



CHAPTER

10 Socio-Cognitive Specializations in Nonhuman Primates: Evidence from Gestural Communication

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Abstract

This chapter reviews primate cognitive abilities in physical, social, and communicative realms and asks (1) whether primates exhibit abilities that differ from those of other animals, and (2) what selective pressures primates face that may have led to the emergence of specific cognitive abilities. The authors focus on communication as the most likely realm for primate cognitive specialization and on the gestural communication of great apes as the modality in which primates exhibit the most advanced cognitive abilities. Findings from studies of natural communication systems of both wild and captive primates as well as studies involving communication with human experimenters are presented and discussed. Apes demonstrate flexibility, learning, and sensitivity to social cues in their gestural communication, but further studies are needed to determine how gestures are acquired and how they are perceived. Studies of comparative development of gestural communication and social cognition have the greatest potential to reveal the cognitive abilities used during gesturing, and they will help to determine whether those abilities are truly specializations for communication.

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Introduction

Primate Cognitive Adaptations

The past 30 years have witnessed an explosion of research on all aspects of primate cognition. Much of this new research has been fueled by the cognitive revolution in psychology and ethology, which prompted a shift from the study of learned behavior to the study of mental representations of the self and of the physical and social environment. A further impetus is the framing of cognitive investigations within ecology and evolutionary biology. This framing has led to a new understanding of the ecological significance and evolutionary origins of cognitive adaptations.

Primate cognitive adaptations can be thought of as complex “behavioral adaptations in which perceptual and behavioral processes (1) are organized flexibly, with the individual organism making decisions among possible courses of action based on an assessment of the current situation in relation to its current goal; and (2) involve some kind of mental representation that goes beyond the information given to direct perception” (Tomasello & Call, 1997, p. 8).

Flexibility is central to cognition, because without some agency in choosing to perform an action or having a range of possible actions to confront a problem or achieve a goal, an animal's response would most likely be an automatic response to a reoccurring environmental situation. Some complex behaviors may seem like cognitive adaptations, but if the behaviors are inflexible responses to the environment, then they are considered behavioral adaptations, not cognitive ones. The idea that an animal has some *agency* over what variables of the environment it attends to and how it acts in response to those variables is at the foundation of attributing cognitive processes to animals, and flexibility lies at the heart of agency.

Mental representation of some type is also a key element in cognition. Complex, human-like representation based on images or symbols is not required or implied. Rather, this representation involves the ability to make decisions based on perceptions of the external world by extracting relevant environmental features, holding information in working or long-term memory, comparing several things, categorizing things, or recognizing similarities between the immediate environment and a previously solved problem. Animals that appear to display “intelligent” choices, generalized learning, or insight are all employing mental representations that allow them to learn or make decisions outside the context of trial-and-error learning (see Tomasello & Call, 1997).

Cognitive adaptations and their underlying neural substrates evolve by natural selection in response to recurrent problems posed by the physical, ecological, or social environment, but they are selected at the cognitive rather than the behavioral level. They involve the ability to make decisions about what to do in a particular situation based on the perception or understanding of contextual variables rather than precise behavioral responses to external stimuli. Cognitive adaptations may be general abilities (e.g., the ability to inhibit a behavior), or they may pertain to specific contexts or environmental problems (e.g., the ability to make probing tools).

In this chapter, we ask first whether the primate order as a whole exhibits cognitive adaptations that differ from those of other animals, and second we ask what pressures primates face that may have led to the emergence of specific cognitive abilities. In the introduction, we discuss primates' abilities in the realms of physical cognition, social cognition, and communication. We focus on communication, and on gestural communication in particular, as an area in which there is great evidence for both flexibility and mental representation. In an attempt to determine whether primates that are phylogenetically closest to humans show evidence of cognitive specializations similar to those of the human species, we discuss facial expressions and body postures in both apes and monkeys. We then concentrate on the manual gestures of great apes as the type of communication that demonstrates the greatest flexibility.

As in many areas of cognitive research, there is a wide gap between the abilities apes demonstrate in experimental settings and those they employ during conspecific communication in wild or captive groups. We compare results from studies of wild and captive conspecific gesture, artificial-language studies, and experiments in which captive apes communicate with humans but by using their natural communication systems. Taken together, these results demonstrate that the cognitive skills apes use during gestural communication should be considered cognitive adaptations, though many questions remain. The captive studies demonstrate the importance of the developmental period in establishing and encouraging the acquisition and use of both cognitive and communicative abilities. Comparative studies focusing on the role of ontogeny in the development of cognitive abilities and on the interaction between cognitive and communicative abilities during ontogeny hold the greatest potential for providing insight into whether the cognitive abilities used in gestural communication evolved as specializations for communication.

Physical Cognition

The study of primate cognitive adaptations has involved many aspects of physical and social cognition. Primate research in the domain of physical cognition has addressed how monkeys and apes acquire information about the physical space in which they live and the inanimate objects in it, how this information is mentally represented and processed, and how it is retrieved and used to make decisions. Free-ranging primates form spatial maps that represent the environment in which they live and use them to make travel decisions as they search for food within their home range (for a review see Janson & Byrne, 2007). In the laboratory, primates exhibit knowledge of movements of objects through space and understanding of object permanence, that is, the notion that objects continue to exist and maintain their features and properties if they have been moved or hidden from view (Barth & Call, 2006; Call, 2001). For example, primates search for hidden objects, and some can solve tasks that require the mental rotation of objects (Call, 2000; Vauclair, Fagot, & Hopkins, 1993). Though primates are proficient at these tasks, there is no evidence that primates have greater understanding of space and objects relative to other mammals, nor is there evidence of significant differences among primate species (e.g., between monkeys and apes).

p. 168 Other research in the domain of physical cognition has involved object manipulation tasks, in which objects are used in relation to other objects, and which require an understanding of causality (e.g., the relation between the use of the tool and the goal to be accomplished with it). Many species of primates, and especially capuchin monkeys and the great apes, are proficient tool users and also show some evidence of understanding of causality (although see Povinelli, 2000). However, primates' tool using skills have been matched or even surpassed by the tool using skills of some corvid birds (e.g., Emery & Clayton, 2004; Hunt, 1996). Discrimination learning studies have addressed whether primates learn to discriminate particular features of objects and assign these objects to categories on the basis of similarities and differences in these features. These studies have shown that primates cannot only discriminate and categorize objects but can also understand complex rules underlying categorization, for example, the notion that categories of objects can be formed on rules such as identity, oddity, sameness, or difference (Tomasello & Call, 1997). Similar to birds and other mammals (e.g., laboratory rats), primates also possess the ability to make accurate estimates of small quantities of items as well as the ability to solve simple tasks involving quantity conservation or summation (Brannon & Terrace, 1998; Cantlon & Brannon, 2006). The exact perceptual or conceptual mechanisms underlying these skills remain unclear.

Taken together, studies of primate physical cognition have shown that monkeys and apes possess the ability to form mental representations of their space and objects, including hidden ones, but they show little evidence of greater learning skills or greater understanding of the physical world and its properties than other vertebrate animals do. The strongest evidence for a potential primate cognitive specialization in the realm of physical cognition involves the use of tools and the understanding of relational properties of objects including causality. This is particularly strong in large-brained primate species that face strong ecological pressures for complex food processing, such as capuchin monkeys and all species of great apes. Comparative studies between the development and transmission of tool manufacture and use in primates and corvids may reveal common social and environmental factors driving the development of these abilities in both lineages (e.g., Emery & Clayton, 2004; Emery, chapter five of this volume).

Social cognition has been a topic of great interest in primate research over the past 50 years, and there is now a growing focus on social cognition research in a wide range of nonprimate species. These studies are driven in part by our desire to understand the evolutionary pressures underlying the development of human social cognition, including the ability to be aware of the self and others; to empathize, cooperate, inform, create, and share symbols; and to hold collective beliefs. Many complex human abilities (including language and understanding others' beliefs) may have foundations in skills of social awareness that evolved to keep track of, predict the behavior of, and manipulate relationships with other individuals in large social groups. Primates have demonstrated advanced capabilities in many areas of social awareness, including self-recognition, awareness of knowledge, social learning, and understanding the social relationships of others. Some nonhuman primate lineages (particularly birds and dogs) demonstrate comparable abilities in certain aspects of social cognition, but primates most consistently demonstrate cognitive adaptations for processing and benefiting from social information. Primates may differ most substantially from nonprimates in the ability to represent other minds. In a recent review, Byrne and Bates (2010) draw a distinction between differences in social cognition based on *degree* (e.g., keeping track of more group members or having more categories) and those based on a deeper *understanding of the mind* (e.g., awareness of the self or understanding of others as having different perceptions and knowledge). The authors argue that “particular skills such as insightful cooperation or deception, perception of intent, imitation of novel skills, and mirror self-recognition, signify a qualitatively different representation of mechanisms and minds.” This difference probably relies on the presence of “specific cognitive architecture that allows for behavior parsing and the formation of hierarchically organized programs of action” (Byrne & Bates, 2010, p. 825). Abilities relating to perception and representation of other minds are good candidates for primate cognitive specializations that set them apart from other species.

p. 169 The ability to be aware of oneself may be one step toward recognizing that other individuals are also “selves” with autonomous behavior and different goals and beliefs. Researchers have conducted many studies of primates' ability to recognize themselves in a mirror, driven by the hypotheses that mirror self-recognition ↪ indicates self-awareness and that knowledge of self forms the basis for theory of mind (Gallup, 1970; Gallup, Anderson, & Shillito, 2002). On the mark test of self-recognition (which measures self-exploratory behavior in front of a mirror after subjects have been unknowingly marked with a salient paint), primates as a whole perform better than other animals (but see Plotnik, de Waal, & Reiss, 2006; Reiss & Marino 2001 for evidence of mirror self recognition in elephants and cetaceans). Apes outperform monkeys on the mirror task (Gallup, Anderson, & Shillito, 2002), but monkeys may have an intermediate level of understanding where they do not recognize the reflection as their own but still understand that it is not a stranger (de Waal, Dindo, Freeman, & Hall, 2005). The notion that learning how to use a mirror to inspect inaccessible aspects of one's body necessarily entails possessing a concept of self has been questioned (e.g., Hayes, 1993), but the tendency of great apes to examine the face in detail, even when it is not marked, provides support for a self-recognition interpretation (Gallup et al., 1995).

