

Studying Social Communication in Primates: From Ethology and Comparative Zoology to Social Primatology, Evolutionary Psychology, and Evolutionary Linguistics

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Abstract Research fields adhere to particular epistemic frameworks that outline the methodological rules of conduct on how to study and interpret primate behavior as both social and communicative. Since the onset of social communication studies, epistemic focus has shifted from behaviorist observations to an examination of the cognitive and neurological capacities that underlie the observed communicative behavior and subsequently, toward an investigation of the evolutionary units, levels, and mechanisms whereby social communication evolved. This volume brings together scholars from within these diverse fields who (1) investigate the historical and epistemic roots of the primate communication/human language divide; (2) identify and analyze the building blocks of social communication; (3) examine how primate social communication strategies are evolutionary precursors of human language; and (4) analyze how social communication differs from human language. In their chapters, the contributors explain the merits and pitfalls of their field-specific epistemic approaches. They compare them to other theoretical frameworks and they give guidelines on how theory formation on the origin and evolution of social communication in primates can be enhanced by allowing for epistemic plurality.

Keywords Social communication • Language • Epistemology • Philosophy of science

Emotions, expressions, vocal signaling, and manual and bodily gestures are evolved means whereby primates, including humans, communicate socially. Additionally, humans have invented signed and vocal languages that not only enable social communication but also abstract, symbolic, and creative thought on the past, present, future, and the inexistent. The development and evolution of

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social communication in humans and other primates has been studied from within multiple disciplines, ranging from ethology and comparative zoology, over primatology and comparative psychology, to evolutionary psychology and evolutionary linguistics. In this volume, contributors examine the epistemic frameworks of these various fields and they give directions for future research.

1 Introduction to the Theme and Outline of the Book

The study of human language is preceded by a rich history reaching back as far as the early Greek philosophers' works. Early philosophers understood language primarily as a knowledge device that enables the expression of abstract thought. The study of social, non-verbal, and verbal communicative behavior in other primate species, and the recognition that human language too can be investigated as a communicative behavior, originated much later in time. From the seventeenth century onward, utopian thinkers and social contract philosophers considered human languages a communicative means to bond societies both socially and politically (see Gontier 2009 for an overview). These ideas were foundational for nineteenth century natural history scholars, and rising fields such as historical linguistics and biology provided the first historical and evolutionary accounts on the origins of verbal and non-verbal communication in our and other species. This history results in the fact that scholars today continue to distinguish human language from other forms of animal and primate communication.

This volume brings together scholars from within diverse fields who:

- (1) Investigate the historical and epistemic roots of the primate communication/human language divide;
- (2) Identify and analyze the building blocks of social communication in primates;
- (3) Examine how primate social communication strategies can be understood as evolutionary precursors of human language; and
- (4) Evaluate how social communication differs from human language.

We make no attempt to provide a complete account on the various data and theories that exist on the origin and evolution of social communication in primates and the origin of language in humans. Indeed, such cannot be the subject of one book alone. With this anthology, we do hope to provide an introductory review of some of the main methodological and theoretical frameworks that are currently available to investigate the origin of both social communication and human language.

Today, due to the nature of academia and how disciplines are structured, beginning scholars often have to make crucial and limited choices on the types of methodologies they will apply and the kind of theoretical frameworks they work from. This has resulted in numerous high-standard and specialized volumes that investigate the subject of this book from within one specific school or theoretical framework. Results of this research are then presented at excellent high-profile conferences such as *Evolang*; *Language, Culture, and Mind*; *Ways to Protolanguage*; or at annual meetings of the International Primatological Society; the International Society of Zoological

Studies; the American Association of Physical Anthropologists; the Animal Behavior Society; the Human Behavior and Evolution Society; the International Cognitive Linguistics Society; the European Society for Philosophy and Psychology; and so on. Nonetheless, these conferences and their proceedings or journals are targeted at field-specific audiences that work within certain but not other disciplines. The unfortunate result is that the scientific outputs often remain juxtaposed.

In this anthology, we have invited our writers to provide reviews of how the research programs that underlie their specific fields define studies on primate communication and human language. The contributors give an overview of the gathered data, they explain the methodologies used to collect them, and they demonstrate how such data contributes to overall theory formation on the subjects at hand. Rather than present new data, the authors thus highlight the numerous methodologies and epistemic frameworks that are currently at a researcher's disposal. This book does not select a "winning methodology" or research school. The aim of this volume is to provide the reader with ways to break into the research, by showing how rich and informed research on the origin of social communication and human language can be when we allow for epistemic plurality. How the results of these various lines of research can be combined into broader, more encompassing theories on the origin of social communication and language goes beyond the scope of this volume.

2 Brief Sketch of the Various Epistemic Frameworks Available for Researching Social Communication and Language in Primates

What are the epistemic frameworks that guide researchers in their studies on primate communication and human language? Current research methodologies and theoretical frameworks on communication and language originated around the turn of the last century, when they emancipated from classic philosophical traditions.

The field of ethology arose in the 1930s, mostly in Europe, as an outgrowth of both naturalized epistemology and comparative zoology. Inspired by early scholars such as von Uexküll (1909), Heinroth (1910), Haldane and Huxley (1927), Lorenz (1937, 1941, 1958) instigated the scientific study of animal "instincts" and developed theories on imprinting and fixed action patterns, and Tinbergen (1963) defined what became known as the 4 questions of ethology. In America, the field of comparative zoology was defined by both Louis and Alexander Agassiz (for a historical account, see Winsor 1991). These scholars contributed by defining how we can observe animal behavior and how we can conduct both comparative developmental and evolutionary research on animal behavior, including communication.

At around the same time, especially in America, modern comparative psychology turned behaviorism into a school. With their focus on learning and conditioning in humans and other primates, scholars such as Thorndike (1911), Watson (1913), and Skinner (1957, 1986) introduced the empirical and experimental study of behavioral

development. Skinner developed a learning theory of human language, averring that language is a behavior and that much of verbal behavior can be learned through operant conditioning.

From within the field of linguistics, Chomsky (1959) fiercely argued against Skinner's behaviorist theories on language learning. Chomsky critiqued behaviorism based upon, what was later called, the poverty of stimulus argument: during development, human children are competent to learn language even though the language performances they are exposed to are imperfect. Chomsky (1965, 1972) therefore postulated an innate language faculty or a brain-based cognitive "language organ."

This I(nternal) language faculty differs from the various E(xternal) languages that exist in the world today, and I-language, Chomsky professed, requires cognitive rather than behaviorist research.

Both the competence/performance and I-language/E-language distinctions divided the field of linguistics into synchronic and diachronic (historical and comparative socio- and anthropological) linguistics. Synchronic linguistics investigated what was structurally universal to all languages, with the assumption that what was universally shared lends insight into the core of I-language. The answer given was that semantically, all languages allow for displacement, or the ability to use symbols that refer to non-observable events in the world, and syntactically, all languages are recursive and compositional.

This characterization of human language held consequences for how animal communication was defined and contended to differ from human language. Chomsky reasoned that animal communication lacks displacement, compositionality, and recursion and that language therefore qualitatively differs from any other type of communication we find in primates. Chomsky never denied that primates have social communicative skills. What he did do was annihilate evolutionary continuity between primate communication and human language, because for Chomsky, the two were incomparable. The defining characteristics of language are not that it enables social communication, but that it enables one to express abstract and creative thought. It is for these reasons that human language is considered qualitatively distinct from primate communication.

The I/E language distinction also held consequences for how communicative and social aspects of human languages became defined and studied. Diachronic studies on the historical origin, dispersal, and death of languages; comparative research on everyday language use; and psychological and behavioral studies on the various types of non-verbal behavior that accompanies human language performance can be investigated from within ethology, comparative psychology, zoology, sociology, and anthropology but, for Chomsky, they contribute little to an understanding of I-language and language competence.

