brosnan et al., 2006; de Waal, 2008; de Waal et al., 2008; Preston and De Waal, 2002). In contrast, anthropoids act selfishly when the possible recipient is out of sight or the distribution of rewards cannot be equitable (de Waal et al., 2008). The social behavior of monkeys and apes is usually docile in natural free-ranging habitats (Sussman and Chapman, 2004), but aggressive competition, threat displays, and violence increase in monkeys and apes in response to social strangers, violation of territorial space with increasing population density, and frustration over restricted access to food and other cravings (Southwick, 1967). The affective quality of anthropoid social behavior is not based on an instinct for either peace or violence; rather it is an adaptive function or tool for emotional competition, social negotiation, and conflict resolution (de Waal, 2000).

The sociality of anthropoid primates can be characterized in terms of its tendency toward "reconciliation" after emotional conflicts. For example, after a fight, chimps often engage in mouth-to-mouth kissing and embraces. Other anthropoid primates reconcile by sexual intercourse, clasping the other's hips, grooming, grunting, and holding hands (de Waal, 2000). Responsiveness to long-distance cues in anthropoid primates facilitates close emotional relationships among triads and larger groups of individuals, so that a third party, such as a high-ranking group leader, can intervene to help pacify and resolve conflicts among members of the social group (de Waal, 1996, 2000; Parr et al., 1997). Affective reconciliation is an important function in anthropoid primates because their survival depends substantially on social cooperation. Consequently, conflict resolution is advantageous to promote fitness and to reduce emotional distress. Monkeys and apes show emotional hypersensitivity with the display of a wide range of prosocial and antisocial behaviors by the same individual depending on the social context rather than a drive for either prosocial or antisocial behavior (de Waal, 2000). Even aggressive monkeys, such as rhesus macaques, can learn conciliatory behaviors as a result of their need for conflict resolution (de Waal, 1996, 2000). Such social learning in anthropoid primates also allows proto-cultural transmission of traditions in courting, foraging, food preparation, and grooming (Kawai, 1965; de Waal, 1999; Whiten et al., 2007).

Among the hominoids, the line to modern humans continues through the first ancestors of Australopiths to members of genus *Homo*. The details of the lineage are intensively debated, but the functional and structural changes are fairly clear even when the precise transitional forms remain uncertain. The earliest hominids lived in what are now the African countries of Chad (*Sahelanthropus*), Ethiopia (*Ardipithecus*), and Kenya (*Orrorin*) around 6.5–4.4 million years ago (Tattersall, 2008b; White et al., 2009). The earliest striding bipedal ape (*Australopithecus anamensis*) is known in Kenya 4.2 mya, and is regarded as ancestral to *Australopithecus afarensis* and *A. garhi* (Kimbel et al., 2006; White et al., 2006; Shreeve, 2010). The australopiths lived at the forest edge and surrounding woodlands in Africa at a time when the dry climate and increasing seasonality were breaking up the forests (Tattersall, 2008a). Despite being bipedal and having a wide environmental niche throughout Africa, they still had small ape-like brains. For example, the endocranial volume of *A. garhi* was about 450 cc (Shreeve, 2010). Australopithecines also retained ape-like body proportions with relatively short legs, narrow shoulders, conical thoraxes, flaring pelves, and long arms for millions of years without developing more modern human features. Bipedal australopiths differed from hominids that emerged later in their ape-like brains and bodies and in their lack of innovation.

Homo habilis is usually classified as the earliest species in the genus *Homo* on the basis of the average brain volume being greater than 600 cc and prominent development in cranial endocasts of brain regions corresponding to Broca's area (BA 44) and the inferior parietal cortex (BA 39/40) in the left, but not the right, hemisphere. However, these asymmetric fronto-parietal prominences are almost certainly related to increasing facility in control of the free hands of bipedal habilines, not speech. In extant apes, Broca's area is an area controlling sequences of movements of the hand and is not involved at all in speech or vocalizations (Passingham, 1981). Damage to Broca's area in nonhuman primates has no effect on the rate or acoustic qualities of vocalization and does not impair social communication (Jurgens, 1982; Kirzinger and Jurgens, 1982). Anthropoid vocalization is sometimes called "limbic language" or "emotional language" because monkey calls are expressed in response to the anterior cingulate cortex (ACC) and amygdala acting on brainstem centers such as the periaqueductal gray area (PAG). The ACC is only necessary for the volitional initiation of vocalization and not for spontaneous vocalization in emotional situations, such as spontaneous monkey calls or human pain groans (Jurgens, 1982, 1983, 2009; Jurgens et al., 1982; Kirzinger and Jurgens, 1982). Accordingly, Broca's area began to regulate vocalization by programming the premotor area's control of the oral and laryngeal musculature for expressive speech early in the hominid lineage, perhaps as early as habilines (Corballis, 2003).

Nevertheless, there is no angular gyrus in anthropoid primates like that in the inferior parietal lobe (IPL) of modern humans (Geschwind, 1965a, b). The parietal lobe of modern humans has a larger size and globular shape that are unlike that of any pre-modern hominid (Bruner et al., 2003; Bruner, 2004; Bruner and Holloway, 2010), so it is likely that *Homo sapiens* was the first hominid with syntactical language, which depends on the angular gyrus in the inferior parietal lobe as part of a distributed frontal-temporal-parietal network supporting self-awareness (Levine, 2004). Other features unique to human beings emerging along with syntactical language are related to the capacities to perceive unity and to shift perspective within that unity (e.g., between self and other viewpoints, between expected and unexpected viewpoints, and across time and place). For example, humor in humans is often based on incongruity (which involves a shift between expected and unexpected viewpoints at the "punch-line") (Taber et al., 2007; D'Argembeau et al., 2007). Altruism in humans is based on feeling engagement and compassion for others (involving shifts between self and other viewpoints) (Moll et al., 2006). The uniquely human functions of self-awareness, perspective taking, humor about incongruity, improvisation (i.e., automatic and fluid inventiveness without intellectual effort or deliberation), altruism, and crucial features of syntactical language (like viewpoint aspect, which involves perspective taking) all depend on the activation of the anterior prefrontal cortex (BA 10) along with other components of the self-aware learning system (Moll et al., 2006; D'Argembeau et al., 2007; Limb and Braun, 2008). The anterior prefrontal cortex of modern human beings (BA 10) is unique in its functions and connectivity; no homologous brain area is present in any extant nonhuman primates (Ongur and Price, 2000). The angular gyrus (BA 39) in the IPC is also unique to modern humans and plays a key interpretive role in language reception and humor detection (Geschwind, 1965a, b; Moran et al., 2004),

There is consensus that there was a qualitative shift in skeletal organization and a general increase in the size of the brain and body of hominids between australopithecines and *H. ergaster* (Hawks et al., 2000). *H. ergaster* had long limbs and femoral-pelvic articulation that was well suited for long-distance walking, providing advantages for hunting and gathering (Lordkipanidze et al., 2007; Pontzer et al., 2010; Rightmire, 2009). They also had an enlarged brain (about 800 cc), reduced arm length with arm/leg proportions like modern humans, forward projection of external nose, narrow pelvis, barrel chest, and reduced sexual dimorphism compared to australopiths and possibly *H. habilis* (Klein, 2009). They were able to emigrate out of Africa and were ancestors of all later species of *Homo*, so they are likely to have been the first largely hairless hominids and developed dark skin replacing the pale skin under the fur of apes and earlier hominids. The external nose and naked dark skin provided adaptation to hot arid climate and seasonal rainfall that occurred at the time of their emergence (Klein, 2009).

Hominids are likely to have had advanced forms of social communication and reenactment using on mime, gesture, and emotional vocalization ("appeal") because of the enlargement of their left fronto-parietal neocortex (Corballis, 2003, 2009a, b), but syntactical language is probably unique to modern human beings, as previously discussed (Donald, 1991; Mithen, 1998; Suddendorf et al., 2009; Tattersall, 2009).