Metacognitive abilities (e.g., awareness of what you do or do not know) may be a better indicator that an animal is aware of itself as a cognitive agent (able to make judgments or possess knowledge). Tests of metacognition typically involve discrimination or memory tasks in which animals have the option to participate in or opt out of the task on each trial (or in some cases to gamble on a trial based on their confidence) (see chapter 15 of this volume). To succeed on a trial, an animal must usually either remember earlier stimuli or be able to categorize a new stimulus correctly. If the animal opts out of a trial, it might receive a smaller reward than it would if it had participated and chosen correctly or it might simply avoid a punishment incurred if a wrong answer is given. To maximize success on these tests, animals should participate when they are confident they will succeed and opt out when they are unsure of their answer. Both primates and cetaceans have performed well in these types of tasks, indicating that they are aware of what they do and do not know (Hampton, 2001; Kornell, 2009; Kornell, Son, & Terrace, 2007; Smith, Shields, & Washburn, 2003; Smith & Washburn, 2005; Smith et al., chapter 15 of this volume). Though there are few comparative studies, monkeys appear to need more training to perform these tasks than apes (see Kornell, 2009; Suda-King, 2008).

Apes also outperform monkeys on tests involving social learning (i.e., learning by observing others) through emulation, imitation, or teaching. Social learning of complex behaviors has been demonstrated by many primate species in captivity, and behavioral differences between groups of wild primates are often considered to be the result of social learning. Primates' demonstrated abilities to learn from observing

others along with observations of naturally occurring regional behaviors provide evidence for the origin and spread of behavioral traditions that may approximate elementary forms of human culture (van Schaik et al., 2003; Whiten et al., 1999). Many other animals have demonstrated the ability to learn from observation of others in captive settings, and they sustained transmission of behavioral traditions (e.g., guppies: Warner, 1988; meerkats: Thornton, Samson, Clutton-Brock, 2010; see further review in Laland & Galef, 2009). Species capable of vocal learning often have local “dialects” that vary between locations (e.g., Deecke, Ford, & Spong, 2006; Jenkins, 1978). There is less evidence for “material culture” (i.e., socially learned behaviors involving the manufacture or manipulation of objects) in nonprimate species, but some observed behaviors might comprise local traditions (e.g., dolphins using sponges as tools Krützen et al., 2005). Unsurprisingly, regardless of whether culture can be considered a cognitive specialization unique to humans or shared by other primates (and/or other animals) rests on how culture is defined and what operational criteria are used for its identification across species (Byrne et al., 2004; Laland & Hoppit, 2003).

Although the question of whether nonhuman primates have the ability to think about other individuals' mental states remains unanswered, it is well recognized that they excel at the task of observing other individuals' behavior, remembering past interactions, and making predictions about future interactions. Primates form complex social relationships with others and have knowledge and memory, not only of their own relationships, but also of relationships between other individuals (e.g., Cheney & Seyfarth, 1999). Studies investigating this aspect of social cognition have assessed primates' ability to recognize kinship, dominance-rank relationships, or friendships among individuals that reside in their social group. Knowledge of social relationships is used in complex cooperative and competitive strategies involving exchange of favors, alliance formation, opportunistic exploitation of social situations, and manipulation of other individuals with deceitful tactics (Byrne & Whiten, 1988).

p. 170 Complex social strategies in group-living monkeys and apes invariably entail the exchange of vocal or visual signals between individuals. Communication can provide a window into the primate social mind, though it is unclear whether the cognitive abilities that underlie communication are adaptations primarily for communication or whether they evolved more generally for group living and simply provide an advantage to communication when they are present. Studies of communication can provide insights into cognitive adaptations; however, they must first demonstrate that the communicative signals studied are not involuntary reactions to the environment but, instead, meet the criteria of flexibility and mental representation. Many features of communication have the potential to shed light on cognitive adaptations. These include the role of learning in the acquisition of signal production, comprehension, and usage; the extent to which signals are under volitional control; the complexity in the structure of signals; and the information content or meaning of signals. The features of the environment that animals attend to when choosing when or how to signal and the ways in which they use communicative strategies to achieve their goals have great potential to reveal when and how animals make choices during communication. Studied features of communicative strategies include the extent to which signals are combined with other signals within the same modality or across different modalities to accomplish different functions; the extent to which combinations of signals exhibit properties of human languages, such as syntax; and the extent to which the production of signals is modified in relation to the presence of particular individuals (audience effects), their attentional states or current behavior, and possibly also their mental states.

Investigations of complexity in primate communication have mainly focused on vocalizations, in part because the shared modality affords direct comparison between monkey vocalizations and human speech. For example, great emphasis has been placed on the finding that vervet monkeys (*Chlorocebus aethiops*) possess different alarm calls for aerial and terrestrial predators and are, therefore, claimed to be capable of *semantic* communication (Cheney & Seyfarth, 1990; Gouzoules, Gouzoules, & Ashley, 1995; Struhsaker, 1967; Zuberbühler, 2000a; 2000b; 2003, chapter 17 of this volume). It is now recognized, however, that this ability is shared by a number of birds and other mammals (Evans & Evans, 2007; Hauser, 1996; Macedonia & Evans, 1993). Food calls have also been given as examples of referential signals because, according to some researchers, they convey information about the type, quantity, and location of food to other conspecifics (e.g., Dittus, 1984). It is unlikely, however, that primate vocalizations about predators or food require a higher degree of cognitive complexity than similar vocalizations used by other mammals or birds. This is because the problems faced by most primates during foraging or escaping predators are simply no different in complexity from those faced by most other animal species. Therefore, it is difficult to argue that these activities posed a special pressure to evolve higher cognitive or communicative abilities in primates.

Vocalizations related to intragroup social interactions are more likely to demonstrate increased cognitive complexity in primates because of the complexity of their social systems and their demonstrated abilities in the realm of social cognition. Rather than being broadcast indiscriminately, social calls may be sensitive to the identity and social rank of listeners. For example, the agonistic screams of macaques appear to elicit different responses from other group members in relation to characteristics of opponents, such as their dominance rank (Gouzoules, Gouzoules, & Marler, 1984), and representational signaling in the context of recruitment of agonistic support is an ability that might have been strongly selected for in the social environment of group-living primates. Social calls may be directed at a specific individual, but they are likely broadcast to at least several individuals, and they can be used to initiate or maintain group behavior. Vocalizations that are emitted in order to coordinate the behavior of group members during travel or to facilitate affiliative and bonding interactions are a particularly interesting area of investigation because, unlike antipredator calls and recruitment screams, these signals are not obviously associated with states of high arousal (e.g., Rendall, Cheney, & Seyfarth, 2000). Contact vocalizations that facilitate coordination of group movements and close-range interactions are particularly well developed in arboreal species such as New World monkeys (Boinski, 1993; Snowdon, 1989). The complexity of vocal structure and vocal sequences in New World monkeys, however, is likely to be the result of the pressures of arboreal life rather than those of social variables (Snowdon, 1993). Moreover, the referential nature of agonistic screams, grunts, or other short-range contact calls has been questioned even for the Old World monkeys and apes (e.g., Rendall, Owren & Ryan, 2009). Controversy over the interpretation of the cognitive underpinnings of primate vocalizations can be reduced to the contrast between two fundamentally different views of primate vocal communication: the “information” view and the “influence” view.

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The “Information” View and The “Influence” View of Primate Vocal Communication

The “information” view of primate vocalizations is grounded in a traditional view of animal communication as a process of cooperation, which involves the exchange of information through signals in a way that benefits both the sender and the recipient of the signal (but see Lachmann, Szamado, & Bergstrom, 2001; Scott-Phillips, 2008 for mechanisms to keep signals honest even when interests do not coincide). The information view assumes that primate vocalizations have meaning and that the speaker and the listener have similar representational processes that ensure corresponding coding and decoding of signal meaning. In this view, primates use vocal signals in a representational fashion, similar to the way humans use words. Implicit in this view is the assumption that speaker and listener make attributions about each other's mental states, such as their thoughts, beliefs or knowledge, because these attributions are what motivate and sustain reciprocal semantic exchange. Given that primates, however, seem to be unaware of the consequences their own vocal signals have on the behavior of the recipients, and do not appear to *intentionally* transfer information to them, the information view assumes that vocalizations are functionally, but not intentionally, referential (Seyfarth & Cheney, 2003). In other words, recipients respond to vocalizations ‘as if’ they contained semantic information.