In the meantime, comparative psychology had indeed developed a tradition of investigating non-verbal communicative behavior such as emotions, expressions, and gestures, in both humans and other primates. Such research had proven that there is quite some overlap in the types of behaviors humans and primates use to communicate socially, which again raised questions about evolutionary continuity. Cross-fostering experiments were introduced where humans taught non-human primates to

sign human languages (Fouts and Mills 1997; Gardner and Gardner 1969; Gardner et al. 1989; Patterson 1978; Terrace 1979); and to learn artificial languages such as Yerkish (Rumbaugh 1977, Savage-Rumbaugh 1986). Many of the original cross-fostering experiments were conducted with the following two goals in mind. One was to flesh out the limits and possibilities of reinforcement or operant learning to gain insight into the boundaries of the nature/nurture, continuity/discontinuity, and quantitative/qualitative debate (for a discussion, see Gontier 2006); another was to test Chomsky's predicaments on human language. The results of these cross-fostering experiments are that primates are competent in learning a limited amount of symbols, and they can compose rudimentary recursive sentences. Another outcome of these experiments was that our cousins learn human language more easily when they are socially motivated to use it as a means to communicate, rather than when they are conditioned to associate ASL constructs with events in the world.

The modern field of primatology emancipated from comparative psychological and ethological schools in the late 1960s, when pioneers such as Fossey (1983) and Goodall (1986) started collecting data on how primates behave and communicate in natural settings. The result of these careful observations was that scholars identified the various ways in which primates interact socially. Maternal care, food sharing, fighting, and sex require interactions with conspecifics. These interactions are accompanied by behavior such as grooming, emotional displays, expressions, vocal calls, manual gestures, eye gazing, and joint attention, and these behaviors can be characterized as socially communicative.

With the rise of sociobiology, the ontogenetic observations and cross-species comparisons were placed in an evolutionary context. Mayr's distinction between ultimate and proximate causes of evolution and the deciphering of the genetic code in the 1950s provided early scholars hope that soon, the genetic basis of primate behavior, cognition, and anatomy would be discovered and that scholars would be able to deduce from that how these traits evolved. In order to understand nurture, we need to understand nature, and early sociobiologists synthesized selection theory with the data obtained from fieldwork and behaviorist experiments, and they developed the first theories on the evolution of human and non-human primate social behavior (Axelrod 1981; Hamilton 1964; Wilson 1975; Morris et al. 1979).

The epistemic tenets of behaviorism were also criticized by cognitive developmental psychologists (Piaget 1972). Overall, advances in the cognitive and neurological sciences allowed scholars to associate postulated mental capacities to specific structures and areas of the brain and to initiate comparative brain research. One important outcome of this cognitive revolution (for discussions, see Baars 1986; Piattelli-Palmarini 1980) was the rise of the field of biolinguistics (Bickerton 1984; Puppel 1995; Jenkins 2000), which investigates how mental capacities and brain structures underlie language. Other outcomes were cognitive research on theory of mind in human and other primates (Byrne and Whiten 1988; Tomasello and Call 1997; Whiten and Byrne 1997). Unanswered questions of these fields today include whether the mind operates in a modular or domain-general fashion.

By the beginning of the 1990s, also the cognitive turn became partly criticized and partly expanded by the "social turn" and "adaptationist turn." By expanding

on the early works in sociobiology, evolutionary psychologists such as Cosmides and Tooby (1994) conjectured that human behavior primarily needs to be understood by making use of natural selection theory and by studying our hominin past, much more than by studying behavior or cognition as it unfolds in modern human infants or non-human primates. They question the possibility to straightforwardly draw inferences on phylogeny from ontogeny, and they underline that chimpanzees are our cousins and thus evolved separately from our hominin ancestors. Such conjectures of course do not invalidate the results of species-specific behavioral research, but it does shift epistemic focus when human behavior in particular is the topic of investigation.

Although a great deal of progress has been made in acquiring knowledge on the physiological, developmental, and sociocultural mechanisms that, respectively, underlie primate anatomy, cognition, and behavior, scholars have so far neither been able to ground these traits either in genes or in specific brain structures (as the early sociobiologists hoped would be the case) nor have they been able to demonstrate how exactly these traits evolved. Because many of the proximate causes of behavior remain poorly identified, evolutionary psychologists place epistemic focus on the ultimate causes of behavior and investigate how natural selection in particular might be the underlying evolutionary mechanism by which these traits evolve (for a discussion, see Gontier 2012a, b). Epistemic questions they ask are: Why did social behavior and cognition evolve? And what are the adaptive benefits?

Pinker and Bloom (1990) followed this shift in epistemic focus and advanced that of primary importance is an understanding of what language is for, i.e., what are the functional adaptive benefits of human language? This differs from Chomsky's epistemic outlook, because he investigated what is unique to human language, and what is unique to human language does not necessarily provide a reason for why it evolved (Gontier 2010). Pinker and Bloom conjectured that language is an adaptation that evolved by means of natural selection. The evolutionary adaptive benefit that language is argued to provide humans is enhanced social communication. Insofar as other primates evolved means to communicate socially, there is epistemic ground to examine how these forms of communication are evolutionary precursors of human language. The field of evolutionary linguistics (Hurford et al. 1998; Knight et al. 2000) and to some extent evolutionary anthropology (Boyle et al. 2007; Mellars and Stringer 1989; McBrearty and Brooks 2000) are direct outgrowths of evolutionary psychology (Barrett et al. 2002). Both fields examine the adaptive functions and selection pressures that enabled verbal and non-verbal communication as well as human sociocultural behavior and how communication is a form of sociocultural behavior (see Gontier 2012b for a discussion). Innovative to their approach is that many of the developed adaptationist theories are currently tested by a varied set of computational and experimental modeling and simulation techniques.

As this brief sketch demonstrates, new disciplines often get established by their adherents overruling the epistemic programs and methodological toolkits of previous disciplines and by reinterpreting the acquired data according to new epistemic rules, or by shifting epistemic focus. The above-described paradigm shifts

have often been characterized as transitions from instructionism or behaviorism over cognitivism to selectionism. But the fact of the matter is that today, scholars remain active in all these fields.

Scholars have developed many methodologies and theoretical frameworks on how we can study and understand primate communication. Currently, researchers remain divided on whether human language is merely one type of social communication that has evolved within the primate lineage, or whether language has non-communicative properties. This divide also continues to impact non-human primate social communication studies. Their social communicative skills are either understood as evolutionary precursors to human communication or, in attempts to demonstrate what is specific and unique to non-human primate communication, their species-specific abilities to communicate socially nonetheless become defined by differentiating their traits from our own. And eventually, both communication and language are studied from within the same theoretical assumptions and by using the same methodologies.

For this book, we have invited representatives of all disciplines who demonstrate how both communication and language can be studied, what scientific data has been gathered, and how theories are build.

3 Introduction to the Contributors and Their Chapters

The volume is divided into four parts. In the first part, the academic origins of the epistemic outlooks on the nature of social communication and human language are analyzed. In the second part, scholars identify the various behaviors that have been understood as socially communicative, in both humans and other primates. In the third part, scholars horn in on how primate social communication evolved and how it can be understood as an evolutionary precursor to human language. And in the final part, scholars highlight how human language differs from other forms of primate social communication.

3.1 Philosophical and Historical Roots of Social Communication Studies

The study of language and social communication has deep historical and philosophical roots in academic culture. Philosophers of science and historians can therefore provide valuable insights into the origin of conceptual frameworks as well as the rhetoric and politics of science that justify or bias how we study the origin of social communication and human language in primates.