The hominids of the Middle Pleistocene had larger prefrontal cortices than earlier hominids (Bruner et al., 2003; Bruner, 2004; Bruner and Holloway, 2010), and they also had more advanced executive abilities, including problem-solving and long-term planning with a mental template, such as mode 3 tool-making ("prepared cores"), domestication of fire, and construction of shelters by the Middle Pleistocene (McBrearty and Brooks, 2000; Tattersall, 2008a). Planning, preparation, and problem solving really involve more than mime and imitation. Long-term planning and preparation to solve problems involves the executive cognitive functions dependent on the prefrontal cortex, which are better described as intellectual abilities. Therefore, we suggest the term "meaning" as an appropriate way to describe the emergent cognitive ability of pre-modern human beings. Meaning refers to the process of non-emotional communication that conveys implicit or explicit significance or purpose in a non-emotional way, which is present to a limited degree even in the early hominids. Meaning is the process of objective communication of understanding and significance, which involves at least the basic use of symbols but not necessarily language with syntax.

The human capacity for music and language may have evolved from both the loud calls and the ability to sing found in apes, and therefore they are expected to be present in hominids with increasing development of Broca's area, the auditory association area (i.e., superior temporal gyrus), and the inferior parietal lobule (Corballis, 2003; Masataka, 2007; Vaneechoutte and Skoyles, 1998). This view does not conflict with the importance of cortical control of gesture in the development of language because both gesture and vocalization begin to be regulated by Broca's area in the frontal cortex of hominids (Corballis, 2003). Monkeys and apes show volitional initiation of phonation, as well as learning of the acoustic qualities of their vocalizations, which is mediated by the anterior cingulate cortex (Jurgens et al., 1982; Jurgens, 2009; Kirzinger and Jurgens, 1982; Masataka, 2007). Although prosimians and monkeys do not produce any multisyllabic utterances (Passingham, 1981), apes produce loud calls and singing of pure tones, stereotyped phrases, and biphasic notes like an 8-month-old human infant (Masataka, 2007).

Nevertheless, the nature of the protolanguage of pre-modern hominids is unknown. The segmentation of song by means of greater working memory and volitional control than is observed in apes produce speech in which the emotional aspect of vocalization becomes less salient than its semantic aspect. However, segmentation of singing produces a hominid protolanguage with little or no syntax, much as is seen in the well-articulated babbling of a 9-month-old human infant or perhaps an 18-month old human child with a vocabulary of 5–20 nouns (Masataka, 2007). By 2 years of age, a modern human child often has a vocabulary of 150–300 words that can be used in noun–verb sentences along with some appropriate use of pronouns and prepositions. The development of further syntactical functions of modern human language and music, like aspect (i.e., viewpoint shifting) and harmony (i.e., knowing what sounds pleasing), depends on the emergence of self-awareness (Schellenberg et al., 2005; Smith, 1997), which does not begin to mature until modern human children begin to be able to recall their past after 3–4 years of age. Viewpoint shifting allows modern humans to shift their contextual focus and to switch in self-aware consciousness from analytical and intuitive modes of reasoning, giving modern people the potential to be inventive and creative (Cloninger, 2004; Gabora, 2004, 2008). The emergence of self-aware consciousness in *H. sapiens* is likely to explain the rapid divergence in learning ability of modern human children from apes after 3 years of age, as well as the complete displacement of pre-modern hominids by modern humans.

The Development of Hominid Cultures

The cultural development of spoken language was associated with an increase in the size and shape of the inferior parietal cortex in *H. sapiens* that is not observed in pre-modern hominids based on detailed morphometric analyses of available brain endocasts of extinct and modern hominids (Bruner et al., 2003; Bruner, 2004; Bruner and Holloway, 2010). There was a correlated increase in left fronto-parietal cortex in early hominids, but there is a novel change in size and shape of the parietal cortex in modern humans not seen in any pre-modern hominid. The function of the fronto-parietal areas for eye–hand coordination, understanding of gesture, and social communication is likely to have served as a precursor for the development of these areas as expressive and receptive modules for syntactical language in modern humans.

The first crude stone tools are known from 2.5 to 2.0 mya in Africa, indicating that the earliest toolmakers had the bodily proportions of an australopithecine (Tattersall, 2008a, b). Early hominid toolmakers not only knew how to make tools but also planned ahead. Their long-term planning is documented by evidence that they carried the right kinds of rocks for miles before making them into tools, and once made they carried the tools in anticipation of using them to butcher carcasses when needed. In contrast, chimpanzees make and use stick tools with materials that do not require long-term planning about things that are out of sight (Povinelli, 2000). The reduced sexual dimorphism and narrowing of the pelvis in *H. ergaster* led to the emergence of the human nuclear family structure with pair-bonding, cooperative and specialized roles of both parents in supporting the family and its children, and a taboo against public sex unlike anything observed in monkeys or apes (Klein, 2009).

Homo heidelbergensis appeared in Ethiopia around 0.6 mya and in Europe around 0.5 mya. Unlike *H. sapiens*, Heidelberg man had no chin and had a thick brow ridge composed of vermiculated bone. The increased brain and body size of *H. ergaster* and later hominids like *H. heidelbergensis, Homo erectus, Homo neanderthalensis*, and *H. sapiens* required a new way of obtaining nutrients to support the greater energy consumption of a larger body and brain, particularly dietary fats from hunting and later from fishing (Bartzokis, 2004; Eaton et al., 1997). There is evidence of the acquisition of meat and marrow by hominids at least by the middle Pleistocene 0.8 mya (Rabinovich et al., 2008) and perhaps as early as the Pliocene 2.5 mya (de Heinzelin et al., 1999). Much as in modern human societies, the hunting of big game by early humans may have been motivated in part by a desire to show off as well as for nutrition. The social prestige of hunting by male hominids is partly related to its importance for reproductive success and health of hunter–gatherer groups. Although women may provide most of the food most of the time in hunter–gatherer societies (Marlowe, 2005), provisioning by men is also crucial for reproduction, particularly when women are unable to forage near the time of child-delivery (Marlowe, 2003). Provisioning of food by men frequently benefits the whole hunter–gather group because large quantities of food are cooperatively shared when intermittently available (Mace and Sear, 2005).

The importance of prestige from hunting is evidenced by protein comprising only a small portion of the diet of extant hunter–gatherers most of the time and the ability of hominids to survive without meat by acquiring essential nutrients from plants alone, as is done by modern vegetarians (Speth, 1991). Nevertheless, the actual nutritional value of hunting by omnivorous hominids is indicated by clear evidence of the systematic butchering of the whole carcasses of deer by hominids around 0.8 mya in the Levant using technologies originating earlier in Africa (Goren-Inbar et al., 2000; McBrearty and Brooks, 2000; Rabinovich et al., 2008). The planned use of Acheulian handaxes and possible planned use of fire by hominids are known from about 1.5 mya in Africa (McBrearty and Brooks, 2000). Later such planned use of tools and fire spread by human movement along the migratory corridor in the rift valley connecting Africa with Eurasia during the early Middle Pleistocene (Goren-Inbar et al., 2000). In depth planning of tool use, controlled use of fire using flint, systematic butchering of the whole carcasses of deer, preparation of nuts and grains with hammers and cooking, and formalized conceptualization of the spatial organization of living space are well documented at Gesher Benot Ya'aqov (i.e., "bridge of the daughters of Jacob") on the river Jordan just south of Lake Galilee in Israel around 750–800 kya, which is well before the emergence of anatomically modern humans (Goren-Inbar et al., 2000, 2002, 2004, 2008; Rabinovich et al., 2008; Alperson-Afil et al., 2009; Sharon et al., 2010). The controlled use of fire and planned organization of ways of processing large game, nuts, and wild seeds of barley and grapes indicates a well-organized hunter–gatherer culture by 790 kya in pre-modern hominids (Goren-Inbar et al., 2004).