In reality, proponents of the information view of primate vocalizations have often oscillated between two highly cognitive interpretations. On the one hand, are interpretations of vocalizations that emphasize their

language-like properties such as semanticity, syntax, and grammar and imply mental representations of call referents (e.g., Hauser, 1996; Seyfarth & Cheney, 2003; Zuberbühler, 2002, 2003). On the other hand, recent interpretations of the information view have taken a more behavioristic approach, in which the only cognitive process involved in vocal communication (and in information acquisition through listening to calls) is thought to be the associative learning process by which a listener acquires the contingent relation between two paired stimuli (a call and an object or an event) (e.g., Seyfarth et al., 2010).

Both interpretations place the bulk of learning in communication on the recipient, who must quickly acquire associations between calls and external events (for a discussion of the different pressures facing signalers and receivers see Seyfarth & Cheney, 2003). Primates are adept at learning contingencies between auditory stimuli and external events and some species have even learned to respond to the alarm calls of other species (e.g., Zuberbühler, 2000b). Though both versions of the information view require the receivers to learn the relationships between calls and the external world, the behaviorist approach does not require that the pairing between a call and stimulus be stored as a mental representation of the external referent. This view has more in common with the interpretation of vocalizations as tools to directly influence others' behavior rather than to inform others' minds.

In contrast to the “information” view's focus on shared representations, the “influence” view of primate vocal communication maintains that the function of calls is to influence the *behavior* of listeners rather than to transmit meaningful information through mental representations (Owren & Rendall, 2001; Rendall, Owren & Ryan, 2009). This view emphasizes that sender and recipient often have different interests (hence communication involves manipulation) and play more distinct roles in the communication process (Dawkins & Krebs, 1978; Owings & Morton, 1998). In this view vocalizations have acoustic features well suited to access and exploit listeners' basic perceptual sensitivities and central nervous system reflexes (Owren & Rendall, 2001). They elicit predictable responses in listeners through *direct* effects on the listener's affective and motivational states and through learning processes by which the listener learns associations between vocalizations and contexts.

The influence view explicitly excludes the notion that mental representations or any type of theory of mind cognitive processes are involved in the exchange of primate vocalizations. Therefore, in this view, primate vocal communication is fundamentally different and evolutionarily discontinuous from human language.

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For example, although communication through language entails similar and ↴ symmetrical cognitive processes in the speaker and the listener, communication through primate calls may involve asymmetries in the mechanisms that support signal production in senders versus reception in perceivers. Moreover, although the acoustic structure of vocalizations is often arbitrary in human language, the influence view maintains that the design of signals is central to the process of nonhuman primate vocal communication.

Evolutionary Trends in Primate Communication

Primate vocal communication can be both referential and complex. However, call production does not display much flexibility and agency on the part of the signaler and may therefore indicate a greater reliance on behavioral rather than cognitive adaptations. In addition, regardless of whether primate calls are interpreted according to an information or influence view, there is little evidence that primates show more complex cognitive specializations in their vocal communication abilities when compared to other animals. Moreover, there is no trend toward increasing complexity in the structure, function, and use of vocal signals from the prosimians to the New World monkeys, the Old World monkeys, and the great apes, suggesting that the evolutionary increase in brain size that occurred in the Cercopithecoids and the ape lineage was not associated with increasing complexity in vocal exchanges or their cognitive substrates. Such an evolutionary trend, however, is observable in the use of *nonvocal* signals (Parr & Maestripereri, 2003).

In the *Cercopithecidae* and in the great apes, there is a clear increase in the role played by facial expressions (associated with the development of complex facial musculature) relative to vocalizations (e.g., Maestripereri & Call, 1996; Parr & Maestripereri, 2003). Moreover, in the great apes, there is an involvement of the arms and hands in making social gestures to a degree that is not observed in other nonhuman primates or other animals (Bard, 1992; Berdecio & Nash, 1981; de Waal, 1988; Goodall, 1968; 1986; Hewes 1973; Kortlandt, 1962; Maestripereri & Call, 1996; McGrew & Tutin, 1978; Plooi, 1978; 1979; Nishida, 1980; Tomasello, George, Kruger, Farrar, & Evans, 1985; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994; Tomasello, Gust, & Frost, 1989). Thus, if any evolutionary trends are apparent in primate communication, these are (1) the preponderance of vocal signals in arboreal species versus the preponderance of gestural (visual and tactile)

signals in terrestrial species, and (2) the increasing complexity of gestural signals from the prosimians to the great apes (Maestripieri, 1999; Parr & Maestripieri, 2003).

It might be speculated that life in the open savannas after departure from the forests selected for the physical characteristics, especially bipedalism, found in Australopithecines and later species, as well as for a further enhancement of the use of gestural communication. Furthermore, bipedalism probably had a more profound influence in freeing the hands for communication than in altering the vocal repertoire (Corballis, 1992; Hewes, 1973). The patterns of gestural communication observed in extant species of primates suggest that gestures could have been used initially in primarily dyadic contexts to communicate information moderating social interactions. Gestures could first have functioned to anticipate the signaler's social actions and to request and command specific actions from others (see; Cartmill & Byrne, 2010; Genty, Breuer, Hobaiter, & Byrne, 2009; King, 2004). Subsequently, gestural communication could have expanded to reference aspects of the external environment such as food, predators, or tools.

In the rest of this chapter, we examine the cognitive underpinnings of social communication, particularly with regard to nonvocal signals, because we believe that the study of gestural communication can elucidate many aspects of primate cognitive adaptations to social life. We begin, in the next section, by reviewing and discussing how nonvocal signals are used in Old World monkeys (especially macaques and baboons) and apes, and what social and communicative functions are accomplished through them in the contexts of competition, mating, affiliation, and parental care.

Natural Gestural Communication of Monkeys and Apes: Description of Patterns

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Primates frequently use nonvocal signals in communication. Many are involuntary responses to external stimuli or internal states of arousal (e.g., piloerection or expanding the chest to seem larger). Though they can be effective signals, these involuntary signals are not *cognitive* adaptations. Rather they are behavioral adaptations selected for communication in reoccurring contexts (e.g., aggression or mating). Some signals, however, demonstrate both flexibility and representation and thus represent cognitive adaptations. Primate gestural communication contains both involuntary responses and voluntary, flexible signals. The first challenge for researchers is to distinguish one from the other; the second is to question whether communication drove or benefited from the evolution of its underlying cognitive abilities.

We review studies of nonvocal communication in both monkeys and apes with an eye toward identifying behaviors that might indicate complex cognitive abilities. We present findings from both wild and captive groups, all involving conspecific communication using the species' own communicative systems. In this section, we contextualize the studies and present results, but we wait until the following section to discuss the potential implications of the findings to the study of primate cognitive adaptations.

Facial Expressions and Body Postures in Old World Monkeys and Apes

Most species of Old World (OW) monkeys and apes live in either one-male groups, or in multimale-multifemale groups. Group-living primates interact with one another on a daily basis and communicate in the context of both competitive and cooperative interactions. Communication in the context of competition allows individuals to negotiate access to resources and reduces the probability of costly fights. Facial expressions of threats typically involve staring at the opponent with eyes wide open, mouth open without showing the teeth, eyebrows raised, and ears flattened (Altmann, 1962; Hinde & Rowell, 1962; Kaufman & Rosenblum, 1966; van Hooff, 1967). Competition over feeding and mating, or simple proximity to another individual can elicit a threat. The threat signals the individual's potential, or motivation to engage in a conflict. The relationship between threat and aggression, however, is not ubiquitous. Aggression may not be preceded by threats and, in most cases, threats are not followed by aggression. Threats, instead, elicit the expression of submissive signals in the individual being threatened.

Submissive signals can include facial expressions or postures that expose vulnerable regions of the body. The most common submissive signal in OW monkeys and chimpanzees is the silent bared-teeth display, also referred to as “fear grin” or grimace. The bared-teeth display occurs primarily in response to threats or aggression, or the approach of a dominant individual (Maestripereri, 1997). The function appears to be to reduce the likelihood of future aggression. The signal, however, may or may not be effective in preventing aggression, depending on the circumstances. In some primates, the bared-teeth display may occur without any prior interaction between two individuals and may be followed by affiliation or mating (Petit & Thierry, 1992; Thierry, Demaria, Preuschoft, & Desportes, 1989). Therefore, the way in which the bared-teeth display is used seems to vary across species. Another common submissive signal is the hindquarter presentation. Similar to the bared-teeth display, subordinates present to dominants upon receiving aggression or in situations with high risk of aggression (Chadwick-Jones, 1989; Maestripereri, 1996a; Maestripereri & Wallen, 1997). The presentation can also be displayed to initiate affiliative interactions. Bared-teeth and hindquarter presentation can occur in conjunction with other submissive signals such as lip-smacking and teeth-chattering (Altmann, 1962; Dixson, 1977; Hadidian, 1979; Hinde & Rowell, 1962).