In his “[Lord Monboddo’s *Ourang Outang* and the Origin and Progress of Language](#)”, the philosopher **Stefaan Blancke** gives a historical account on the origin and evolution of language debates as they emerged in the Enlightenment literature. In the eighteenth century, trade and colonization confronted Western civilization with

other cultures. Incoming travel accounts reported on the observations of “ape-men” in the woods, or “*Homo Sylvestris*” (Tyson 1699), today designated as orangutans, that demonstrate anatomical form and communicative skills comparable to our own. Blancke first reviews how, from within the Romantic Movement, debates on human nature set forth the groundwork of dichotomies that still plague current theorizing on non-verbal communication and human language. These dichotomies include the innate/acquired or nature/nurture debate (is language the result of learning and enculturation in civilization or is it an innate biological capacity); the qualitative/quantitative distinction (does human rational, abstract linguistic thought differ qualitatively from non-verbal social communication in animals and primates; and can one find grades of complexity in the various languages man uses to communicate); and the continuity/discontinuity debate (does man, with his capacity for language stand apart from nature, or is there continuity with other types of communication). Blancke relates these dichotomies to ideas of nature being created and creation being orderly structured into a Great Chain of Being that steadily progresses from the simple to the complex. Accordingly, the first languages were understood to be more “passionate” and construed of iconic gestures and vocalizations strung together with little syntactic rules, while younger languages were considered to be more “rational” and containing more abstract symbolizations and complex grammar. In the second part of his chapter, Blancke zooms in on James Burnett aka Lord Monboddo, a Scottish intellectual of the eighteenth century who published one of the first Romantic accounts on the natural (meaning historical, not evolutionary) origins of language in his work *The Origin and Progress of Language*. As Blancke demonstrates, Lord Monboddo entertained a somewhat idiosyncratic view on the nature of human language, for he ascertained that it is not a defining feature of our species. He further conjectured that humans demonstrate affinity with non-human primates, especially orangutans. Orangutans, he contended, are “lower” humans that can provide insight into our emotional, rational, and linguistic capacities; and to make his point, he hypothesized that if orangutans were enculturated properly, they would be able to acquire language and other traits associated with civilization.

This challenge of enculturating non-human primates with the hope to finally settle on the innate/acquired, continuity/discontinuity, and qualitative/quantitative dichotomies was put to test during the numerous cross-fostering experiments conducted in the beginning of the twentieth century. The early cross-fostering experiments where the chimpanzee Gua was raised together with a human child by the Kellog family (Kellog and Kellog 1933), as well as the speech experiments conducted by the Heyes family with the chimpanzee Vicky are reviewed by **Sandra Swart**, in her chapter on “[Ferality and Morality: The Politics of the “Forbidden Experiment” in the Twentieth Century](#)”. Swart is a historian, and she sketches the broader historical and scientific contexts in which these reinforcement-based behavioristic learning experiments were conducted; how incoming results were received by the larger scientific community; and she investigates the scientific motivations the researchers entertained to justify comparison of human ontogeny with non-human primate behavior. Why conduct such experiments; what results were the researchers aiming for; and which ideologies on human nature

were they supporting or fighting? In fact, why were such experiments “allowed”? Swart demonstrates that rather than providing insight into the origin and evolution of communication, these experiments aimed to understand the beginnings of human nature and thus the limits of non-human primates. Language skills were a mere example of the latter boundary. In the second part of her paper, she turns to debates on the “forbidden experiment,” i.e., raising human children by non-human primates. Although raising a series of ethical issues, Swart demonstrates that scholars such as Winthrop Kellogg took the idea of such experiments seriously. In attempts to find leverage, Kellogg even referred to intellectuals such as Montesquieu who similarly had speculated on the potential of such experiments. Experiments where humans were reared by other primates were never conducted in practice, which made scholars resort to the quest for alternatives. Inspired by Linnaeus, Darwin, and Galton, who had referred to “beast-children” in their works, such alternatives were found by reports on “feral” children. Reports on real “Tarzans” and “Mowglis” in the wild, such as Lucas, the “Baboon Boy” of South Africa, were often dubious and fraudulent, but nonetheless taken quite seriously by these early intellectuals. Swart reviews how pioneering and leading scholars, including Raymond Dart and John Foley, authenticated several of the cases reported, and she analyzes the polemics of the scholars involved. She ends with a critical assessment of the usefulness of the results obtained from such studies and weighs them against the ethical concerns they raised.

3.2 The Elements of Social Communication in Primates and Humans

Many scholars agree that social communication can make use of gestures, vocalizations, and expressions. But what do such behaviors communicate? Do they convey emotions, shared intention, or symbolic abstract thought? Is joint attention sufficient to communicate, or does it require intentionality and theory of mind? In fact, when do behavioral acts become understood as communicative and as social? And how does one study all of the above? In the second part of the volume, and from within ethology, primatology, and psychology, scholars introduce the building blocks of social communication; they highlight the biological, cognitive, and cultural requirements to communicate socially; and they theorize when it originates in primates.

From the mid-1960s onward, interspecies cross-fostering and language learning experiments took on a more scientific approach. Because vocal language learning experiments had proven unsuccessful, several experimental projects were launched where psychologists, primatologists, and linguists investigated non-human primates' capacity to learn signed and artificial languages. The famous Project Washoe, launched by Beatrix and Allen Gardner at the University of Nevada in Reno, was the first experiment whereby a chimpanzee was taught lexical and grammatical structures of American Sign Language. Later, the project was expanded to include other

chimpanzees. This expansion enabled the study of chimpanzee–chimpanzee ASL conversations as well as transmission modes among chimpanzees across multiple generations. Many of the language-trained chimpanzees eventually found their home at Central Washington University, in the Chimpanzee and Human Communication Institute. Originally run by Roger Fouts, this Institute then became directed by **Mary Lee Jensvold**. In her chapter “[Experimental Conversations: Sign Language Studies with Chimpanzees](#)”, Jensvold reviews the historico-theoretical context, methodological preliminaries, and various experimental setups used over more than 40 years of inter-specific and intra-generational research on ASL comprehension, conversation, and transmission. One of the major outcomes of this research is that reinforcement learning had but limited success. Rather, chimpanzees more successfully learned ASL constructions when social immersion techniques were used, i.e., when a socio-cultural environment was created that made communicating in ASL constructs meaningful. This research therefore demonstrates, as is the case with human children, that language learning not merely depends upon having a cognitive capacity to learn language, but that language learning is a culturally embedded practice that requires social motivation. A second major outcome of these experiments was that chimpanzees were able to learn not only a lexicon, but also basic grammar. Finally, she demonstrates that once learned, ASL becomes a permanent and meaningful way to communicate with caregivers as well as with other chimpanzees. Jensvold discusses cases of displacement (that demonstrate successful use of arbitrary signs); wh-question experiments (that indicate syntactic skills such as compositionality); and conversation analyses that focused on turn-taking, on topic/off topic conversations, and reactions to negative-response statements (that prove correct comprehension, usage and additivity); and she compares the chimpanzee’s skills with that of human ASL learners. Numerous cases of the expansions of the message to facilitate comprehension of the communicative partner, private signing in contexts of imaginative play, and successful transmission of signing to offspring (as was the case with Washoe’s adopted son Loulis) prove that chimpanzees are, to a certain extent, able to learn, comprehend, meaningfully apply, and transmit human language. Jensvold therefore pleads for continuity.

When primatologists, ethologists, or developmental psychologists observe, study, or theorize on the nature of communicative interactions in primates, including mother–infant relationships or non-verbal and verbal social communication, these researchers have to have a minimal working definition of “communication,” “social interaction,” and “information.” What are these working definitions; how do they influence methodology; and how do they relate to a larger theoretical paradigm from wherein the results of observation and analysis are interpreted? These meta-theoretical questions are addressed by **Maria Botero** in her chapter on “[How Primate Mothers and Infants Communicate: Characterizing Interaction in Mother–Infant Studies](#)”. Taking mother–infant interactions as exemplar, she historically and paradigmatically contextualizes how theoretical assumptions have shaped our understanding of social non-verbal communication. She distinguishes between two alternative methodological approaches to study primate mother–infant interactions: the ecological-linear model as it was introduced by Jeanne Altmann to study social