Still later there is archeological evidence of further spread of hunter–gatherer technologies to Europe. Wooden spears dating from about 400 kya were preserved in a peat bog in Schoeningen, Germany along with cut-marked animal bones and flint artifacts. Huts with hearths constructed by *H. Heidelbergensis* are also known from 400 kya at Terra Amata in southern France.

Even later, pre-modern and modern hominids both existed at the same time and had contact with one another, as shown by the evolution of divergent strains of head lice (Reed et al., 2004). Around 80 kya pre-modern hominids were competent hunters and fishers who planned their settlement choices around the seasonal availability of game and fish, such as the spawning of large catfish rich in omega-3 fatty acids at the beginning of the rainy season in the rift valley (McBrearty and Brooks, 2000). The skills of pre-modern hominids in obtaining of an abundant source of preformed omega-3 fatty acids from fish available from lakes and ocean sources appear to have been important as a means of supporting the expansion of the pre-modern hominid brain with nutrients essential for the more extensive and prolonged myelination of the modern human brain (Crawford et al., 1999; Bartzokis, 2004; Cunnane et al., 2007). Thus pre-modern hominids showed in-depth conceptual planning in their making and use of stone tools, spears for hunting, systematic butchering of big game, domestication of fire, the building of shelters, organization of living spaces, and flexible utilization of seasonal resources throughout the Pleistocene (1.6–0.1 mya), which are executive cognitive skills unknown in non-hominids (Tattersall, 2008a, b). The capacity for planning allowed pre-modern hominids to exploit the flexibility inherent in their generalized digestive system to adapt to a wide range of habitats and external conditions beyond their control, utilizing plants, game, or fish according to whatever was available. Evidence for what happened to be abundant when modern hominids emerged is indicated by nutrients that are essential for modern humans, such as plant and animal sources of omega-3 fatty acids, such as rift valley catfish, for healthy brain development and functioning (Crawford et al., 1999; Cunnane et al., 2007). The influence of an abundant contextual source of omega-3 fatty acids in the transition from pre-modern to modern human brain structure can be understood as an example of context-driven actualization of potential in evolution (Gabora, 2006). The influence of dietary context on evolution provides an example of the pervasive importance of cooperative interactions in ecology and development rather than selfish competition between individuals within social groups or competition between socio-cultural groups (Weiss and Buchanan, 2009).

The executive cognitive skills and social life of early hominids were distinct from both apes and modern *H. sapiens*. The prefrontal cortex (PFC) serves as the senior executive system in hominids. In modern human beings, the PFC’s executive functions include working memory (dorsolateral PFC, BA 11/46), evaluation of internal stimuli (medial PFC, BA 8/9), long-term planning for a main goal while problem solving and carrying out multiple intermediate tasks (anterior PFC, frontal poles, BA 10) (Bengtsson et al., 2009; Burgess et al., 2000; Fuster, 2000; Passingham et al., 2010; Rowe et al., 2007). Hence the emergence of evidence for long-term planning and problem solving in pre-modern hominids suggests that the development of the prefrontal cortex had an important role in pre-modern hominid development. The hypothesis of prefrontal development in pre-modern hominids is supported directly by the increasing height and width of the frontal cortex in the anterior part of hominid endocasts, which largely accounts for the increasing total brain in the pre-modern hominid lineages (Bruner et al., 2003; Bruner, 2004; Bruner and Holloway, 2010).

The development of the prefrontal cortex of hominids allowed improvements in motor planning and control of manual gestures, which are important precursors for the later development of vocal control and syntactical language (Corballis, 2003, 2009a). By the Middle Pleistocene (781–126 kya), there is direct evidence of hominids hunting large mammals and indirect evidence of their social cooperation, division of labor, and sharing of food (McBrearty and Brooks, 2000; Goren-Inbar et al., 2002; Rabinovich et al., 2008; Sharon et al., 2010). The divergence of body lice from head lice between 83 and 170 kya in Africa suggests that closely tailored clothing were produced and worn by hominids at that time (Toups et al., 2010). Adult men and women organized and divided their labor in a cooperative manner in a hunter–gatherer culture (Zihlman, 1997; Marlowe, 2005). The greater size and strength of men and the child-bearing ability of women led to gender-based division of labor with both genders playing complementary and essential roles. The adult women and children often gathered most of the food, and men provided defense from predators and some hunting (Marlowe, 2005). Given difficulties in traveling when pregnant and the short-life span at the time, women are likely to have maintained a temporary home base where young, weak, and sick could be nursed. The bands of nomadic hunter–gatherers may have included 15–30 or so individuals. Adaptations for bipedalism meant that the bipedal hominid foot could no longer grasp the hair of the mother, so the mother had to hold infants actively. With narrower pelvis and larger brains, much of the development of hominid infants occurred after birth, leading to a need for extended child care (Klein, 2009). Hominid children had prolonged periods of dependence on parental care for food, safety, and education. Artisans could develop expertise in tool-making for hunters (McBrearty and Brooks, 2000), and food could be processed and prepared by others in temporary camps or settlements (Goren-Inbar et al., 2002, 2008; Rabinovich et al., 2008; Sharon et al., 2010). The division of labor was needed to care for the young while providing a stable food supply and food preparation and storage for a cooperative group of several adults and their dependents. *H. ergaster* and its descendents were able to migrate widely throughout Eurasia during the middle and late Pleistocene. To do so, they needed a way to survive injuries that would have precluded their keeping up with a mobile hunting or gathering troop. Consequently, pre-modern hominid social groups maintained temporary camps as a relatively secure home base with a formal conceptualization of living space with specialized areas for tool-making, food preparation, cooking, and sleeping, as is documented at Gesher Benot Ya'aqov in the Levant around 0.8 mya (Alperson-Afil et al., 2009) and earlier around 1.5 mya in Africa (McBrearty and Brooks, 2000). Such home bases provided for pregnant women, children, and the infirm as a conceptualized extension of the anthropoid mother–infant attachment pattern in which a secure home base is fundamental (Mineka and Suomi, 1978; Bowlby, 1983). The home base changed sprained ankles and fevers from fatal events to minor ailments, allowing hominids to migrate more safely to areas without prior immunity to local diseases than could apes. Chimps also hunt in cooperative groups that share meat with one another, but the sharing of meat is reciprocal among hunters as an aspect of male social bonding during times of food abundance and not for nutrition or sexual reproduction (Mitani and Watts, 1999, 2001; Mitani et al., 2000).

Hence, the cooperative sharing and division of labor in hominids involved a greater degree of long-term planning, intellectual awareness, and social organization than the emotion-based reconciliation and social cooperation observed in monkeys and apes (de Waal, 1996, 2000). The intellectual basis of cooperation in humans meant that conflicts between social groups can be better reconciled than in monkeys and apes, whereas emotion-based reconciliation based on social affiliation and prestige are effective *within* social groups but not *between* them (Southwick, 2000).

The division of labor between men and women for food acquisition, child care, and defense is likely to have motivated customs that culturally reinforced sexual and emotional predispositions that favor exogamy and the incest taboo in Pleistocene hominids. All group-living primates and some other social mammals avoid mating with familiar relatives and non-relatives with which they live in close conditions (Lumsden and Wilson, 1980). Among nomadic hunter–gatherers, children were often nursed and reared together in close domestic conditions that involve cooperative interactions among both parents, grandparents, and other members of the group (Mace and Sear, 2005). Such domestic familiarity during childhood predisposes modern humans to express a strong aversion to sexual intercourse with familiar people later in life, even when customs and social pressures actually favor it (e.g., marriage among children reared communally in kibbutzim) (Lumsden and Wilson, 1980). The incest taboo is in part culturally constructed in hominids, even though it depends on emotional disinterest or aversion to breeding with co-resident kin, as well as on social dependency for status (Chapais, 2008). Social status in anthropoid primates depends substantially on the ability to recruit social support by means of alliances with both kin and non-kin (Chapais, 1988, 1995; de Waal, 2000). However, taboos are defined as customs and cultural expectations that create concern for the cultural meaning that others in one's social group give to particular behaviors. The meaning-based nature of taboo in hominids is illustrated by the taboo against public sex, which does not occur in apes but is likely to have emerged along with reduced sexual dimorphism and pair-bonding that led to the emergence of the human nuclear family in *H. ergaster* and all its later descendents (Wade, 2006). Such culturally defined meaning may be biologically arbitrary or even unnatural (e.g., fashion designers suggesting women should be ultrathin anorexics and that it is shameful for women to be well-fed and reproductively fit) (Brinch et al., 1988; Gendall et al., 1998). Thus culturally constructed taboos give both form and force to social norms about what behaviors are likely to elicit social support or exclusion (Krill and Platek, 2009).