Mating and Affiliation

Facial expressions and body postures play an important role also in mating interactions. Females in estrus signal their readiness to mate by approaching males and presenting their hindquarters to them. Macaque males use facial expressions such as the pucker, bared-teeth, lip-smack, or teeth-chatter while approaching an estrous female (Christopher & Gelini, 1977; Goosen & Kortmulder, 1979; Maestripereri, 1996a). Once the distance between males and females is reduced, males use tactile signals such as hip-touches to induce the female to present her hindquarters. During copulation, the female often reaches back grasping the male's flank or leg with her hand and lip-smacks while the male displays bared-teeth, squeaks, or teeth-chatters (Maestripereri, 1996a). In this context, facial expressions could simply reflect an underlying orgasm-related emotion (Goldfoot, Westerborg-Van Loon, Groeneveld, & Slob, 1980).

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Mating interactions are often preceded or followed by affiliative behavior such as grooming and a range of signals are used to entice another individual to approach or to indicate affiliative intent during approach. An individual may use the pucker, lip-smack, teeth-chatter, the bared-teeth, or the hindquarter presentation while approaching, or to induce another individual to come closer. Once distance is reduced, grooming is usually requested by lying on the ground and exposing the part of the body to be groomed. Postural changes are also used to signal the intention to terminate the interaction (Boccia, 1986). The facial expressions and body postures used to reduce distance between adults are also used between adults and infants. Macaque mothers retrieve their infants from a distance by using the pucker, the bared-teeth, the lip-smack, or the presentation, depending on the species or the circumstance (Ferrari, Paukner, Ionica, & Suomi, 2009; Jensen & Gordon 1970; Maestripereri, 1996b; Maestripereri & Wallen, 1997). Some of these signals are used interchangeably and often occur in rapid succession, that is, a mother will first lip-smack or bare-teeth to her infant and then turn around and raise her tail (Maestripereri, 1995). These interactions are particularly frequent in the first weeks of an infant's life when mothers display these expressions to their infants while walking backward as a way to encourage their infants' independent locomotion (Ferrari et al., 2009; Maestripereri, 1995; 1996b).

Affiliative communication between males often involves hip-clasping, mounting, and genital manipulation (i.e., one individual reaches out and fondles the other's genitalia). In contrast, females often embrace each other (Dixson, 1977; Maestripereri, 1996a). Mounting, clasping, and embracing may be accompanied by lip-smacking or teeth-chattering by one or both partners (Chevalier-Skolnikoff, 1974; Maestripereri, 1996a). These signals are most likely expressions of excitement and might function to minimize risk of aggression and promote bonding. Particular affiliative interactions between adult males known as “greetings” probably serve to negotiate dominance relationships, alliance formation, and decision-making processes relative to the direction of travel (in baboons, see Colmenares, 1991; Smuts & Watanabe, 1990; Whitham & Maestripereri, 2003).

Play

Play is characterized by the occurrence of a distinctive facial expression known as the “play face” (van Hooff, 1962; 1967). This expression consists of a wide opening of the mouth, as if attempting to bite, but without clenching the teeth. The top teeth are typically covered but the bottom teeth may be visible. Play faces are usually displayed simultaneously by two play partners and may be associated with soft vocalizations (Symons, 1978). Typically, the play face does not occur in contexts other than play. It is not used to initiate play from a distance, and it most often occurs during contact play involving struggle (Preuschoft, 1992). Traditional explanations of play signals in monkeys and other animals maintain that they are a form of “metacommunication,” that is, they communicate to the partner “I want you to know that this is only play” (Altmann, 1962). This explanation, however, implies quite sophisticated cognitive processes, notably the ability to attribute knowledge to others. It is also possible that the play face is produced spontaneously in situations of ambiguous threat (when it is unclear whether a conspecific is being aggressive or playing). In this scenario, the signaler does not produce the play face purposefully as a signal, but play partners learn to use the spontaneous expression as an indication that the interaction will be affiliative and not aggressive (e.g., Pellis & Pellis, 1996). Some authors have hypothesized that the play face may simply be a form of play rather than a signal with a complex meaning (Maestripieri, 1997; Pellis & Pellis, 1996; Tanner & Byrne, 1999). In addition to the typical play face, chimpanzees, bonobos and orangutans also exhibit “smile” and “laughter” (Chevalier-Skolnikoff, 1982; van Hooff, 1967). These expressions are believed to be homologous in macaques, chimpanzees, and humans (Preuschoft & van Hooff, 1995). Unlike monkeys, all great apes are reported to frequently exhibit novel facial expressions, particularly in the context of play, in which the facial muscles are contorted in highly variable shapes and combinations (Chevalier-Skolnikoff, 1982; de Waal, 1988).

Development and Use

Although little research has been done on the mechanisms underlying communication through nonvocal signals in primates, it is very likely that many facial expressions and whole body postures in Old World monkeys and apes reflect underlying emotional states or induce emotional changes in the recipient (Parr & Maestripieri, 2003). Many of these signals appear to be graded rather than discrete. The flexibility in the combination of elements in each signal (e.g., exposure of the teeth along with raising the shoulders) would be an adaptation to reflect the intensity of the emotion or motivation underlying the signal. Similarly, the structural similarities among signals may allow the expression of rapid transitions in emotional or motivational states (Shirek-Ellefson, 1972). Functionally, facial expressions and body postures may communicate information about the signaler's impending behavior, requests to approach and engage in affiliation, mating, or play, or requests to inhibit behaviors such as aggression or fleeing. Unlike vocalizations, they are not used to communicate about aspects of the external environment, such as the presence of food or predators; rather, they may convey information about a range of social activities occurring in the group, and postures often also contain an indication of the location where the activity will take place (e.g., grooming or direction of travel).

Facial expressions and body postures rarely show any context-specificity linking them to the external environment. The same signal is used in different contexts and the same communicative function can often be served by different signals. This contextual flexibility is considered an important feature of manual gesture in great apes, but unlike gestures, facial expressions and body postures show little evidence that they are used in an intentionally communicative way with the expectation of eliciting a particular response. The relation between the structure of signals and their function seems to be probabilistic rather than fixed, with much information being provided by the social context. Though facial expressions and body postures are likely spontaneous expressions of internal emotional states, appropriate use and interpretation of signals in relation to social context probably requires some social learning during development.

Manual Gestures in Great Apes

Although facial expressions and their contexts of occurrence are rather similar in Old World monkeys and the great apes (see Berdecio & Nash, 1981; de Waal 1988; Goodall, 1968; 1986; van Hooff, 1973, for great apes), apes differentiate themselves when it comes to the use of manual gestures. Apes use gestures in a wide range of social contexts and they appear to have a level of volitional control over when and how to use them that sets both apes and gesture apart from other primates and other types of communication. Apes produce a range of gestural forms that are not typically observed in monkeys and use many of them in ways that indicate a deeper sensitivity to the minds of other individuals and, in many cases, an *intention* to communicate.

Hand begging gestures, for instance, are rare or nonexistent among Old World monkeys but have been reported in all four species of great apes. De Waal (1988) believes that bonobos use this gesture as an overture for reconciliation after a fight more than chimpanzees do, whereas chimpanzees use this gesture to request food or agonistic support more than bonobos do. Other gestures and postures observed among chimpanzees and bonobos include wrist shaking, arm waving, arm up, stretch over, hunch over, hand and foot clapping, chest beating, and various types of rhythmic movements involving the hands and feet, and embraces (see Goodall, 1968). Some of these signals are presumably used as attention-getters (e.g., arm waving) whereas others are more explicit requests for sex or grooming. McGrew and Tutin (1978) reported a cultural tradition involving a “hand-clasp” posture that occurs between wild chimpanzees engaged in allogrooming, and this was later observed in a captive group as well (de Waal & Seres, 1997). It is unclear, however, if the posture has any communicative significance to the individuals engaged in this behavior, or to other group members. A form of attention-getting behavior (“leaf clipping”), in which leaves are held and torn apart with the teeth producing an audible sound, has been reported among chimpanzees in the Mahale mountains, mostly in the context of requesting sex or food (Nishida, 1980).

Intentional Gestures

The distinction between intentional and nonintentional gestures in chimpanzees was first explicitly made by Plooij (1978, 1984). Plooij described several gestures used by infants during interactions with their mothers or with their peers: a “hands around the head” gesture to request tickling, an “arm-high” gesture to initiate grooming; a “food-beg” gesture to request food; “leaf-grooming” and “running away with an object” gestures to encourage social play. Plooij identified gestures as being intentional when they were used “flexibly” and/or were accompanied by gaze alternation. By *flexibly*, he meant that the same signal could be used to achieve different goals, and different signals could be used for the same goal. For example, Plooij observed a juvenile who, in some cases, used an “arm-high” gesture to invite grooming under its arm, and in other cases used the same gesture in an appeasement context. This flexibility in relation to goal indicates that the gesture is not produced as an automatic response to an external stimulus. Gaze alternation involved monitoring the response of another individual to the signal and suggested that the sender had some understanding of the effect of the signal on the recipient. For example, Plooij observed that when begging for food, infants alternated their gaze between their mother's face and their hand (see also p. 176 Bard, 1992, for similar interactions in orangutans). Plooij (1984) argued that some gestures develop ontogenetically from goal-directed actions, but then become signals in part due to the influence of social learning and shaping. He suggested that, at some point during development, the infant understands that the mother is an independent agent with her own communicative ability and, at this point, most gestures begin to be used intentionally.