mother–infant interactions in non-human primates; and the interactional model advanced by Jerome Bruner to study mother–infant interactions in humans. Because it was introduced for investigating communicative interactions in non-human primates, the ecological-linear model avoids assumptions on the presence or absence of belief states such as intentionality or theory of mind, but focuses on the immediate and observable outputs of communicative behavior (action–reaction schemes or does behavior *x* in the mother chimpanzee trigger a behavior *y* in the infant). Information, Botero demonstrates, is therefore understood from within Shannon’s classic information theory as a message that is transmitted between a sender and a receiver. From within the school of ethology, the message (a vocal call or behavioral pattern) is often understood as “instinctive” or fixed, and thus informed neither by environmental context or social situation, nor learning. This in turn reinforces a methodological emphasis on the transmission mode (the onset, duration, and ending) of communicative messages, rather than an emphasis on the context and the meaning of the message. This epistemic stance, Botero points out, limits research on semantics of the message and the sociocultural situatedness wherein communication takes place. In contrast, the interactional model, designed to investigate human mother–infant communication, works from within the explicit assumption that there exists a functional sociocultural and communicative context. Such communication is understood as interactional, because it is assumed to be the outcome of ritualized sociocultural practice at both the level of the mother–child dyad, and at higher levels such as the group. The mother–infant dyad is therefore evaluated as embedded in a set of other communicative group interactions that affect and result in social, cognitive, and cultural learning. Such a stance, Botero demonstrates, also does not require assumptions on intentionality of the communicative process. Rather, the messages are considered semantically meaningful when one can observe that they are communicatively functional. Such functional assessments can only be made when one contextualizes the communicative behaviors as a sociocultural dyad. Botero demonstrates how this interactional approach to communication can be implemented into the study of chimpanzee mother–infant interactions.

Facial expressions are the most outstanding examples of non-verbal communication. How facial expressions are means of communication and how they in particular enable the articulation of emotions in both humans and other primates has long been the subject of social communication studies. Charles Darwin (1872) pioneered the study in his seminal work *On the Expression of the Emotions in Man and Animals*. He first linked specific expressions to certain emotions, and secondly, he contended that such expressions are instinctive and innate within a variety of species. Expressions of emotions are exemplar of adaptive behavior that evolved by means of natural selection to enable recognizable social communication among members of the same and different species. This work was revived and expanded by Paul Ekman, a clinical psychologist who introduced the facial affects theory. In humans, he differentiated between 7 “archetypical” and universal expressions for emotions of joy, fear, anger, sadness, surprise, disgust, and contempt. Ekman also devised several methodologies and testing devices with the goal to standardize comparative cross-cultural research on both expressions and emotions within the human lineage. In the

chapter “[On Prototypical Facial Expressions versus Variation in Facial Behavior: What Have We Learned on the “Visibility” of Emotions from Measuring Facial Actions in Humans and Apes](#)”, **Augusta Gaspar, Francisco Esteves, and Patrícia Arriaga** give a historical review on how the facial affect theory became the standard paradigm within comparative psychology. The authors critically assess the basic tenets of the theory. First, they demonstrate that although humans have a distinguishable set of emotions and expressions and associated action recognitions, scholars active in ethnological/anthropological and cross-cultural psychological research discovered quite some cross-cultural variability in how certain emotions link to specific expressions. Secondly, their own comparative work on the development of expressions and emotions in human children and adults shows that both expressions and emotions are much more variable and behaviorally flexible during the course of development than assumed by adherents of the facial affect theory (in a state of anger, for example, people sometimes smile). Gaspar and co-authors identify many more non-verbal clues that accompany the behaviors, and both the expressions and their linkage to certain emotions are the outcome of considerable learning of the behaviors in a sociocultural context. This also has consequences for evolutionary comparative research that often straightforwardly assumes the universality of emotions and expressions. Gaspar and co-authors demonstrate significant difference between which emotions are linked to specific expressions in humans, and how such linkage is expressed in our phylogenetic cousins. The authors emphasize the continued need for observational descriptive, comparative ethological research to further flesh out how enculturation, learning, and the general sociocultural environment help shape both expressions and emotions and the linkage between the two.

Any type of social communication, be it linguistic, emotional, expressive, or gestural, requires a capacity for the communicative partners to share attention toward the communicative signal. **Timothy Racine, Tyler Wereha, Olga Vasileva, Donna Tafreshi, and Joseph Thompson** contribute a chapter on “[The Evolution of Joint Attention: A Review and Critique](#)”. Reviewing the literature, they list the various cognitive, behavioral, and social capacities that have been proposed either to enable or to associate with joint attention. These include intersubjectivity, attentional focus through gaze following or pointing, exchange of emotions, shared beliefs, and mind reading (also discussed in **Nagataki**, this volume). They show that most scholars therefore agree that joint attention is a form of social cognition that ontogenetically precedes the development of either social communication or language. This gives credibility to the idea that joint attention also evolutionary precedes social communication of any kind. Considerable debate arises, however, on whether non-human primates and human infants are able to share attention intentionally. In the second part of their chapter, Racine and co-authors demonstrate that the various theoretical and empirical problems associated with comparative developmental research on joint attention also hinder evolutionary research on its origin. The authors critically assess several theories on the evolutionary origin of social behavior and how they can or cannot be applied to examine the evolutionary origin of joint attention. These theories include the secondary intersubjectivity theory that was developed by Trevarthen,

evolutionary psychology approaches as they were introduced by scholars such as Cosmides and Tooby, Pinker and Buss, and Tomasello's (2000) shared intentionality hypothesis. Trevarthen assumes intersubjective behavior to be innate and thus unlearned, but Racine et al. demonstrate that such a claim adds little explanatory value. Evolutionary psychologists are notorious for countering classic social science models that emphasize learning and instruction to the neglect of phylogenetic research. But the phylogenetic research such scholars deem necessary involves assuming that social behavior evolved by means of natural selection, as an adaptation to a Pleistocene environment. They also content that the social cognition required for joint attention is domain-specific and modular. Racine and co-workers point out that such a stance requires evolutionary psychologists to assume that "core knowledge" exists and that it is readily available during ontogeny, which again eliminates learning as a potential mechanism underlying the behavior. Racine and co-workers therefore evaluate these theories to contribute little explanatory insight into the onset of joint attention during ontogeny. Tomasello's theory on joint attention does integrate and rely on comparative ontogenetic research of joint attention in chimpanzees and human infants; and he concludes from these experimental observations that chimpanzees do not have the same number of mental states as humans and do not understand them in the same way as humans do. But here too, the difference is argued to be shared intentionality which is contended to be an adaptation, which again contributes little to overall theory formation or experimental research. Racine and co-workers criticize these adaptationist accounts on several grounds. For one, the latter is associated with the modern synthesis, which in biology is more and more discredited in favor of an extended synthesis. Secondly, the scholars involved do not take ontogeny into account. Evo-devo and epigenetics are evolutionary theories that developed within the extended synthesis and that do take both development as well as evolution into account when advancing evolutionary theories (see also **Boeckx, Tattersall, and Tamariz**, this volume). The authors therefore suggest that psychological research on joint attention is conducted from within evo-devo in order to further flesh out the origin of joint attention, during both ontogeny and phylogeny.

What is Theory of Mind? How does it unfold in humans? And how can scholars study it? In his "[Describing Mental States: From Brain Science to a Science of Mind Reading](#)", **Shoji Nagataki** guides us through distinct psychological theories and associated methodologies that enable researchers to investigate mind sets, especially emotional and mental states, in oneself and other humans. Historically, investigations into theory of mind have been conducted by simply asking the research subjects to describe their mental and emotional states (the method of introspection), by observing the outcomes of cognized behaviors such as language in experimental settings (the behavioristic approach), and by mapping the types of brain activity that are associated with certain states of mind (neuroimaging). Nagataki demonstrates how all these approaches fall short. Introspection is based upon subjective interpretations of the research subject and assumes an immediate reciprocal and intuitive understanding of the belief states by the investigator. Behaviorism merely focusses on the outputs of behavior and does not investigate