Likewise, there was strong norm-favoring for peaceful negotiation that made fighting within the group and war with other groups rare, as is the case among extant nomadic hunter–gatherers (Fry, 2009). Cooperation between neighboring bands of hunter–gatherers would be favored by exchange of mates among neighboring bands, thereby reducing fighting over territorial borders (Chapais, 1995). Cooperativeness in women would also have favored their survival for reproduction, which may contribute to the fact that women are substantially higher than men in the heritable personality trait of cooperativeness (Cloninger, 1995). Likewise, communication between groups of long-distance trading partners would have facilitated exchange of mates, as well as the exchange of locally rare materials (McBrearty and Brooks, 2000). A custom of exogamy is suggested by the fairly frequent occurrence in the Middle Pleistocene of hominids who had mixtures of robust and gracile morphological features (Tianyuan and Etler, 1992). The existence of a taboo against public sex during the Pleistocene cannot be proven, but the intellectual capacities that made such customs possible and the social conditions that made them advantageous arose at that time.

Hence it is likely that a hunter–gatherer culture with cooperative division of labor, trade, sharing, norm-favoring, and taboo arose in pre-sapiens hominids before the emergence of a "mythic" culture with totemism, animism, or a concept of the sacred (Donald, 1991; McBrearty and Brooks, 2000; Marlowe, 2003, 2005; Mace and Sear, 2005). Mythical, self-transcendent, or spiritual thinking requires a capacity for autobiographical narrative, whereas taboo is a more instinctive aspect of intellectual understanding of what is prohibited that may have arisen along with other norm-favoring customs. Cultural norm-favoring is a strong component of social cooperation in modern humans (Cloninger and Svrakic, 1997) and reproductively advantageous (Mace and Sear, 2005; Chapais, 2008).

It is noteworthy that the hunter–gatherer culture of pre-sapiens hominids was characterized by the accumulation of mechanisms for cooperation that facilitated coping with the increasing size and complexity of social organization. Such predisposition for cooperation makes it possible for human beings to be healthy and reproductively fit when functioning coherently (as in states of calm allowing perception of unity). On the other hand, people also have predispositions toward violence when reacting for the sake of physical survival (as in states of fear or hunger promoting perception of separateness reminiscent of a tree shrew threatened by an intruder). The conditions of a hunter–gatherer society favored a combination of both self-directedness and cooperativeness in hominids, with some bias toward assertiveness in men and cooperativeness in women for survival and reproductive success.

Skill in walking and social cooperation facilitated the widespread migration of hominids long before the emergence of any evidence of theoretical thinking characteristic of syntactical language or scientific understanding of natural phenomena in terms of uniform laws. The migration of hominids from Africa to Europe and Asia occurred in successive waves of migration at 1.8–1.6 mya, 1 mya, 500 kya, and 70–40 kya (Tattersall, 2008b). The first two waves of emigration by *H. ergaster* led to the emergence of *H. erectus* in Asia. The adaptive radiation of hominids in Europe following the emergence of *H. heidelbergensis* around 500 kya in Africa led to the emergence of *H. neanderthalensis*. The emigration of anatomically modern hominids out of Africa around 50 kya led to the worldwide spread of modern *H. sapiens* and the eventual extinction of other hominids (Krause et al., 2010; Ian Tattersall, 2008b). The DNA of Neandertals differs equally from all groups of modern humans, supporting the hypothesis that modern humans emerged as part of an adaptive radiation of hominids in Africa independent of the radiation of hominids leading to Neandertals in Europe (Ovchinnikov et al., 2000).

Neandertals functioned in small bands of 15–30 individuals that roamed from one campsite to another when local resources were exhausted. They were highly flexible and able to survive the numerous climatic changes that occurred between their emergence around 200,000 years ago and their extinction 27,000 year ago. They had large brains, ranging from 1200 to 1740 cc in volume compared to the modern human range of about 1000–2000 cc (Tattersall, 2008b). Neandertals appear to have sometimes scavenged meat and at other times to have used ambush-hunting techniques, resulting in frequent skeletal fractures (Trinkaus and Zimmerman, 2005). Neandertals showed their capacity for planning by controlled use of fire, and beginning about 50,000 year ago invented the tradition of burying their dead occasionally and in simple ways without the grave artifacts characteristic of later Cro-Magnon burials (Tattersall, 2008b). There is evidence at Shandigar cave in northern Iraq of Neandertals surviving to advanced age despite severe handicaps (like a useless arm), suggesting social cooperation with empathy for others (Tattersall, 2008b).

Anatomically modern humans appeared outside Africa for the first time about 90,000 ago. The Cro-magnons became widespread and produced impressive artifacts that indicate a new kind of awareness that allowed the development of art, science, and spirituality. Geometrically incised ochre tablets were created in South Africa 75,000 years ago. The earliest known cave paintings, musical instruments, figurines, and notations were created by Cro-magnons in Europe around 34,000 years ago at the beginning of the Upper Paleolithic period. Cro-magnons buried their dead with body ornamentation and grave goods beginning about 28,000 years ago. Shortly afterwards, Neandertals became extinct, and Cro-magnons flourished to achieve the unusual distinction of being the single hominid species in existence (Tattersall, 2008a, b).

What Brain Structures Emerged Coincident with the Functional Changes?

Ecological shifts elicited adaptive changes in brain structure and function, as detailed elsewhere (Cloninger, 2009). The emergent brain structures and functions for the lineage of craniates leading to human beings, detailed in Table 5.1, will be briefly summarized to provide an overview of the major transitions in the central integration of brain functions from the midbrain in early vertebrates, the hypothalamus in reptiles, and the neocortex in mammals.

In early vertebrates (i.e., anamniotes, including fish and amphibia), the midbrain is the dominant association center for integration of sensory input and regulation of motor output, including large optic lobes for processing visual input (Darling, 2010). The forebrain (including cortex dorsally, hypothalamus, and basal ganglia ventrally) of anamniotes receives sensory input, particularly about smell, but exerts no feedback control of sensory integration or motor output by the midbrain. The hypothalamic–pituitary axis of anamniotes does regulate endocrine functions, much as in amniotes (Goos, 1978). The basal ganglia of anamniotes have few cells and receive little if any cortical input or dopaminergic input from the ventral tegmental area (VTA) of the midbrain (Reiner et al., 1998). In contrast, in all amniotes (reptiles, birds, and mammals) the basal ganglia are neuron-rich and receive extensive cortical input and dopaminergic input from the midbrain, thereby allowing amniotes to learn and execute a more sophisticated repertoire of behaviors and movements on land than do anamniotes in water (Reiner et al., 1998; Reiner, 2002). It seems likely that the common ancestor of amniotes developed greater forebrain organization of both the dorsal cortex and basal ganglia because the organization of the basal ganglia of early vertebrates is less elaborate than that of amniotes. In particular, cortical-striatal-cortical loops (i.e., feedback connections between cortex and basal ganglia) are present in all amniotes and are lacking in all earlier vertebrates (Reiner, 2002).