Building upon Plooij's work, Tomasello and colleagues (Tomasello et al., 1985, 1989) focused on intentional gestures used by juvenile chimpanzees during interactions with their mother or other group members. In addition to flexibility in the use of signals and gaze alternation, response waiting and audience effects were also included as evidence of intentional gesture use. Response waiting meant that the individual waited for a response from another individual after sending the signal, thus suggesting that the goal of the gesture was to communicate. Finally, audience effects occurred when an individual used a signal differently depending on the identity or attentional state of the recipient. Some of the intentional gestures studied by Tomasello and collaborators were used to get the mother's attention and initiate nursing (e.g., touching her body), solicit carrying (placing one arm on the back of another individual or pulling another individual along), request grooming (exposing the body part to be groomed or placing the other individual's hand on this part), request food sharing (placing the hand under the adult's mouth in a begging gesture), or invite play

(arm raising, ground slapping, head bobbing, hand clapping, foot stomping, running away and looking back). Tomasello et al. (1985) reported that some gestures were used quite flexibly in different contexts and that the older juveniles used some novel behaviors not observed among other individuals. Tomasello et al. (1989) also reported the creation of new gestures when new materials were introduced to the group (e.g., newly introduced wood chips were used to initiate play by throwing them at others).

Longitudinal Study

In a follow-up to their original study of chimpanzee gestures, Tomasello and colleagues (Tomasello, Call, Nagell, Olguin, & Carpenter, 1994) returned to the same group to see whether gesture repertoires or use had changed over time. They reported that juvenile chimpanzees used eight different gestures to initiate play, three different gestures to solicit nursing, three to request carrying, and two to beg for food. Visual signals were used only if the recipient was looking and tactile signals only if the recipient was attending to the behavior of the signaler. Many social interactions (e.g., play) were initiated with an “attention-getter” gesture such as “throwing chips,” “poking at,” or “ground slapping.”

The comparison of gestures across time periods and generations showed that there was little overlap among gestures either within or between groups, indicating that the gestures were not acquired via social learning. Specifically, (1) some juveniles used gestures that no other group member used; (2) some juveniles used gestures that had not been directed to them and that they had little opportunity to observe; (3) juveniles raised only with peers ended up developing some of the same gestures as those raised with adults; (4) within-group variability in the use of gestures was very high. These findings suggested that younger individuals were not acquiring their gestures by watching older, more experienced ones. To determine whether these findings were typical of the species, Tomasello and Camaioni (1997) extended the longitudinal study of chimpanzee gestures to include additional groups. This study replicated some of the earlier findings, including low concordance rates in gestures within groups and generations. Two individuals in this study were taught new food begging gestures by human experimenters and then reintroduced into the group, but the novel gestures did not spread within the group: other individuals kept using their own gestures and did not adopt the new ones during the course of the study.

p. 177 Tomasello and Camaioni (1997) argued that chimpanzees use two basic types of intentional gestures with their conspecifics: “attractors” and “incipient actions.” Attractors are imperative gestures aimed at getting other individuals' attention, whereas incipient actions are also imperative gestures, but they are used to communicate information about impending behavior or to request specific activities. According to Tomasello and Camaioni (1997), both attractors and incipient actions are mostly used in dyadic contexts and are never used for declarative purposes, that is, to share interest in, or comment on, something or someone. Furthermore, many gestures rely on physical contact between signaler and recipient or are incipient movements that anticipate contact. Thus, in Tomasello and Camaioni's (1997) view, gestures are more closely related to the mechanical manipulation of another's body than to the psychological manipulation of another's mind. Tomasello and Camaioni (1997) emphasized the differences between the intentional gestures of chimpanzees and those of human children and adults. In their view, the latter are often used triadically and for declarative purposes, are often indexical or symbolic, are meant to influence others psychologically, not mechanically, and are learned through social observation rather than individual learning (we discuss this distinction further in a later section). Tomasello and Camaioni conclude that intentional gestures in chimpanzees are probably learned by a process of ontogenetic ritualization and not by observational learning. Ontogenetic ritualization is a form of individual learning in which each individual learns the effects of its behavior on the other's behavior. Gestures described as incipient actions support this proposed learning mechanism since the process of ritualization would naturally yield gestures that were comprised of the initial movements or other parts of actions.

To determine whether the features of chimpanzee gesture were typical of all apes, Tomasello and his colleagues expanded their study to include gorillas, bonobos, orangutans, and siamangs (Call & Tomasello, 2007; Liebal, Call, & Tomasello, 2004; Liebal, Pika, Call, & Tomasello, 2004; Liebal, Pika, & Tomasello, 2004, 2006; Pika, Liebal, & Tomasello, 2003; Pika, Liebal, & Tomasello 2005). The researchers gathered focal video data from two groups of each species and identified intentional gestures according to the same criteria. In this way, the repertoires and gesture use of each species could be directly compared. Somewhat surprisingly, the authors found far more similarities than differences between species in both the number and use of gestures. The authors identified repertoires of between 20 and 30 gestures for each species, and all of them involved a combination of visual and tactile elements. Notably, only the African apes (*Pan* and *Gorilla*) used auditory gestures such as clapping or banging objects. This inclusion of auditory elements may be related to the propensity for bimanual drumming, an ability found in only the African apes that some have claimed is linked to the origins of music and language (Fitch, 2006). Aside from the differences in auditory gesture, all species included in the large comparative study appeared to use gestures in very similar ways. For example, all species were sensitive to the gaze of others when choosing between tactile and visual gestural modalities: visual gestures were used more frequently when the gesturer could be seen, whereas tactile gestures were used similarly regardless of gaze. The authors looked for group differences as well as species differences comparing gestural repertoires between conspecific individuals within and between different groups. They found that individual repertoires varied as much within as between groups. This was used as evidence against the possibility that gestures are acquired through social learning and as support for the theory of ontogenetic ritualization posited by Tomasello and Camaioni (1997).

One may argue that the characterization of chimpanzee gestures as imperative signals acquired through individual learning that manipulate behavior rather than transmit information used by Tomasello and Camaioni (1997) is overly strict, and that the differences that Tomasello and colleagues draw between ape and human gestures are overstated. For example, chimpanzees and other primates can use both attention getters and requests for action in triadic ways (e.g., alarm calls, food begs, or recruitment solicitations). Furthermore, among both human and nonhuman primates, many gestures are used to manipulate behavior rather than either the body or the mind. It is also likely that the gestural repertoires of both primates and humans are the result of a combination of genetic expression and individual and social learning processes. Finally, some of the distal and declarative (i.e., commenting rather than requesting) uses of human gestures are strictly related to language, and there is evidence that when great apes learn rudiments of human language, the use of indexical and symbolic gestures follows closely (see section on ape-human communication).

Iconic Gestures

One way in which ape and human gestures appear to differ sharply from one another is their use of representational elements. Humans use iconic gestures to represent objects or events by recreating an aspect of their referent's shape, size, or movement. Producing and interpreting this type of gesture requires the ability to represent real-world referents by their salient aspects (e.g., using a round gesture to refer to a ball). Iconic gestures are importantly different from incipient actions because they represent actions through recreating a particular physical feature rather than indicate desired actions by performing the initial movement of an uncompleted action. There is scant evidence that nonhuman primates are capable of spontaneously producing signals with this type of representational relationship to objects or events in the world. Apes can be specifically trained to make iconic gestures; however, a handful of studies have also reported use of spontaneous iconic gestures with conspecifics in bonobos and gorillas. Savage-Rumbaugh, Wilkerson, and Bakeman (1977), and Savage-Rumbaugh and Wilkerson (1978) reported high variability in both bonobo copulation positions and the facial expressions and gestures that accompanied them, including prolonged mutual gaze, and a number of different gestural and postural signals. Savage-Rumbaugh et al. (1977) argued that some gestures were iconically related to the desired change in the partner's behavior. For example, they observed that a male would often physically push the female's body into a desired copulatory position, but sometimes he would move his hand across the female's body rather than pushing her. This latter movement was interpreted as an iconic indication of what he wanted the female to do (but see Tomasello & Call, 1997 for a different interpretation).

Tanner and Byrne (1993; 1996; 1999) argued that some captive lowland gorillas use iconic gestures similar to those observed by Savage-Rumbaugh et al. (1977) among bonobos. Most of the observed gestures

occurred during play, a few in agonistic contexts, and none in feeding situations. In the context of play, an adult male appeared to use his arms iconically to indicate to another individual the direction in which he wanted her to move or the action he wanted her to perform. Many of these gestures appeared interchangeable in function. The authors observed individual differences in the use of gestures, including an increase in their expression during development, as well as changes in the preferred types of gestures as individuals matured (Tanner & Byrne, 1999). Although some of their developmental data were consistent with the ontogenetic ritualization hypothesis, Tanner and Byrne (1999) also argued that *some* aspects of gestural communication, notably the comprehension of gestures, are not learned but somehow “biologically encoded” (e.g., innate; Byrne and colleagues have developed this hypothesis in subsequent work, which we discuss in the section on acquisition mechanisms). Furthermore, they argued that gorillas have the potential for symbolic communication and are anatomically and cognitively preadapted to use iconic gestures. For example, they noted some similarities between the iconic gestures used by zoo gorillas and the signs used by language-trained gorillas, which often elaborated upon species-typical gestures in their symbolic communication. In their view, although certain aspects of gesture are heritable (e.g., the predisposition to produce and recognize certain movements as gestures), the cognitive abilities great apes use during gestural communication (e.g., selection of appropriate gestures, awareness of gaze, flexible use of different gestures) are not so different from human communication. They argue that the sharp distinction made by some authors between the symbolic use of gestures in humans and the nonsymbolic nature of primate gestures is not as dramatic as it could be (though Byrne's later findings support sharp contrasts in acquisition and symbolic use of gesture; see Genty et al., 2009; Hobaiter & Byrne, 2011). This issue is further explored in the next section.