the underlying mechanisms that enable cognizing. And neuroimaging techniques are troubled by the explanatory gap for how do the brain activation patterns relate to the mental states. Nagataki further demonstrates that all of these methods are conducted within a social experimental context where it is assumed that both the researcher and the subjects under investigation already understand one another's mental states. Whether it involves asking for personal descriptions, interpreting results from observation, or asking a patient to respond to, or to imagine mental states during PET or fMRI scans, such experiments are done within a social context where "mind reading" already and necessarily occurs in order to be successful. Where does this "common ground" stem from? Answering this question involves an inquiry into folk psychology. Folk psychology takes this "common ground" as a given, and there exist three theories that investigate its origin: rationality theory, simulation theory, and theory–theory. Rationality theory goes back to Kant and assumes that there is a psychic unity, all humans share a universal reason as well as universal mental categories that enable one to understand others as intentional agents. Simulation theory is more empiricist-informed and assumes that all humans share a common sense apparatus, which enables one to "simulate" or take on the perspective of others, via empathy, imitation, or imagination, and as such, to infer understanding. Questions for both theories then become whether the assumed common sense apparatus or universal reason is innate or acquired, and how either evolved. Theory–theory assumes a less universal and fixed state, and contends that humans develop theories on the mental states of others through learning and enculturation, which enables perspective taking. Nagataki demonstrates that all these theories assume that mind reading, whether it is through reason or through investigating bodily expressions, assume either inferential or intuitive learning, and the question then becomes how we are to interpret the latter. The author pleads for a "detranscendentalized" form of intuition and points to verbal communication and especially language as the locus of this folk psychology. (Linguistic) Communication itself is an empirically acquired behavior that infers meanings from bodily actions such as sound production, and this learning occurs within and across generations. According to Nagataki, languages therefore provide a "third-person" perspective of folk psychology, and folk psychology itself is a means to communicate socially. Once acquired, language is often a means to understand and interpret others' mental states. Language itself is a socially evolved means that enables intuitive understanding. He ends his chapter with an application of his approach in an experimental setup, where therapists were evaluated to read anger states in normal individuals.

3.3 Evolutionary Transitions from Social Communication Systems to Language

How can primate social communication be understood as an evolutionary precursor to human language, and how did the transition occur? For years, scholars have been

debating what the anatomical–physiological modalities are wherefrom language evolved. Traditionally, two schools can be distinguished: scholars either defend that speech evolved first and thus that the evolution of language proceeded from vocal–auditory adaptations (for an overview, see Fitch 2000); or scholars defend that vocal language evolved from gestural (proto-)language, in which case the evolution of human language required both visual–gestural and later vocal–auditory modifications (Armstrong et al. 1995; Corballis 2002; MacNeilage 1998). Today, synergies of both ideas can be found, and several scholars suggest that the postulated protolanguage might have been prosodic, where rhythmic sounds and gestures that holistically conveyed semantically complete messages transitioned into fractioned, compositional language (for a discussion, see Arbib and Bickerton 2010; Mithen 2006; Tallerman 2007). In this part, and from within primatology, psychology, and linguistics, scholars investigate how gesture-first theories can be expanded to include other types of bodily communication, how non-human primates have more voluntary control over their vocalizations than originally presumed, and how both gestural and vocal communication might have transitioned into human language.

Given that there exist so many means by which primates can communicate non-linguistically, and accepting these communicative modes as evolutionary precursors to human language, how then, did human language evolve from these non-verbal modalities? This is the question raised by **Jordan Zlatev**, in his chapter on “**Bodily Mimesis and the Transition to Speech**”. Zlatev expands on the work of Donald (1991), a neuropsychologist who in his *Origins of the Modern Mind*, defends that symbolic thought, language, and our human-specific consciousness primarily evolved from sociocultural stimuli. Rather than evolve from modular brain adaptations, the capacity for complex culture evolved from changes in how different brain regions functionally connected and associated with the expanding neocortex. He distinguishes between three consecutive stages of cognitive-cultural evolution in our species: the mimetic, mythic, and technology-supported stage. These stages are differentiated based upon the predominant means in which culture is individually and collectively expressed and memorized: first in bodily expressions, then in language, and eventually cultural inventions such as art and written language allow for external information storage of symbolic thought. Donald’s theory has been adapted and expanded by many scholars interested in the evolutionary origin of language. Especially, adherents of a gesture-first origin of language investigate how a mimetic, primarily gestural expressive communication systems, could have originated from the communication systems present in other primates. Zlatev synthesizes gesture-first theories with Donald’s concept of mimesis developing the bodily mimesis hypothesis. The bodily mimesis hypothesis assumes that our ancestors acquired more volitional control over bodily actions such as expressions and gestures enabling them to consciously initiate and rehearse such behavior, as well as imitate or re-enact bodily actions. Such rehearsals and re-enactments enable a more developed form of empathy and intersubjectivity and thus increase group cohesion and sociocultural learning where pantomime and ritualized behavior become a means to intentionally communicate non-linguistically. Zlatev’s chapter first reviews the evidence in favor of the bodily

mimesis hypothesis. For Zlatev, the first hominins who possessed a more advanced control over bodily actions were *Homo ergaster* and *Homo erectus*. These species invented symmetric Acheulean artifacts and fire, and the production of both require fine motoric skills if not craftsmanship (indicating rehearsal and re-enactment). In comparison, the action recognition that occurs in monkeys during the activation of mirror neuron systems might enable basic empathy, but not the development of systems of shared symbolic meaning (also see Nolan, this volume). In order to make such a transition, Zlatev contends that actions need not merely become recognized, but volitionally and intentionally imitated. Comparative psychology demonstrates that chimpanzees and other great apes already possess voluntary control over manual gestures. Nonetheless, Zlatev suggests that chimpanzee's cognitive abilities for hand–eye coordination, causal reasoning, executive control, social learning, teaching, social intelligence, and functional representation are different from our own. Evidence for a gestural, mimetic origin of language can also be found in the fact that in humans, vocal language learning is often preceded by mimetic types of communication and also adult vocal language use is often accompanied by gestures. From this, Zlatev concludes that a mimetic form of communication evolved first and later co-evolved with vocal language. The transition from mimetic to vocal language is clarified by referring to Cognitive Semiotics, a field that investigates the symbolism of vocal, gestural, or artistic signs in relation to the cognitive capacities that enable them. Vocal language is less iconic and more arbitrary than manual communication systems, which enables more conventionalization and standardization of the message across larger groups. It is also less costly to learn vocal arbitrary sounds than to repeat whole sets of ritualized behavior to convey a message, which is why, according to Zlatev, speech at the expense of gesture became selectively favored, resulting in the multimodal communication system of modern humans.

David Leavens, Jared Tagliatela, and William Hopkins combine experimental and observational data on voluntarily produced vocal–auditory communicative signals in primates, with manual and gestural origin theories of social communication, into a multi-modal theory on the origin of human language. In their “[From Grasping to Grooming to Gossip: Innovative Use of Chimpanzee Signals in Novel Environments Supports both Vocal and Gestural Theories of Language Origins](#)”, the authors take an ecological and epigenetic approach to both communication and language. This implies adhering to the following two tenets: first, the many means there exist for non-human primates to communicate, both vocally and gesturally, are deemed sufficient for communication, so neither modality is maladaptive; and secondly, although human language requires enhancements in the physiological capacity to communicate both manually or vocally, language did not solely evolve from these features. Rather, in line with Dunbar (1996), they assert that human language evolved particularly to enhance social communication in larger groups, and they present empirical evidence that supports this hypothesis. The structure of non-human primates' supralaryngeal vocal tract and breathing apparatus limits the types of vocal calls they can produce, and it is the main reason why non-human primates cannot speak. One of the major contributions

of Leavens et al.'s work is that they demonstrate that non-human primates have more voluntary control over their supralaryngeal vocal tract than traditionally conceived. Their spectrum of vocal calls is also much larger. Sounds produced in the front of the mouth, such as lip smacks, sputters, kisses, and teeth chomps and also pants and grunts that are produced lower in the tract, can be understood not merely as behavioral actions, but as vocal-auditory communicative signals. The authors review both their own experimental research as well as reports on observations in the wild, and they demonstrate that primates possess voluntary control over such vocal signals; that such signaling behaviors are often co-opted innovatively and voluntarily to communicate (to acquire attention, for example); and that there is significant cultural variation in how and which vocal signals are used to communicate, which in turn implicates social learning. Leavens, Tagliabue, and Hopkins' work furthermore provides functional and neurobiological evidence that proves that it is primarily the left hemisphere that is active during such lip-produced sounds and that the activated brain regions show considerable homologous overlap with the regions active during speech in humans. They conclude that the evidence necessitates us to accept that our hominin ancestors, just as non-human primates, already possessed significant voluntary control over the production of vocal sounds and that such sounds were readily available to be co-opted to create novel intentional communicative signals (see also **Tattersall** and **Tamariz**' contributions). The consequence of these findings is that manual and vocal origin of language theories can be combined: language evolved simultaneously from both vocal as well as gestural communication systems. The reason vocal language is the dominant mode for human language today is explained by referring to Dunbar's theory: Evidence supports that vocal communication increases with group size, in humans as well as other primates, for it enables more rapid social bonding.