The clade of amniotes are divided into two sub-clades: *Sauris* (i.e, reptiles and birds) and *Mammalia*. The last common ancestor of sauropsids (i.e., lizard-like reptiles and birds) and synapsids (i.e., mammal-like reptiles and mammals) lived in the late Cretaceous period around 320 mya. Within the sub-clade *Sauris*, lizards and snakes are grouped together in the order *Squamata*. In squamates and other reptiles, the central regulation of brain function is invariably organized in the hypothalamus of the basal forebrain (Bruce and Neary, 1995; Nieuwenhuys, 1994). Sensory information is first processed in the basal forebrain of lizard-like animals before being relayed to their thalamus and dorsal cortex. Like earlier vertebrates, the dorsal cortex and thalamus of lizard-like animals receive sensory input, but do not reciprocate with output that could modulate the hypothalamus (Butler and Cotterill, 2006; Nieuwenhuys, 1994).

Hence squamates and their ancestors are probably limited to the experience of mental images in the present, which is called “primary” or “perceptual” consciousness (Butler and Cotterill, 2006). In squamates, the hypothalamus in the basal forebrain is the dominant association center that integrates external and internal sensory inputs and regulates motor output (Bruce and Neary, 1995; Nieuwenhuys, 1994). In contrast, both mammals and birds have developed forebrain systems that permit higher level control of the hypothalamus by thalamic and cortical structures, although mammals and birds do so with structures that are only partly homologous (Butler and Cotterill, 2006). The dorsal cortex of early mammals was differentiated into a multilayered neocortex, and there is a progressive series of transitions in brain function along the ancestral lineage from synapsids to human beings whereby neocortex took control of central regulatory functions from the hypothalamus (Cloninger, 2009).

Like mammals, the dorsal cortex of birds developed forebrain structures that are not found in lizard-like reptiles and that are comparable in function to that of mammalian neocortex, including functional counterparts to mammalian prefrontal cortex (Butler and Cotterill, 2006; Jarvis et al., 2005; Reiner et al., 2004). Unlike their ancestors (i.e., fish, amphibians, and reptiles), birds have cortical-striatal-cortical loops like the prefrontal-striatal-prefrontal loops that regulate movement and emotion in anthropoid primates (Levy and Dubois, 2006).

Compared to reptiles, both mammals and birds have high brain–body ratios, forebrains with a relatively large volume of non-limbic cortex, and multiple cortical association areas that process multi-sensory input and support executive planning of movement (Butler and Cotterill, 2006). However, birds lack the multilayered neocortical architecture of all mammals, as well as the claustrum and the highly stratified organization of afferent innervation observed in therian mammals. The supervisory thalamic-cortical circuits of birds support functions that have sometimes been claimed to be unique capacities of mammals or humans, such as working memory, number sense, episodic memory in scrub jays and pigeons, complex vocalization and communication abilities in songbirds and parrots, use of available twigs as tools to obtain food in New Caledonian crows, and the capacity for deception by jays and ravens (Butler and Cotterill, 2006). However, birds lack self-awareness comparable to that of modern human beings. No single region on the avian brain has been shown to be homologous to mammalian prefrontal cortex, but there are regions that play analogous roles to prefrontal cortex in the complex cognitive functions displayed by birds and not by reptiles or amphibians (Butler and Cotterill, 2006).

The homologies and functional analogies between mammalian and avian thalamo-cortical structures and functions are examples of independent evolution of similar higher level cognitive functions beyond perceptual consciousness of the present moment. Here I will follow only along the human lineage without any claim that the abilities that develop are unique to that lineage.

The five major transitions in brain structure and function in mammals are summarized in Table 5.2. In early mammals and tree shrews, the major neocortical function is facultative control of mating, which is reflexive in squamates (Emmons, 2000; Wersinger and Baum, 1997). Primary somatosensory cortex is clearly developed in tree shrews (clade designated here as 2b), but there is little or no differentiation of sensory neocortex from motor neocortex (Kaas, 2006, 2008).

Compared to tree shrews, strepsirhines have greater motoric agility (e.g., adaptation for grasping and leaping) (Bloch et al., 2007; Szalay and Delson, 2001), greater dietary flexibility (Chivers and Hladik, 1980; Hladik et al., 1999), more maternal care of young (Broad et al., 2006), and more time spent in allogrooming (Emery and Amaral, 2002; Emmons, 2000; Moynihan, 2006). These functions involve regulation of material things like acquisition of food and related activities of daily living. Unlike rodents, in primates there is no direct path from the brainstem taste areas like the Nucleus of the Solitary Tract to the hypothalamus and amygdala. Information about taste in primates, in contrast, reaches the amygdala and orbitofrontal cortex from the primary taste cortex, which is in the frontal operculum and insula (Verhagen et al., 2004).

Table 5.2 Cladistic staging of evolution of the functional components of self-aware consciousness in human beings: five basic transitions from the common ancestor of squamates and mammals to modern human beings

Transitional clades	Emergent brain structural networks	Major function (voluntary)	Component functions
Early mammals	Somatosensory neocortex regulating bodily functions of midbrain for sex and survival	Mating (i.e., rudimentary intentionality influencing whether to copulate and reproduce conditional on success in foraging for adequate nutrient resources)	Sex drive Foraging
Proto-primates and early primates	Differentiation of sensory and motor neocortex; neocortex regulating taste; social relations controlled by smell	Physicality (i.e., preferences regarding taste of food, enhanced physical agility for grasping, and capacity for digestion of fruits)	Rhythmicity Agility Discrimination
Anthropoids	Prefrontal cortex regulating hypothalamic functions of the limbic system (Semendeferi et al., 2001); PFC inputs replaces olfactory inputs regulating brain reward centers, facilitating emotion regulation (Smith et al., 2001; Broad et al., 2006); Von Economo neurons in AIC/ACC allowing rapid coordination of emotional preferences and behavior (Craig, 2008); mirror neuron system enhancing eye–hand coordination and emotional regulation of gesture, vocalization, and social interaction (Corballis, 2003; Rizzolatti and Craighero, 2004)	Emotionality (i.e., emotional regulation of individual behavior and social relationships leading to individual and social traditions, as well as awareness and expression of subjective feelings in gestures and vocalizations)	Receptivity Closeness Reconciliation Tradition

Table 5.2 (continued)

Transitional clades	Emergent brain structural networks	Major function (voluntary)	Component functions
Early Homo	Fronto-parietal perceptual-motor praxis system permits refined tool-making (Stout et al., 2000, 2008). Linkage of prefrontal cortex and auditory association cortex regulates cross-modal representation for meaningful and purposeful planning in solving social and physical problems (Pinker, 2010); coupling of terminal associative neo-neocortical regions in brain default network regulates attention and daydreaming; the communication of pre-modern hominids is probably based on coordination of gesture and vocalization with its meaning expressed by rudimentary cross-modal representation and interpreted by metaphoric understanding of action and sound production with greater involvement of the enlarged prefrontal cortex in hominids (Bruner, 2004) compared to anthropoids that have volitional initiation of vocalization regulated by the ACC and interpreted by the superior temporal gyrus and inferior parietal cortex (Hauser, 1997; Rauschecker and Tian, 2000; Hauser et al., 2002; Corballis, 2003)	Meaning (i.e., the process of reasoning and understanding objectively, which allows executive non-emotional problem-, long-term planning, and cooperation according to a mental template. Communication is by body language and volitional initiation of vocalization, but not with syntactical language, scientific notation, or abstract art. Hence meaning is a rudimentary and concrete form of symbolic learning and episodic memory that allows asking what, where, when, who, and how, but not abstract theoretical questions about why or what if. Accordingly it favors tradition and imitation, rather than symbolic invention. Hence pre-modern hominid intellect allows the proposal of plans, problem-solving with learning set formation (i.e., inter-set improvement in performance in subjects given discriminations involving different pairs of stimuli), elaboration of methods of implementation, evocation of feelings, and interpretation of the meaning of concrete cross-modal representations. Such long-term planning and problem solving is observed in hominids (e.g., mode 3 tool making, building shelters, domestication of fire), and similar	Taboo Metaphor Empathy Judgment Subliminal