Natural Gestural Communication of Apes: Implications for Cognition

The increased interest in primate gesture in the last 30 years has been largely motivated by a desire to identify *complex*, *flexible*, and *intentional* communication in great apes. Reacting to findings that apes are poor vocal learners and their vocal repertoire appears largely fixed, researchers turned to gestural communication for clues to cognitive adaptations underlying ape communication and possible antecedents to human language. Here we review what great apes' gestures reveal about their potential for complex, flexible, intentional communication, and we discuss what cognitive mechanisms are involved in gesture.

The fact that apes can acquire novel manual skills and movements through observation of others makes great ape gesture a likely candidate in the search for social-cognitive adaptations and prelinguistic cognitive foundations of language. Because the focus on the gestural modality was, in large part, a reaction to the growing understanding of the vocal modality as inflexible and unlearned, it is unsurprising that most of the research on and discussion of ape gestures has focused on either the flexibility of gesture use or potential mechanisms of gesture acquisition.

Flexibility

p. 179 The flexibility with which apes use gestures is mentioned in nearly every recent study (Arbib, Liebal, & Pika, 2008; Call & Tomasello, 2007; Genty, Breuer, ↵ Hobaiter, & Byrne, 2009; Liebal et al., 2006; Pika et al., 2003; Pika, Liebal, & Tomasello, 2005; Pollick & de Waal, 2007). Flexibility is usually defined as the number of different contexts in which a gesture is used, but it may also refer to the number of “functional contexts” (i.e., social goal resulting from the gesture rather than type of social interaction in which the gesture occurs). Pollick and de Waal (2007) measured the relative flexibility of gestures and vocalizations in captive groups of chimpanzees and bonobos and compared them within and among groups and species. They observed that manual gestures were used in a wide range of contexts both within and between groups, but that the use of vocalizations and facial expressions was limited to specific contexts and did not vary between groups.

Pollick and de Waal (2007) also found that multimodal signals (gestures accompanied by vocalizations) were more likely to elicit responses in bonobos than in chimpanzees. This combination of gesture with vocalization (which occurs rarely in gorillas and orangutans) may have particular importance in the origins of language. In adult humans who are fluent speakers of a language, gesture and speech are tightly linked in time (McNeill, 1992), and synchronization of gesture and vocalization occurs as early as 9–15 weeks of age (Fogel & Hannan, 1985). The extent to which apes are able to synchronize vocalizations with gestures when

communicating with conspecifics has not received much attention, though it appears to occur only rarely (if at all in some species). Chimpanzees' ability to produce synchronous vocal and gestural signals to communicate with humans is currently being studied (see later).

Meaning

The fact that apes use gestures in more than one context and use more than one gesture in each context is often used as evidence that gestures are used intentionally. This lack of one-to-one correspondence between stimulus and signal is often referred to as “means-ends disassociation” (Bruner, 1981) and provides evidence that gestures are not automatic responses to specific external stimuli but are rather employed voluntarily. Establishing that ape gestures are not mechanical responses is important when comparing them to language or attributing cognitive processes to signalers, but the focus on establishing flexibility has, in some cases, led to a view in which all gestures are multifunctional. If all gestures are truly multifunctional, then it is unlikely that they carry any meaning outside the context in which they are produced, and recipients must, therefore, rely on the surrounding social context to respond appropriately. If gestures cannot be interpreted outside their social contexts, then they are weak signals, and their relevance to human language origins is more questionable. Recently, Cartmill and Byrne (2010) proposed analyzing ape gestures for “intentional meaning,” categorizing them by how probabilistically they are associated with achieving specific social goals. By identifying examples of gestures that have “goal-outcome matches” (where the outcome of the interaction matches the goal attributed to the signaler), one can determine how often a particular gesture is associated with a particular goal. Cartmill and Byrne argue that gestures used frequently with a single goal-outcome match have specific meanings. The authors applied this analysis to gestures made by three captive groups of orangutans and found that more than half of the gestures had predictable meanings. Importantly, the authors attempted to validate their attributions of meaning by observing whether gesturers persisted in their communicative attempts following different types of recipient reactions, and found that orangutans were more likely to persist when the reaction did not match the gesture's presumed meaning. Their persistence demonstrated that the gesturers' goals had not been fulfilled by the responses to the initial gestures and, thus, supported the experimenters' attributions of meaning to those gestures.

The balance between flexibility and meaning poses a problem for the discussion of gesture and its usefulness as a tool to understand the cognition underlying ape communication. On the one hand, if gestures have very specific meanings, then they should demonstrate a very tight correspondence with specific contexts, and it might be difficult to determine whether they are used intentionally or reflexively in response to environmental stimuli. On the other hand, if gestures are too flexible, they cannot be useful as communicative signals and their function is unclear. One way in which gestures could demonstrate flexibility without sacrificing meaning is in apes' ability to use them strategically in response to various properties of the intended recipients (e.g., attention, knowledge, social status). By investigating the behavior of the recipient prior to the gesture, it is possible to study what social factors are important in predicting the choice and use of a gesture.

Because gestures are not broadcast openly like vocalizations, it is often trivial to identify the gesturer's intended recipient (and indeed many studies use directedness as a criterion of intentional use). Because the recipient is usually apparent, researchers can ask more detailed questions about what aspects of the recipient the signaler takes into account when gesturing. Several studies have indicated, for example, that apes are able to take the recipient's visual attention into account, choosing appropriate modalities based on whether they can or cannot be seen (Call & Tomasello, 2007; Tanner & Byrne, 1993). There is also some indication that they may continue to monitor the other's visual attention throughout a communicative exchange (Genty et al., 2009). Apes also combine gesture into sequences or exchanges with others, and the transitions between different gestures may reveal more about communicative strategies than the specific gestures used. For example, apes might quickly escalate to a fully functional shove when trying to displace a subordinate individual, but attempt a wider range of gestures when attempting to coerce a dominant individual to move from a choice spot. Such strategies have the potential to reveal the decision process underlying gesture use. It can be difficult, however, to interpret the cognitive processes underlying communication with conspecifics because of the inability to control environmental and social factors. Because of this, many studies of strategic use of gesture are conducted using ape-to-human communication (see section on human-directed communication).

Acquisition Mechanisms

One of the most important questions raised by studies of ape gesture is the problem of acquisition. In nonhuman primates, gesture is regarded as having greater potential for social learning and cultural transmission than vocalization. Both apes and monkeys are able to learn new manual actions by observing others performing them (see review in Whiten, 2000), and apes can acquire novel communicative signs and gestures from humans (e.g., Gardner & Gardner, 1969; Shapiro & Galdikas, 1999; Tomasello & Camaioni, 1997). Additionally, most of the population-specific behaviors described in reports of culture in wild apes involve manual tasks, such as tool use or grooming techniques, indicating that social learning of manual actions occurs in wild populations (van Schaik et al., 2003; Whiten et al., 1999). It is clear that apes have the potential to learn novel manual actions from others, and they are able to use acquired actions to communicate when encouraged by human experimenters. Given this potential, one might expect that ape communicative gestures would be socially learned and would display cultural variation in their forms or uses between different sites.

Local traditions involving the presence or variation of manual actions, such as tool use, food processing, and grooming, have been reported in wild great apes (e.g., Whiten et al., 2001; van Schaik et al., 2003; Hobaiter & Byrne, 2010; also see Byrne, 2004; Byrne et al. 2004 for review and discussion of studying nonhuman culture.). There is no evidence, however, that manual *gestures* show similar levels of group specificity. Studies consistently report that gestures are either highly idiosyncratic or highly shared by all individuals of a species and that there are few (if any) group-specific gestures or traditions involving gesture. The gestures of a gorilla in a Brazilian zoo are just as likely to resemble those of a gorilla in a Swedish zoo as they are those of a gorilla in the same group. Because no local gestural traditions have developed, there is no evidence that gestures are socially learned. Only two plausible alternatives have been offered: gestures are either ritualized from the first movements of functional actions (ontogenetic ritualization) or they are genetically inherited.

Ontogenetic ritualization of functional movements into communicative signals is exemplified in human infants during the development of some early gestures such as raising the arms to indicate a desire to be carried. In this process, what was once a functional movement (raising both arms to grab onto the mother while she picks up the infant) becomes stereotyped into only the first part of the action (the arm raise) as the recipient learns to respond to the first part of the action. This is an effective mechanism for creating gestures from actions, and it seems a likely candidate for many ape gestures (Tomasello & Camaioni, 1997; Tomasello & Call, 2007), particularly for tactile gestures that resemble functional movements such as brushing, pulling, or pushing. It is more difficult, however, to attribute ontogenetic ritualization to gestures that do not resemble a movement associated with a functional action (as in the case of clapping or performing a headstand). It is also important to note that ritualization is primarily an *individual* learning process. No social learning is implied and thus every individual must undergo the same process of reducing functional actions to ritualized gestures.