Chimpanzee's ability to produce voluntary and intentional vocal signals in socially communicative settings is also the theme of **Adam See's** chapter on "[Reevaluating Chimpanzee Vocal Signals from the Ground Up](#)". Problems he touches upon include the following: When do vocal sounds become communicative signals? Do communicative signals require learning? Does that learning need to be social and if so, when does learning become social? And when does communication become intentional? See reviews the recent scientific data obtained on chimpanzees' ability to voluntarily produce vocal sounds (including the work of Leavens et al. (2005), and this volume), and compares it with the criteria Tomasello introduced to understand chimpanzee's manual gestures as both communicative and intentional. Tomasello (2000) has asserted that, unlike in their vocalizations, non-human primates demonstrate significant evolutionary innovation in their voluntary control over manual gestures. They are often intentionally produced as communicative signals during dyadic reciprocal relationships, and many of these gestures can be learned. From a careful reading of Tomasello's work, See deduces that his main criteria for understanding several of these manual gestures as communicative signals are threefold: they are socially learned, voluntarily produced and used flexibly depending on the context, and they invoke attention to the attention of others. By using these criteria, he analyzes the literature

on chimpanzee vocalizations and provides evidence for all three criteria being equally applicable to certain vocalizations. A specific category of chimpanzee vocalizations, namely those that are produced to acquire attention, differ from other vocal displays and vocal calls (such as uncontrollable alarm calls or food grunts), because they are less associated with emotional or environmental stimuli and more the result of socially learning to direct the behavior of others. For Tomasello, there must be intentional usage of gestures before they can become understood as signals: they must be directed toward others in a social context in order to trigger behavioral responses or mental states (such as acquiring attention). Tomasello therefore relates research on gestural signals to debates on the presence or absence of theory of mind in chimpanzees. See asserts that although there is reason to debate the issue whether primates' manual attention-getting gestures demonstrate second-order intentionality, there is no more reason to doubt its presence in the production of vocal signals than there is in regard to manual gestures. See thus concludes that the criteria Tomasello uses to understand manual gestures as communicative and intentional signals are met in regard to the voluntarily uttered attention-getting vocal sounds. See consequently agrees with scholars such as Leavens, Tagliatalata and Hopkins that human language evolved from both vocal as well as manual signaling.

3.4 Evolutionary Origins of Human Language

How does human language differ from social communication as it unfolds in non-human primates? When did human language originate in time? Can the archeological and hominin fossil record provide insight into the origin of language? And by which evolutionary, biological, and cultural mechanisms did human language evolve? In the final part of this volume, authors analyze these questions from within anthropological, archeological, evolutionary, and linguistic sciences.

In the chapter on “[Communication and Human Uniqueness](#)”, **Ian Tattersall** explains how, or better how little inferences we can make on the origin and evolution of language by studying either hominin fossil remains or archeological finds. To examine the onset of vocal linguistic sounds, anthropologists draw inferences on the length of the supralaryngeal vocal tract (the sound box) from the position of the cranial vault (the skull base) and how flexible the basicranium is. Inferences on the larynx are drawn from the hyoid bone (a floating bone supported by muscles located above the thyroid in the neck, in turn positioned above the larynx). Both basicranial flexion and hyoid bones enable scholars to calculate the position of the tongue and the air space available to produce the spectrum of sounds. Middle ear bone remains allow inferences on hearing capacities. But, Tattersall demonstrates, comparison of these anatomical features across later-evolving *Homo* species (especially Neanderthals and humans) displays both significant variation within species and similarity between species, thereby providing inconclusive evidence for or against these species' capacity

to produce human(-like) vocal language. Recent insights coming from the newly emerging field of paleogenetics have also proven that Neanderthals share the specific mutations of the *FOXP2* gene. Fixed in our species, it is associated with articulate speech. But even if one postulates from these findings that Neanderthals possessed the capacity for articulate speech, the archeological record shows no compelling evidence they did actually speak a symbolic and syntactic language. The archeological record demonstrates a transition between four types of tool-technologies: the Oldowan (mode 1), Acheulean (mode 2), African Middle Stone Age and European Middle Paleolithic (mode 3), and African Later Stone Age and European Upper Paleolithic tools (mode 4). These archeological remnants provide behavioral proxies, i.e., scholars can speculate upon the cognitive and behavioral capacities that are required to produce these artifacts. Tattersall endorses the likelihood that from the onset, the hominins who produced these artifacts had an emotional, manual, and vocal communicative system, but there is little evidence that they possessed a linguistic mind. Only during the life span of *Homo heidelbergensis*, who is presumably the direct predecessor of our kind, archeologists find more complex and composite tools associated with the Middle Stone Age technological complex. Even Archaic *Homo sapiens*, first found in Ethiopia and 200,000 years old, produced artifacts not much different or more elaborate than the tools associated with older species. It is only with the appearance of anatomically modern humans, which happened around 100,000 years ago in Africa, that the archeological record undeniably demonstrates the presence of symbolic artifacts and ornamentation that include the 70,000-year-old geometric artwork and personal ornaments found in the South African Blombos Cave. The newly evolved skeletal features of anatomically modern humans demonstrate a major developmental reorganization of several bodily structures. According to Tattersall, this plausibly extended to the synaptic wiring of the neocortex, providing our species with new cognitive capacities for symbolization and abstract thought. These capacities remained dormant until they were triggered by cultural stimuli such as the described symbolic artifacts, which enabled a rapid evolution of semantic and syntactic language. For vocal language to emerge, several anatomical structures, including the vocal apparatus, became exapted and language evolved rapidly and exclusively in our species. Tattersall emphasizes that the vocal apparatus was already in place and of functional use in existing communicative systems, but that cultural stimuli triggered such features to become exapted for new use: language, which was vocal-auditory in kind. For Tattersall, the emergence of Nicaraguan Sign Language demonstrates another contingent evolutionary scenario where this time, due to other sociocultural circumstances, existing anatomical and cognitive structures became exapted for gestural language.

In the chapter on “[How did Humans become Behaviorally Modern? Revisiting the “Art First” Hypothesis](#)”, **Rita Nolan** battles the standard philosophical model of human cognition that understand symbolization as the result of logic and computation, and language as that what uniquely features semantic-syntactic structures, recursion, unbounded productivity, and displacement. Nolan provides an