Table 5.2 (continued)

Transitional clades	Emergent brain structural networks	Major function (voluntary)	Component functions
		operation with shorter working memory capacity is seen in apes and cetaceans (Macphail, 1982; Gaskin, 1982). However, such planning, problem-solving, and interpretation do not involve self-awareness, theoretical abstraction, or flexibility in shifting one's viewpoint in time or attitude because there is little or no capacity for mental time travel or theoretical creativity to ask "what if" or why except in special states of calm passive fixation like rituals)	
Modern *Homo sapiens*	Auto-noetic system unifying fronto-parieto-temporal neo-neocortical association areas (linked by visual projection system) (Levine, 2004; Tulving, 1987). Parietal cortex of modern humans is more rounded in shape and larger in volume than in pre-modern hominids (Bruner, 2004; Bruner and Holloway, 2010).	Apperception of unity (i.e., self-awareness of omni-sensory information as aspects of coherent and transcendental whole in which the components are interdependent and inseparable, as in the perception of harmony in music, awareness of the continuity of the self in personal narratives over time and place, and need for fairness in social relationships, compassion and altruistic concern for the weak or disadvantaged, and sometimes perception of universally uniform scientific laws and/or a universal unity of being)	Harmony Sublimation Aesthetics Science Awareness of unity

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What is the Functional Architecture of Human Brain Functions?

Before continuing with a description of the evolution of brain functions in anthropoids, it is essential to describe the method of summarizing information about the phylogeny of brain functions. Without a systematic way of organizing information, patterns in evolution can be difficult to recognize. An outline of my proposed model of the functional architecture of human beings is given in Table 5.3 as a matrix of functional abilities that emerged in mammalian evolution.

Each of the proposed functional labels has been defined psychologically and described in terms of comparative neuroanatomy and behavior. This information will be published elsewhere because of space limitations here. The reality of human evolution is a bushy nonlinear dynamic system as a whole (Wright, 1982; Tattersall, 2008a), but by following only the ancestral lineage leading to humans, it is adequate as a first approximation to describe the local process as a linear sequence of steps. The matrix given in Table 5.3 describes the functional organization of information processing by brain circuitry as it emerges in phylogeny from lizard-like animals to modern human beings. The matrix of functions represents the homologous modular structure of the human brain, which is comprised of domain- or situation-specific functions organized in terms of information processing systems with nested sub-systems and sub-subsystems (Cole and Schneider, 2007; Mithen, 1998). These brain modules are functionally dissociable but highly interactive, like components of a quantum field (Eccles, 1989; Pribram, 1993). The theoretical specification of a general functional model in this way is designed to allow predictions and interpretations of data from paleontology and anthropology that are ambiguous when taken one fossil or one extant animal at a time.

What we present must be considered as a working model to be tested, corrected, and refined. Such synthesis of data from psychology, cognitive neuroscience, and phylogeny offers a way for anthropologists and psychobiologists to begin to make adequate tests and interpretations of the wealth of data available about the evolution of brain functions.

We want to emphasize the importance of the matrix structure: a nested matrix structure is essential in order to take into account the holographic and modular nature of human consciousness and brain functions (Pribram, 1993; Cloninger, 2009). The matrix structure has crucial dividends because it requires a systematic approach and also suggests a testable mechanism for cladogenesis based on precursor functions that become generalized at transitions in response to adaptive challenges and natural selection, as described in subsequent tables. The strongest evidence for the matrix structure is the consistent evidence for the same brain system to regulate converse functions (i.e., functions that are the reverse of one another in the sense of involving the same elements but with the direction of effects transposed). For example, handicraft, such as planning how to build stone tools, is the material aspect of intellectual functioning (designated as 5–3, as explained in the next paragraph), whereas its converse function, gesture, is communicating by means of parts of the body (designated as 3–5). The same lateral prefrontal network regulates planning of motor sequences in both handicraft and gestural expression (Koechlin et al., 2000; Passingham et al., 2010). Such symmetries reveal a matrix

Table 5.3 Functional architecture of human beings as it emerges from **core functions** (in bold) and other precursor functions in mammalian evolution[a]

Plane	Sexual sub-plane—2	Material sub-plane—3	Emotional sub-plane—4	Intellectual sub-plane—5	Spiritual sub-plane—7
7—Spiritual	Moderation [7]	Spontaneity [7]	Altruism [7]	Dialog [7]	**Unity [7]**
5—Intellectual	Planning [5]	Handicraft [5]	Rapport [5]	**Meaning [5]**	Diplomacy [7]
4—Emotional	Intimacy [4]	Motive [4]	**Mood [4]**	Appeal [5]	Humor [7]
3—Material	Parenting [3]	**Physicality [3]**	Sensibility [4]	Gesture [5]	Charity [7]
2—Sexual	**Mating [2]**	Gratification [3]	Sensuality [4]	Community [5]	Egalitarianism [7]

[a] The clade in which functions emerge are indicated in brackets [ ]. The labels of sub-planes given here describe examples of functions that emerge or are qualitatively enhanced in a stepwise function along the evolutionary lineage of clades leading to human beings, represented here as an expanding matrix of functions. The only aspect of dialog discussed here is syntactical language

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pattern that helps to recognize the same causal processes as they are reflected in converse or transposed situations.

The sequence of emergence of function involves the emergence of precursor functions within a matrix prior to each major transition. For example, in early mammals (stage 2a involving sexuality of the common ancestor of monotremes, marsupials, and tree shrews), the most basic function regulated by neocortex is mating (designated as functional sub-plane 2–2 in which the first number specifies the plane and the second number specifies the sub-plane). Then in tree shrews (stage 2b) there is emergence of an enhanced ability to restrain sexual activity intentionally for other functions like feeding by neocortical regulation of the ventromedial hypothalamius (VMH). Tree shrews spend most of their time foraging and do not reproduce unless they obtain sufficient nutrients for childbearing.

The emergence of neocortical modulation of taste in early primates was coincident with new adaptive functions regulating gratification (sub-plane 2–3, material aspects of sexuality) and parenting (sub-plane 3–2, sexual aspects of materiality). Precursors of emotionality emerge in strepsirhines (i.e., stage 3b) including enhanced sensory discrimination, enhanced maternal care, and preference bonding, which are late emotional aspects of sub-planes 3–3, 3–2, and 2–3, respectively. Accordingly, each stage is divided into an early phase that is followed by a late phase in which there are precursors that provide a foundation for future major transitions.

Brain Development in Anthropoid Primates

Strepsirhines have well-differentiated sensory and motor neocortical areas in contrast to tree shrews. Detailed studies of galagos revealed several changes in brain structure that support enhanced motor agility with advanced grasping and leaping adaptations compared to tree shrews (Kaas, 2006, 2008). The findings include greater topographical ordering of sensory input for the hands and feet, premotor and supplementary motor areas, at least two motor areas in cingulate cortex, and feedback circuits among prefrontal cortex, premotor cortex, and primary motor cortex. In addition, strepsirhines have an enlarged posterior parietal cortex for processing visual, auditory, and somatosensory information to form and relay instructions about hand and eye movements to premotor areas.

In anthropoids there is emergence of emotionality with patterns of mood regulation, intimacy, motive, sensuality, and sensibility (see Table 5.3) that are similar to human affectivity, as noted by Darwin, Bowlby, and others (Preston and De Waal, 2002; Sussman and Chapman, 2004). Related brain changes include the development of prefrontal cortex for regulation of emotional functions (Semendeferi et al., 2001), a distinctive system for interoceptive processing of sensual aspects of touch (Craig, 2004, 2005, 2009), and the emergence of the mirror neuron system to provide rapid functional coordination of frontal and parietal cortical areas (Rizzolatti and Craighero, 2004). The orbital prefrontal network regulates the sensory awareness of the affective qualities of stimuli, and the medial prefrontal network organizes emotional expression along with other visceral functions (Ongur and Price, 2000).