The theory of ontogenetic ritualization has been criticized recently by Byrne and his colleagues (Genty et al., 2009; Hobaiter & Byrne, 2011). They argue that, because ontogenetic ritualization must occur *de novo* with every individual and every gesture, the chances of each individual acquiring a similar form for a gesture ritualized from an action are very low. Furthermore, although the conditioning inherent in ritualization might lead an individual to use an incipient movement as a gesture, it does not require that either individual understand the gesture as a means of communicating a particular desire and, thus, would not necessarily lead to the ability for one individual to both produce and comprehend the same gesture. Even assuming that the production or comprehension of a gesture could be generalized from use with a specific individual to the rest of the group, each individual must (at minimum) acquire each gesture from the perspective of both signaler and receiver through ontogenetic ritualization. Byrne and his colleagues stress that ontogenetic ritualization is a likely acquisition mechanism only for those gestures that resemble incipient actions of common species-typical actions, for which every individual has frequently both initiated and been the recipient of the original actions. Furthermore, close analysis of two gorilla actions and gestures that seemed likely candidates for ontogenetic ritualization revealed little similarity between the specific movements of the gestures and those that initiated the actions, weakening the theory that the gestures were ritualized from the actions (Hobaiter & Byrne, 2011). Byrne and colleagues further argue that, for ontogenetic ritualization to result in the same gesture in several individuals, the same ritualization process must have taken place for each individual in exactly the same way; otherwise, we would expect that each might use a different gesture to initiate a particular type of interaction, arising from differences in the actions or responses during ritualization.

Hobaiter and Byrne (2011) report high overlap of gestural repertoires between groups of the same species studied at different sites, and also between species of great apes. The authors report a 60% overlap between chimpanzee and gorilla gestural repertoires and an 80% overlap between chimpanzee and orangutan repertoires. They report 24 gesture types shared between the 3 genera and conclude that many ape gestures are not only species-typical but are, indeed, ifamily-typical. They propose that the natural repertoire of ape gestures are a result of “genetic canalization into physical forms and potential messages that are species-typical” (Hobaiter & Byrne, 2011). This explanation does not imply that there would be no individual differences in gesture form or use, that social interactions would not influence the form and use of gestures, or that gestures would be used in a hardwired reflexive way, but rather that all members of a species are biologically predisposed to use a certain set of gestural forms and meanings given a typical rearing environment.

It may not be reasonable to assume that a single mechanism underlies the development of all ape gestures. It seems most likely that gestures are acquired through a variety of mechanisms. Even the gestures of prelinguistic human infants are probably acquired through a range of mechanisms including ritualization (for incipient actions such as the arm raise) and observation (for conventional gestures, such as nodding to mean yes).

A detailed longitudinal study early in development would be needed to determine whether apes acquire gestures through ontogenetic ritualization. If so, one would expect to see young infants begin with functional actions and slowly reduce down the size and effort of their gestures until they are ineffective and somewhat standardized. Through this type of study, one could also determine whether infants had to receive the same ritualization process to comprehend the same gesture directed toward them. It might also be the case that an ontogenetic ritualization process is combined with something like imitation recognition (e.g., Nielsen, Collier-Baker, Davis, & Suddendorf, 2005) such that once an ape had ritualized an action to a gesture, it could recognize similar movements produced by others and ascribe the same goals to the other ape. This combination of individual learning and generalization is attractive as a potential mechanism for gesture acquisition and use, but it relies heavily on the assumption that apes can attribute goals to one another. Though the patterns of gesture use suggest that apes respond to one another's attention, gestures, and responses in a dynamic way, there is no evidence that they attribute goals to gesturing individuals. Controlled laboratory studies can assess the ability of apes to attribute goals to others, but whether they do so in their natural communication is likely to remain a question for speculation and debate.

It is clear that ape gestures are different from those used by humans. Human gestures are almost always framed within linguistic exchanges and ↪ reference external objects, events, or ideas through symbolic, metaphoric, or iconic means. It is unclear, however, exactly how the gestures of great apes differ. Tomasello and Camaioni (1997) characterized apes' gestures as dyadic, imperative, and ritualized, and children's gestures as triadic, declarative, and learned. This distinction provides an excellent framework for comparison, but may be an oversimplification: the difference might be one of degree rather than kind. There is some indication that apes use gesture triadically; for example, when they offer or request food or objects (e.g., Liebal et al., 2006). These interactions are triadic in that they involve an object external to both animals in the dyad, but in all cases one of the animals is touching the object, so they could also be perceived as part of the dyad. Something similar seems to occur when apes use gesture to indicate places they would like to be groomed (Pika & Mitani, 2006). Chimpanzees use an exaggerated scratch on their own bodies to indicate where they would like another to groom them. This gesture seems to have deictic and triadic properties by drawing attention to a specific area, but it is different from a human mother and infant sharing attention and gesturing toward an external object. Again, the question remains whether it is a difference of kind or degree.

The question of whether apes are capable of iconic gesture has also been the subject of some debate. The cases of iconic gesture in captive gorillas that Tanner and Byrne (1993; 1996; 1999) reported mainly consisted of indications of where one individual wanted another to travel or what position one wanted the other to take. These types of gestures are iconic because of their similarity to the movement the recipient would make when fulfilling the request. However, if these gestures began as direct manipulation of the other's body and were ritualized into gestures that resembled either the start of the manipulative action or an ineffective smaller version of the action, it is possible that they would have much the same form as they would if the gorillas were representing the desired action iconically: moving the arm along the path that it would take if manipulating the other.

In human gesture research, iconic gestures are defined as “representational” gestures because they refer to objects, actions, or relations by recreating an aspect of their referent's shape or movement (McNeill, 1992). Moreover, in an iconic gesture, the hand can represent either a hand grasping an object or performing an action (e.g., throwing a ball), or represent an object or action itself (e.g., indicating the path of a ball after it was thrown). Only the first type would directly resemble the action a person would take when performing an action. Though some ape gestures do bear resemblance to the actions an ape would take when directly manipulating another (e.g., grabbing the air near another individual without coming into contact or shooing another away), it is not apparent whether any of these gestures “represent” objects or events. Without evidence that apes are using these gestures representationally, it is unclear what can be gained by labeling some gestures “iconic.” If iconic gestures do, however, provide some indication that apes can use, elicit, and share mental representations through gesture, then one would expect the strongest indications of intentional use (response waiting, persistence, elaboration, etc.) to accompany these gestures. Unfortunately, because iconic gestures are described only rarely in great apes, it would be difficult to fully answer this question beyond cataloguing and describing anecdotal examples of iconic gesture when they occur (but see Bates and Byrne, 2007 for a discussion of using anecdotes to study complex cognition).

Recently, Russon and Andrews (2010) addressed the issues of very rare events and iconicity by analyzing descriptions of extended iconic gesture sequences used to elaborate a message (described by the authors as “pantomime”). Using observations of forest-living rehabilitant orangutans obtained from 20 years of descriptive data, they identified 18 cases of pantomime (14 of which were addressed to humans). These extremely rare cases of elaborated iconic gesture did display numerous markers of intentionality, and the signalers usually had clear goals. However, most of the events were taken from written descriptions that had been initially recorded for other purposes, so systematic analysis of goals, types of elaboration, and measures of social cognition could not be performed. It is also notable that the vast majority of examples of pantomime described were performed to humans, and all orangutans had prolonged contact with humans during the process of rehabilitation. Given the paucity of observations in this study and the orangutans' extensive exposure to human culture, it remains unclear to what extent apes can use spontaneous gesture representationally with one another, or at all.

So what have studies of gesture revealed about the cognitive specializations of apes? It seems that apes use at least some of their gestures intentionally with the expectation of a specific behavioral response (as indicated by response waiting, persistence, and elaboration). It is unclear whether apes gesture with the intention to *communicate desires* or with the intention of *eliciting particular behaviors* from others. Though the philosophical and cognitive implications of these two possibilities differ, the functional outcome is much the same: gestures are used to fulfill the gesturer's goals by causing specific behaviors in others. The preferential use of visual gestures when the recipient is watching demonstrates that apes take the visual attention of others into account before signaling. All studies indicate that apes are able to use gesture voluntarily (i.e., they do not gesture automatically in response to certain stimuli). Gestures also seem less likely than facial expressions or vocalizations to be designed to elicit emotional reactions in recipients—they can be subtle movements, are directed at specific individuals, and often get no reaction whatsoever. Ape gestures may or may not have meanings that can be interpreted outside of the context in which they are produced. As with most primate signals, it is likely that the recipient learns to extract a gesture's meaning from a combination of signal form and context. Only playback studies or carefully designed experiments will allow us to determine whether gestures themselves are perceived as having meaning without being contextualized in an ongoing interaction.

Future studies should be designed to provide evidence for mechanisms of gesture acquisition and how gestures are perceived. Gesture has thus far proven itself a useful tool for studying the cognition of the signaler prior to and during gesture use, but it has not yet been used to address questions of the recipient's perceptions or understanding. It is our hope that future studies will attempt to determine how much apes understand about gesture events. For example, do recipients attribute goals and/or intentions to the gesturer? Do gesturers have intent to inform or merely to affect behavior? Because gesture often occurs in bouts during which both parties produce signals, there is great potential to investigate the changing dynamics during which a signaler becomes recipient and then signaler again. One might also ask whether gesture is used to “negotiate” or arrive at a compromised outcome in extended interactions in which the goals of two individuals are competing.