alternative to this view, which goes back to philosophers such as Cassirer and Langer and she makes a case for art, or deliberate symbolic artifacts of material culture as she calls it, sharing these features. This has consequences for the origin of modern behavior in humans. Traditionally, language, art, and abstract thinking are assumed to distinguish us from other animals, and in our evolution toward modern behavior, language has been theorized to have evolved first, thereby enabling art, abstract thought, and other behaviorally modern traits such as navigation over water. Based upon the recent Blombos archeological findings—which include deliberately engraved ochre that is presumed to be of a symbolic nature as well as shell beads that served as personal ornaments and presumably symbolized status, gender, or other sociocultural features of the person who wore it—Nolan says that the capacity to produce deliberate symbolic material artifacts evolved first. Art facilitated the evolution of displacement, abstract thought or symbolization, recursion, and unbounded productivity, and eventually language. In making her case, Nolan provides a rich philosophical contextualization and critical assessment of many of the theories that have developed in regard to human language, human uniqueness, and modern behavior. Although agreeing with Chomsky's poverty of stimulus argument that in turn functioned as a critique against Skinner's verbal imitation and operant learning theory, Nolan criticizes Chomsky by making reference to Tomasello's theory that, following Grice, emphasizes that language requires and enables shared intentionality. But Tomasello's theory in turn is balanced against Grice's second requirement for language, which is shared semantics: all members of a language community more often than not attribute the same meaning to the same linguistic constructions. Gestural origin theories of language, which find proof of the evolutionary origins of shared intentionality and imitation in the discovery of mirror neuron systems (MNS), cannot by themselves explain the origin of abstract symbolization or features such as displacement, because actions and perceptions triggered and activated by the MNS require the presence of the object, the observer, and the performer of the behavioral scheme. If what makes language unique is its features such as semantic-syntactic structures, recursion, unbounded productivity, and symbolic displacement, then Nolan emphasizes that these features first and foremost have no immediate perceptual aspect. Following Harnad, language origin theories need to answer the symbol grounding problem: i.e., symbolization occurs without immediate empirical grounding or associating of the symbolized objects or behaviors to the physical or sociocultural world. Such decoupling or movement away from present and visible objects and behaviors allows for displacement, a term defined by Sterelny as the ability to talk about the past, present, or future. Combining these ideas and critiques, Nolan demonstrates how the late Middle Stone Age Art of Blombos already possesses these features traditionally attributed exclusively to language, and how the deliberate manufacture of material symbolic artifacts triggered and facilitated human language which is consequently assumed to have evolved later in time. She ends her contribution with guidelines on how to empirically test the theory.

How much of language evolution can be explained by referring to cultural rather than biological evolutionary processes? How does one define cultural

evolution? And how does cultural evolution underlie the evolution of language? These are the questions raised by **Mónica Tamariz** in the chapter titled “[Experiments and Simulations Can Inform Evolutionary Theories of the Cultural Evolution of Language](#)”. Tamariz elucidates how a combination of new experimental and computational techniques developed in the fields of evolutionary psychology, anthropology, and linguistics provide research tools that can complement cross-species comparative psychological research on cultural transmission (e.g., Gaspar et al., Botero, Jensvold, Leavens et al., this volume). Tamariz illustrates several of the iterated learning experiments and mathematical and computational agent-based simulations as they were developed by, among others, the James Hurford/Simon Kirby and the Luc Steels/Bart de Boer groups, which demonstrate that key linguistic features can evolve by means of cultural evolutionary mechanisms. More specifically, the creation of communicative symbols and conventions among individuals, the spread and stabilization (faithful sharing) of linguistic conventions within and across populations over time, the emergence of linguistics systems such as vowel systems, and compositionality of linguistic structure can be experimentally modeled and simulated by solely invoking cultural evolutionary dynamics. In the second part of the paper, she links these experiments and simulations to existing theories on babbling, social and imitation theories, and musical and gestural protolanguages, and she puts forward a theoretical framework for the cultural evolution of language. In this framework, she breaks with some of the long-standing ideas on how we are to conceptualize cultural evolution (how similar or different is it to biological evolution), how we can define cultural and linguistic evolutionary units (replicators), and how they are inherited and transmitted over generations. Tamariz advances that languages are complex adaptive systems that exist not so much because of biological, neuro-cognitive, or genetic adaptations for recursion or abstract thought, rather they emerge from contingent cultural evolutionary processes operating at both local and population levels. Following Maynard Smith and Szathmáry’s (1995) work on the major evolutionary transitions, she reasons that the cultural evolution of language involved two key transitions: a selection for replicability and a selection for function. Babbling phases or presumed protolinguistic phases in language development or language evolution occur because there exists selection of replicators: Sounds or gestures are faithfully replicated through imitative social learning. Eventually, these replicating cultural units become co-opted or exapted (see **Tattersall’s** contribution) for function: They are attributed communicative value between individuals at a local level. Innovative to Tamariz’ approach is that she suggests that individual concepts or perceptions (such as memes or linguemes) are not constant entities, because they result from “statistical” social learning: they can change during the course of an individual’s life time, and for this reason, they cannot be replicating units. What does replicate are social constructs that emerge as a consensus at the population level. At the population level, social interaction patterns that influence imitative learning and teaching, as well as the easiness with which certain symbols are (re-)produced, provide selection pressures on the type of linguistic features

that evolve. Cumulative learning and transmission to new generations is necessary for linguistic systems to emerge. And such systems evolve more by random drift than natural selection and eventually demonstrate remarkable stability and complex features such as compositionality and arbitrariness of signs, due to constraints imposed by how we learn socially. In short, language is not so much a biological capacity that evolved in our species, but an emerging outcome of individual and group behavior that includes social learning and cultural transmission. By demonstrating how cultural transmission systems itself are both evolving and evolutionary systems, she concludes that we need to prioritize cultural evolutionary explanations of language over biological ones.

What is it that makes human language specific and unique, and how exactly does it differ from animal and primate communication? That is the main question tackled by **Antonio Benítez-Burraco, Ana Mineiro, and Alexandre Castro-Caldas** who, in their chapter “[The Emergence of Modern Communication in Primates: a Computational Approach](#)”, present a summary and review of the Biolinguistic tradition. The authors recognize the diverse means there are in the animal and primate taxa to communicate. Nonetheless, in line with Chomsky, they contend that such communicative systems cannot be understood as a semantic or symbolic coding system that is so typical of human language. They assert that human language neither evolved from animal cognition nor animal communication systems. Rather, human language evolved from our species’ unique cognitive and neurologically underlain abilities to “compute” complex structures. Language is typified by symbols that function as displaced conceptual representations and that are syntactically stringed together into semantic compositional structures. Such computational binding is recursive and enables humans to make an infinite series of meaningful linguistic structures that enables us to demonstrate abstract knowledge processes such as creative thought. Again in line with the Chomskyan tradition, they emphasize that social communication is but one function of human language. Other functions of human language, in particular these cognitive–neurological computations that underlie both the competence and performance of language, are what characterizes and defines its uniqueness. After having outlined the theoretical framework they work from, Benítez-Burraco and co-workers review how recursion, binding, compositionality, and displacement are evidenced in current human, vocal, and gestural languages. Afterward, they present archeological and paleontological fossil evidence for the evolutionary emergence of these types of computational behavior. Problems investigated include how the tying of knots and the production of complex composite tools can allow scholars to draw inferences on the presence of recursive cognitive thought; and how endocasts hint at the origin of brain lateralization, brain size, and increased neural connectivity required for language. They end with inferences on the evolution of language from recent genetic studies on the *FOXP2* gene (in humans correlated to the rise of articulate speech) and the *MICROCEPHALIN* gene (associated with brain size).

Cedric Boeckx, in his “[What Can an Extended Synthesis do for Biolinguistics: On the Need and Benefits of the Eco-Evo-Devo Program](#)”, zooms in on the distinction Chomsky made, together with Marc Hauser and Tecumseh Fitch, between