The medial prefrontal cortex operates as a component of a brain circuit that first emerges in anthropoids, called the "default mode network" (Raichle et al., 2001; Rilling et al., 2007; Buckner et al., 2008). It is called the default mode because it is most active in states of restful calm. The medial prefrontal network, but not the orbital network, expands and differentiates in a multi-step progression of size and number of areas and functions in the transition from anthropoid to human (Ongur and Price, 2000). The expansion and differentiation of the medial PFC and the default mode network are implicated in the stepwise progression from medial prefrontal regulation of emotionality in simians to that of symbolism in pre-modern humans and the perception of unity in modern humans (Cloninger, 2009).

Apes represent the transitional group in which precursor functions emerge that serve as a foundation for the emergence of intellectual learning (i.e., "meaning" with objective problem solving and long-term planning) in early humans. The precursor functions for meaning observed in apes include intergroup proto-cultural variation in traditions for courting, foraging, tool-use, food preparation, and grooming styles (aspects of 4–3, motive) (Kawai, 1965; Whiten et al., 2007; Bonnie et al., 2007) along with enhanced observational learning involving imitation (Beck, 1974) and secondary representation including mirror self-recognition (see 4–3) (de Waal, 1996; de Waal et al., 2005), reconciliation after fights (de Waal, 2000), melodious loud calls (aspects of 3–4, sensibility) (Geissmann, 2002), daydreaming (an aspect of 4–2, intimacy), and the ability to recognize when others may not see what they intend to do (de Waal, 2008), such as mating with a receptive partner when out of sight of the dominant male (an aspect of 2–4, sensuality). Monkeys do show some observational learning, as in for using tools and other skills and traditions (Beck, 1973a, b), but such learning in apes is more frequent and involves learning arbitrary proto-cultural conventions independent of conditioning to obtain rewards (Beck, 1974; de Waal, 1999; Bonnie et al., 2007). These precursor functions emerged as useful abilities in cooperative group foraging in anthropoid primates (Deacon, 1997), thereby setting the stage for the emergence of language and other unique aspects of modern human cognition later in evolution (Tattersall, 2004).

In early hominids (i.e., members of the genus *Homo*), there is emergence of neocortical regions with several unique functional properties, which has been called "neo-neocortex" (Eccles, 1989). In addition to being late to emerge in evolution, neo-neocortex is also late to myelinate in modern humans and has delayed dendritic and synaptic developments when compared to the "old" neocortex present in the sensory, motor, and emotional systems of non-hominids. When lesions of neo-neocortical areas occur in young people, especially before puberty, neo-neocortical development is able to compensate functionally by reallocating functions to intact areas. The protracted development of these "terminal zones" of associative neocortex is regulated by oligodendrocytes, which continue to differentiate into myelin-producing cells late into the fifth decade of life (Bartzokis, 2004). The unique metabolic demands of producing and maintaining the myelination of the expanded hominid neocortex created an increased demand for essential nutrients from fishing and the brains of game in hominids as sources of dietary fats, such as omega-3 fatty acids (Eaton et al., 1997; Crawford et al., 1999; Cunnane et al., 2007). The nutrient and metabolic demands of neo-neocortex also resulted in the vulnerability of unique human cognitive functions to Alzheimer's dementia and other uniquely human brain dysfunctions (Bartzokis, 2004).

The emergence of neo-neocortex is documented in early hominids by evidence of cerebral asymmetry in brain endocasts and of right-handedness in the clockwise rotation of stone cores during flaking by 1.8 mya in Africa (Toth, 1985; Holloway, 2009). In modern humans, there is marked lateralization of the functions of neo-neocortex in the two cerebral hemispheres. The right neo-neocortex carries out geometrical and spatial processing, and processing of music, prosody, holistic images, and synthesis over time, whereas the left neo-neocortex processes conceptual similarities and analysis of details over time algorithmically (Sperry, 1982).

The regions of neo-neocortex that function asymmetrically are terminal association areas, which include the polar and medial prefrontal cortex, inferior temporal cortex, and inferior parietal cortex, and other regions that are jointly activated through the Default Mode Network (DMN). The rudimentary core of the DMN was already present in anthropoids (Buckner et al., 2008), in which it regulates emotionality (Drevets et al., 2008; Price and Drevets, 2010). In hominids, its functional capacity expanded with emergence of neo-neocortex for intellectual functions that are activated when hominids are in a state of calm (e.g., eyes closed resting) or passive alertness (e.g., passive visual fixation), as when meditating, in reverie, or in fantasy (Raichle et al., 2001; Rilling et al., 2007; Travis et al., 2010). Later in evolution, the functions of neo-neocortical regions expanded into a proactive functional fronto-temporo-parietal circuit serving autobiographical memory and self-aware consciousness in modern *H. sapiens* (Levine, 2004), rather than being functionally active mainly at rest in pre-modern hominids (Raichle et al., 2001; Rilling et al., 2007; Buckner et al., 2008). The potential for greater cognitive flexibility and creativity of modern human thinking under stressful conditions provided an adaptive advantage that may explain the extinction of all other hominid species after the emergence of modern *H. sapiens*. Hence the evolution of neocortex in hominids involves not just quantitative growth in size, but a succession of two qualitative functional shifts marked by the emergence of cerebral asymmetry in pre-modern hominids and of self-awareness in modern humans.

Symbolic activity like symbol-based cognitive control and other executive functions are possible with the neo-neocortical enhancement of the anthropoid Brain Default Network in hominids, which allowed first-person perspective taking and daydreaming, as when a person is letting his or her mind freely wander about inner thoughts and feelings (Buckner et al., 2008; Raichle et al., 2001; Rilling et al., 2007). Meaning builds on the emotion-regulating functions needed for cooperative group foraging in anthropoids (Deacon, 1997). For example, *H. erectus* showed executive skills and craftsmanship in the making of refined tools in their Acheulian culture (Stout et al., 2000, 2008). These symbolic functions depend on processing in the inferior parietal lobule (IPL), which is a convergence area for touch, hearing, and vision, allowing cross-modal transformations important for symbolism and language (Deacon, 1997; Eccles, 1989; McGeoch et al., 2007). In modern humans, the angular gyrus (BA 39) of the IPL in particular has an important role in the comprehension of metaphor and allegory (Ramachandran, 2005). The core functions of meaning or basic hominid symbolism involve cross-modal transformation, such as capacities for taboo, metaphor, empathy, and intellectual problem solving (Cloninger, 2009).

In modern human beings, the evolution of functional connectivity among all the regions of neo-neocortex allows self-awareness and the transcendental apperception of unity. For example, the emotional aspects of the perception of unity involve the unique modern hominid perception of unity that can be described as "humanism". Humanism is composed of feelings of engagement and altruism. Such humanistic engagement and altruism have been investigated in studies of child development and of brain imaging while adults make voluntary charitable donations as a personal sacrifice. Modern human children are selfish at age 3–4 before their brain network for self-awareness begins to mature, but then develop altruistic attitudes by the ages of 5–7 years (Fehr and Rockenbach, 2004; de Quervain et al., 2004; Fehr et al., 2008). Altruism, as measured by costly donations to humanitarian causes, was strongly associated with activation of anterior prefrontal cortex (BA 10/11/32). The subgenual cingulate (BA 25) was also activated by altruistically motivated decisions and not by monetary rewards (Moll et al., 2006). The activation of the frontal poles (BA 10) during altruistic acts by humans is noteworthy because there is no brain region homologous to the human frontal polar cortex (BA10) in monkeys (Ongur and Price, 2000).