the faculty of language in the broad sense (FLB) and the faculty of language in the narrow sense (FLN) (Hauser et al. 2002). The author demonstrates that the reception of this article has mostly resulted in a focus on FLN and how it contributes to human uniqueness, while Boeckx' thinks through the consequences of recognizing that language is decomposable into subunits and accepting that many of these subunits (FLB) are shared with other primates. His main argument is that recognizing FLB enables, if not altogether necessitates the introduction of a sub-branch of biolinguistics, namely "comparative" biolinguistics. Originally, the field of biolinguistics focused on the human neurocognitive and ontogenetic capacity to develop I-language or language competence. By acknowledging, first of all, that there is no discrete and homogenous "language organ" in the brain; and secondly, by recognizing that multiple components of the FLB are shared with other primates and thus have an evolutionary history and continuity, biolinguistics now has to move beyond ontogeny and investigate how the subcomponents of the FLB evolved phylogenetically. From this, it also follows that one needs to investigate how the various elements of the FLB combined into our current language capacity, as well as how the unique properties of FLN (especially recursion and displacement), evolved. Boeckx argues that the Eco-Evo-Devo program holds potential to address these questions (see Racine et al., this volume). The Evo-Devo field originated exactly with the goal to reconcile phylogenetic evolutionary research with development. This field also takes on a more systems-theoretical approach, and studies on self-organization, exaptation, and emergence are key concepts in theory formation. Such concepts, Boeckx contends, enable a synthesis between synchronic, diachronic, and evolutionary linguistics. E-language is an emergent property of language users and self-organizes outside human individuals in language communities (see **Tamariz** contribution), while I-language appears to be an emergent property that results from the co-optation of various brain structures and cognitive capacities (see **Tattersall**, this volume). In pleading for the adoption of an Evo-Devo perspective, and following pioneering scholars such as Gould, Boeckx emphasizes that a functional-adaptationist approach, so characteristic of mainstream evolutionary linguistics and evolutionary psychology, is insufficient to explain the origin of anatomical form or the neurocognitive brain structures that underlie I-language. Without making the claim explicit, he argues that not only the ultimate (functional-adaptationist) causes of E-language, but also the proximate causes of I-language, or the physiological neurocognitive brain structures that underlie our human capacity for language, need to be the subject of scientific investigation. Here too, Boeckx hopes that taking on an Evo-Devo perspective will provide the answers to the questions long asked. Boeckx' paper is a programmatic one, wherein he most of all pleads for a moderation of several of the traditional, synchronic, and biolinguistic claims, in favor of the incorporation and integration of evolutionary and comparative studies in order to examine both the ontogenetic and phylogenetic emergence of I-and E-language. The incorporation of the Evo-Devo perspective will, according to the author, enable evolutionary pluralistic accounts that can complement the functionalist-adaptationist, modular and gene-centered theories of our time.

4 Current Trends, Future Questions, and Concluding Remarks

Every school of thought comes with scientific leaders, and all scientific leaders are visionaries that oppose the standard thoughts of their time and propose new ideas as well as methodologies to test them. These methodologies then serve as a canon for subsequent generations of researchers who, when following outlined ideas and methodologies, either confirm the postulated hypotheses and contribute to theory formation; or they find anomalies, contradictions, or new methodologies that lead to criticism and new ideas, which in turn enables theory formation by more clearly delineating the research problem (Kuhn 1962).

Behaviorists such as Skinner and Watson battled the phenomenological and nativist philosophers of their time by focusing on visible behavior and learning. With the goal to extend evolutionary theory to behavior and taking an instructionist approach in their behavioral studies, primatologists and experimental psychologists sought the observable continuation and boundaries of animal and human communication. Chomsky and Piaget battled Skinner and Watson by emphasizing the importance of cognition, and evolutionary psychologists and evolutionary linguists opposed both instructionist and cognitive thought by evolutionizing the existing theories. None of these advances could have been made if not for the previous work that had been done in the fields they eventually opposed, for theories do not come into existence *de novo*. Rather, scientific theories themselves are a shared learning experience of our species.

From within a variety of disciplines, scholars are now able to more clearly demarcate the means by which primates communicate gesturally, vocally, and linguistically. They have been able to point out many of the cognitive and anatomical requirements that enable communication and language. And they have been able to more scientifically ground that much of non-linguistic and linguistic communication is socioculturally embedded. The means used to communicate not merely depend upon anatomical structures and individual cognitive learning abilities, they also depend upon group behavior and sociocultural modes of information storage and teaching thereof. What anthropologists used to call the “super-organic structure” has equally become evolutionized, and today, the cultural dominion is either theorized to co-evolve with the biological realm or to form a complex emerging (adaptive) system (Steels 2002).

In sum, the various new epistemic frameworks that have been proposed to investigate the origin of social communication demonstrate that research is more successful when, rather than provide old answers, it creates new ways in which to formulate the questions and re-evaluate the obtained data. Having read the various chapters that make up this volume, we are happy to distinguish plenty new research avenues. How can we characterize the current trends in research on communication and language? And which directions should future scholars take?

What characterizes current research on emotions, expressions, vocal calls, or mental states is that the researchers involved first and foremost situate the

sociocultural context in which these behaviors are displayed. And it is becoming more and more accepted that it is the sociocultural context that to a large extent facilitates if not initiates the rise of these communicative behaviors. The study of social communication therefore falsifies many of the original philosophical assumptions on the nature of perception, cognizing, and mental states. Expressions, perceptions, symbols, grammatical rules, and mental states become understood less as prototypical cognition-based entities, or static biologically or genetically determined instincts, and more as malleable and learnable sociocultural constructs. Consequently, what evolved on a biological level are not the various types of communicative behavior or specific cognitive traits, but the anatomical and cognitive means there are to initiate behavior that can become interpreted as communicative. As the various observations and experiments demonstrate, all primates, to a lesser or larger extent, are able to transform random behavior into functional and communicative behavior; to attribute meaning to meaningless gestures, expressions, sounds, or eye gazes; and to reach some level of mutual understanding. But questions that remain pertinent are whether, and to what extent, the biological evolution of anatomical modalities and neurocognitive features that facilitate communication are sufficient to explain the origin of social communicative behavior, and how sociocultural (evolutionary) mechanisms provide additional explanations. Where do we put epistemic importance? What is causally relevant? Anatomical structure, behavior, cognition, or culture?

Another pertinent question that remains is how human language differs from social communication. Does sociocultural communication suffice to define human language and explain its evolutionary origin? Volitional control, levels of arbitrariness, types of symbolization, intentionality and awareness of course vary in gradation between human and other primates, and our species indeed by far surpasses the capacities of other primates in how we attribute meaning and communicate on the past, present, and future of events. When does primate communication end, and when does language begin, or is there no difference? Stated otherwise, what is non-linguistic about primate communication? And what is non-communicative about language? If there is no difference, then distinguishing between primate communication and human language is unnecessary from an epistemic point of view. If there is a difference, one can ask whether that is sufficiently characterized by referring to recursivity, compositionality, and displaced symbolism; or by referring to the larger outreach human language appears to have.

A distinguishable trend is that while linguistic, cognitive, and behavioral studies used to focus on ontogenetic research, and even oppose evolutionary research, it is safe to say that today, all these fields have taken on an evolutionary perspective to examine the sources and the means by which communicative behavior evolved. For many years, evolutionary scholars merely had the modern synthesis framework at their disposal, and so they examined how social communication could have evolved by means of natural selection. Today, with the recognition that evolution can proceed by a myriad of evolutionary mechanisms, scholars are just beginning to investigate how epigenetics and evo-devo frameworks, drift theory, exaptation and niche construction theory, and cultural evolutionary processes can be put to use to make sense of the evolutionary origin of social communication.

Future research on social communication will be greatly advanced by examining how the myriad of evolutionary mechanisms, both biological and cultural, that are currently identified within an extended synthesis, can identify the proximate and ultimate causes of social communication in primates.

Finally, it is good to keep in mind that shifting epistemic outlooks and applying new methodologies might call for a reinterpretation of the data and the theory that explains it, but it does not falsify the data obtained. None of the theories that have developed through the years demonstrate less or more scientific rigor. A behavioral experiment that quantifies empirically measurable actions is not methodologically more or less impaired than a neurocognitive experiment that examines the presence or absence of voluntary control over these actions. Scientists expand on the different means there are to theoretically conceptualize, as well as methodologically and experimentally delineate research problems, and it is through this expansion that science progresses. It enables comparison of conceptual frameworks, methodologies, and experimental setups, and most of all, it enables combining the results of the latter. Both comparison and combination can only lead to a richer demarcation as well as understanding of the problem. Both are highly necessary, for neither of the theories on their own are able to answer the question how social communication or language evolved in primates. What adherents of these various frameworks have done, every single one of them, is provide perspectives on how the problem can be defined, examined, and experimentalized. The result in the end is that more data, theories, and methodologies are available to the researcher, which enables epistemic plurality. A future question therefore becomes how the various data and theories can be combined into fuller and more encompassing theories that explain the biological, developmental, cognitive, neurological, and cultural evolution of social communication in primates.

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