Pre-modern hominids such as Neandertals and ancient *H. sapiens* represent the transitional group in which precursor functions emerge that serve as a foundation for the emergence of self-aware consciousness in modern human beings. The precursor functions for self-aware consciousness involve activation of neo-neocortex in restful states by means of the Default Mode Network, such as passive visual fixation or ritualized burying of the dead by Neandertals and ancient *H. sapiens*.

Finally, modern human beings have the potential for stable self-aware perception of a sense of unity in all aspects of life, manifest by emergent capacities for harmony, sublimation, aesthetics, science, spirituality, humor, and inventiveness (Cloninger, 2004). These integrative abilities give modern human beings their potential in art, science, and spirituality, which sometimes lead to transcendent joy about beauty, truth, or goodness (Mithen, 1996; Cloninger, 2004). The self-aware perception of unity is fundamental for art, science, and spirituality. Modern human art involves aesthetic qualities beyond the artistic craftsmanship observed in premodern hominids. With modern aesthetic sensibility, art has become the creative search for the awareness of beauty by an integrated representation and organization of diverse parts that make up a harmonious whole (Merriam-Webster, 2003). Science is the search for knowledge of general truth by systematic theorem-like study of the operation of uniform laws to explain and predict particular events that comprise a coherent model of space and time within the universe (Merriam-Webster, 2003). Science is described as "theorem-like" or hypothetical and deductive (i.e., If…, then….) because it is a search for specific conditions that predict particular consequences, which depends on an understanding of the relationships of parts to one another in a whole. Likewise, spirituality with the capacity for transcendence observed in modern humanity involves the search for personal knowledge of what is divine or good by self-awareness of the universal unity of being, particularly including what is beyond transient individual existence (Cloninger, 2007). As a result of the transcendental unity of apperception (Kant, 1781), modern human beings have the extraordinary Promethean potential to plan for the future while consciously recollecting the lessons of their past, which is variously called foresight, "pure reason" (Kant, 1797), "conscious time-binding" (Stebbins, 1982), or "mental time travel" (Suddendorf et al., 2009; Tulving, 2001).

Such integrated awareness of unity in art, science, and spirituality is supported by the auto-noetic system of learning and memory (Tulving, 2001, 2002). Such self-aware consciousness allows a person to travel in space and time in their recollection of episodic events, which is essential for self-awareness of a person's own life narrative. Such autobiographical or holistic thinking involves a distributed fronto-temporo-parietal network (Levine, 2004) in which memory is encoded by the left MPFC and hippocampus and is retrieved by the right MPFC (Tulving and Lepage, 2001; Tulving, 2002). Essentially the visual projection system connects regions of neo-neocortex in all tertiary association cortices so that the brain can function as a coherent whole. Whereas in pre-modern hominids, the terminal association areas of neo-neocortex can be transiently engaged in states of calm passive alertness, these areas can be stably coupled in self-awareness even under stressful conditions in modern human beings.

Modern human language with syntax is an important example of the functions that emerge with the perception of unity. The abilities that depend on the perception of unity emerge along with the ability to shift temporal perspective, as well as the ability to recollect one's personal past after age 4 years. In linguistics, viewpoint aspect is the temporal organization of situations (e.g., events or states) and temporal perspective (Smith, 1997). In music, harmony is the simultaneous combination of notes into chords and the sequential temporal ordering of chords (i.e., chord progressions). Human children normally have implicit knowledge and ability to perceive the syntactic functions that typify harmony in music and viewpoint aspect in language by age 6 or 7 years with no special musical or linguistic training. In other words, they know what sounds good (i.e., consonant) and what sounds bad (i.e., dissonant) (Schellenberg et al., 2005). Syntactic functions, such as the perception of harmony or the ability to appreciate shifts in viewpoint aspect (McColgan and McCormack, 2008), depend on the perception of unity, which is the core function of the self-aware consciousness system. Self-awareness begins to mature after age 4 years and is fairly well developed by age 7 years in most children at the same time that harmony (Schellenberg et al., 2005), the theorem-like understanding of grammatical rules (including rules for representation of contextual perspective, such as tense and viewpoint aspect) (Crain, 2005; Lind and Bowler, 2008), and preferences for egalitarianism (Fehr et al., 2008) emerge. The dependence of syntactical and grammatical functions on the self-aware consciousness system suggests that the meta-perceptual functions required for modern language emerged for the first time in modern humans.

The perception of unity permits the personal integration of values, thoughts, and actions. Despite the capacity of modern human beings for integration, there are substantial differences between individuals in the development of their self-awareness, humor, creativity, and well-being (Cloninger, 2004).

Implications for the Anthropology of Cooperation

The complex phylogeny of human functional abilities presents both opportunities and challenges for both anthropologists and psychobiologists. Such core functions never operate in isolation because adaptation involves the whole person, not separate organs or functions. Accordingly, the emergence of a new functional ability leads to interactions with all the individual's other abilities. Detailed observational studies are needed in other mammalian species in order to distinguish the functional abilities that are possible with the brain structures of those species. For example, dogs do not have the type of slow-conducting sensory nerves that allows anthropoids to distinguish the affective quality of what is pleasant versus unpleasant. They can experience pain and pleasure, but do not have the nervous system that allows processing of affective valence in the same way as anthropoid primates (Craig, 2004, 2009). People can observe the behavioral expressions and responses of dogs and may empathically project what another human being would feel if they showed the same expressions and behavioral responses. However, dogs simply cannot have the same affective experience that human beings can imagine they might be having.

As a result, we must be careful in deconstructing the components of cooperation and suggesting what other species can or cannot experience. For example, it is essential that we distinguish between altruism and the social affiliation seen in anthropoids. I would reserve the word "altruism" for an attitude that is only possible in an animal that has the capacity for self-transcendence, which requires identification with what is beyond the existence of the individual. Altruism is an expression of self-awareness that emerges for the first time in modern human beings along with self-aware consciousness and the capacity for sublimation. Altruism depends on brain structures that are only present in human beings and not in nonhuman primates. Altruism emerges in human beings along with other aspects of the perception of unity, such as science, art, and spirituality. Hence animals without self-awareness and a capacity for self-transcendence are incapable of altruism as defined here. Even chimpanzees do not have the capacity for self-transcendence, as indicated by abilities like "mental time travel" (Povinelli, 2000; Rilling et al., 2007; Suddendorf and Whiten, 2001; Tulving, 2001). Of course the word altruism can be used for other cooperative behaviors, but then what word can we use to distinguish "the intentional practice of disinterested and selfless concern for the well-being of others" from other kinds of cooperation seen in strepsirhines or the cooperation seen in haplorhines? Even in modern human children, altruistic thinking, as commonly defined (i.e., selfless concern for the welfare of others) only emerges between 4 and 7 years of age along with the maturation of self-aware consciousness and the capacity for theory of mind (Fehr et al., 2008).

My point is that we need to use our knowledge of phylogeny and comparative neuroanatomy to develop a systematic terminology with practical definitions and descriptions of the terms so that we do not anthropomorphize our interpretations of behavior in other species. Communication and understanding are compromised when people attribute functions like intimacy to species that have no brain capacity for emotionality, taboo or culture to species that have no capacity for symbolization, or altruism to species that have no capacity for self-awareness. Likewise debates about whether human beings are either prosocial or antisocial only serve to polarize and confuse discussion when the reality is that human beings are capable of peace and violence under different conditions. We all have the primitive functions of an "inner tree shrew" within us, which may be expressed when we fail to utilize the higher cognitive functions of human self-awareness that allow the perception of unity even under stressful conditions, like when we are hungry, frustrated, or threatened. The pretense that we can make theory-free observations is naïve, and an understanding of brain-behavior relationships requires a theory that integrates neurobiology and behavior in their joint evolutionary context. As Kant said, "intuitions without concepts are blind, and concepts without intuitions are empty (Kant, 1781)." Unless we have clear concepts of functional abilities in terms of the mode of information processing and the situational context, then our observations are blind and cannot lead to real understanding.

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