Human-Directed Gestural Communication

Observational studies of communication between nonhuman primates are limited in their conclusions by the difficulty of controlling for various social and environmental variables. Attributing particular cognitive processes to either signaler or receiver in a communicative exchange is tricky, and it is difficult to narrow down the range of possible explanations for an animal signaling or responding to a signal in a particular way. Experiments performed on captive populations attempt to introduce environmental controls (e.g., by restricting visibility or introducing specific items as a way to manipulate the probability of observing communication about a specific type of stimulus (e.g., Barros, Boere, Mello, & Tomaz, 2002; Cheney & Seyfarth, 1990). Observers then record subsequent changes in animals' signaling or in how they respond. This can be an effective method for testing changes in animals' actions or reactions to a particular type of environment, but the behavior of other individuals in the group remains an essential but uncontrolled variable. This means that it is difficult to ask questions about how animals react to particular types of behavior. One must either wait until the right animal produces the desired behavior in exactly the right conditions, or forgo the naturalness of the exchange and opt instead to use a human experimenter as a communication partner.

Experiments in which apes communicate with human experimenters fall into two categories: those in which the animals are taught to interact using a human-designed communication system (“artificial” or “taught” language studies), and those that attempt to elicit the animals' natural communicative signals or responses. Each contributes something to our understanding of the abilities and communicative potential of different species and, in turn, each presents challenges and limitations on what can be learned about the scope and use of communicative abilities in apes.

Artificial language studies attempt to teach infant apes to use and respond to symbolic communication with human caretakers. Usually, the apes are reared with human caregivers in enriched, often human-like, environments focusing on fostering communicative play and encouraging the apes to use the taught linguistic medium to request treats and activities. The earliest attempts used spoken English (Hayes & Hayes, 1951), but after discovering that apes lack the ability to mimic vocal sounds, researchers focused their attempts on systems of written or manual signs. Following the success of ↵ Gardner and Gardner (1969) in teaching an infant chimpanzee American Sign Language (ASL), interest in exploring ape communication in the visual modality (using either American Sign Language or visual symbols) took off.

Learning and Use

Artificial language studies have been conducted on gorillas, chimpanzees, bonobos, and orangutans, and all have demonstrated extensive ability in producing and comprehending manual signs or symbols (Gardner & Gardner, 1969; Miles, 1990; Patterson & Linden 1981; Savage-Rumbaugh, Shanker, & Taylor, 1998). These studies with signed or symbolic languages revealed that great apes possess many communicative abilities once attributed only to humans—most importantly, perhaps, the ability to communicate using *arbitrary* symbols that are not linked to internal states.

Though techniques and successes have varied from study to study, all taught-language experiments have demonstrated that apes can learn to map arbitrary symbols onto real world referents and to use these symbols to communicate their desires. Moreover, several have indicated that apes can acquire these symbols from passive observation of others as well as from direct instruction (Fouts, Fouts, & van Canfort, 1989; Gardner & Gardner, 1969; Savage-Rumbaugh et al., 1998). This ability to acquire communicative signs through passive observation is of great interest to those interested in comparisons between primate communication and human language. Apes can be trained to associate symbols with objects through conditioning or shaping (where an experimenter physically manipulates the ape's hands to perform the desired behavior), but the acquisition of such symbols through observation of others is a characteristic most often associated with human language learning. However, it is notable that at least some of the communicative abilities (using arbitrary symbols and learning these symbols from observation of others) have also been shown in free-ranging apes when taught to request specific foods at a feeding station (Shapiro & Galdikas, 1999).

Syntax

It was hoped that, once apes were given the right environment and an arbitrary symbolic system, they would show many elements of human language that were apparently lacking in their own communication systems. Evidence for use of syntax or the creation of new signs, however, has been significantly lacking. There have been a few reports of apes inventing or combining known signs to refer to novel ideas or objects (e.g., Fouts & Mills, 1997; Patterson, 1980; Patterson & Cohn, 1990), but no ape habitually combined or created new signs to dramatically increase its vocabulary. This is an important observation because studies of primate communication have overwhelmingly focused on the search for syntactic rules in primate communication systems as clues to the origins of human language (e.g., Arnold & Zuberbühler, 2006; Genty & Byrne, 2010). It is notable, then, that even when provided with individual units that are analogous to human words (i.e., referential, arbitrary, taught), apes do not display any aptitude in combining the units in a systematic or meaningful way. The only consistent “syntactic” rule observed in taught language studies was a modality ordering preference in which an ape consistently used a keyboard symbol first followed by a gesture (Greenfield & Savage-Rumbaugh, 1990). This ordering rule was likely based on facilitating movement following communication and it lacked the added meaning associated with syntactic structure in human language. Although their abilities to employ syntax during language production appear very limited, apes in these studies have demonstrated great success at perceiving and responding to syntactic changes in human language. The best example is the bonobo, Kanzi, who was able to respond appropriately to a range of commands varying different syntactic properties (e.g., “place the X on the Y” and “place the Y on the X in the Z”). Kanzi even responded more appropriately than a two-year-old child to commands containing recursive changes (Savage-Rumbaugh et al., 1993).

Overall, the ape language studies have left us with more questions than answers (see also chapter 19 of this volume). As we become more aware of the extent of apes' ability to use complex symbolic communication in

experimental settings, the gap between their potential for such communication and the apparent lack of such features in their natural communication systems is widened. Artificial language studies demonstrate what a species is capable of given exactly the right configuration of environmental influences, but they cannot provide much information about how the abilities would have arisen in the first place in a natural environment without devoted teachers and a preexisting linguistic framework.

p. 185 **Spontaneous Human-Directed Communication**

Studies in which apes are encouraged to communicate with a human experimenter through their own spontaneous (i.e., not taught) behavior attempt to remove some of the artificiality from the taught language studies and yet elicit behavior that might be difficult to observe in conspecific interactions. By requiring apes to communicate with a human, researchers can more effectively control for social variables such as the eye gaze, location, and response of the communication partner. In many of these paradigms, apes must communicate with humans in order to obtain a food or another resource that they cannot obtain directly. This design introduces what some have called the “problem space,” an artificially imposed distance between signaler and receiver that elicits different types of behaviors than those one would see if the apes were free to act directly on their environment (e.g., Leavens, Hopkins & Bard, 2005). In these situations, apes must figure out a way to cross the problem space by using the human experimenter as a tool to obtain a result they cannot achieve directly. These types of experiments are very effective at identifying the cognitive processes underlying communication, but they tell us little about how and whether these processes operate in communicative interactions with conspecifics.

Communicative Strategies

Experimenters have used the problem space created by the distance between ape and human to study the types and sequences of gestures apes produce when they cannot move freely in relation to their recipient. In these studies, experimenters are able to control the reactions and the attention of the human recipient and thus observe what apes do in situations where recipients do not perceive the communicative attempts or do not respond as expected. Studies in which apes must request food from human experimenters who are either looking away or have their backs turned have largely supported the conclusions of observational studies that apes attend to the visual attention of others and use visual gestures more often when they can be seen (Liebal, Call et al., 2004; Liebal, Pika, Call, et al., 2004; Poss, Kubar, Stoinski, & Hopkins, 2006). These studies have also gone beyond the findings of the observational work, concluding that, when the recipient is looking away, some apes use attention-getting behaviors (such as auditory gestures) or move to locations where they can be seen (Leavens, Hostetter, Wesley, & Hopkins, 2004; Liebal, Pika, Call, et al., 2004).

Studies in which human experimenters respond “inappropriately” or do not fulfill the desires of the ape provide information about what apes do to overcome failed communicative attempts. Leavens, Russell, and Hopkins (2005) designed an experiment in which chimpanzees that have requested one food item from an experimenter are then given only part of the food or an undesirable food instead. They found that the chimpanzees persisted in their communicative attempts and elaborated the attempts by using new gestures when they were not given the entire desired food. Expanding on this analysis, Cartmill and Byrne (2007) presented orangutans with a similar protocol and found that their strategies differed based on whether they had been partially successful in communicating (given part of the desired food) or unsuccessful (given the undesirable food). When partially successful, orangutans used previously attempted gestures and repeated each gesture more. When unsuccessful, orangutans avoided failed signals and attempted more novel gestures, trying each only once or twice. Because the orangutans were not more likely to repeat the last signal they attempted following a partial reward, the results cannot be explained by a simple operant conditioning account. Subjects remembered which gestures and actions they attempted; reattempting behaviors from the full set when they had been partially successful in obtaining the desired food and avoiding them when they had failed. This study demonstrated that apes have a greater sensitivity to the responses of the recipient and to the success of their own communication than had been previously thought.

Pointing

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Many ape-to-human communication experiments have focused on the forms of communication rather than the strategies. These studies mostly address the questions of whether apes understand pointing and whether they themselves point. Pointing is one of the important milestones in child development (Bates, Camaioni, & Volterra, 1975; Bruner 1983). It is thought to be important in allowing triadic communication, establishing joint attention, and developing theory of mind (Akhtar & Tomasello, 2000; Baldwin, 1993; Butterworth, 2003). The cognitive mechanism behind pointing in infants is hotly debated, with infant pointing having both “rich” and “lean” interpretations according to whether the researcher believes that infants are attempting to change the minds or merely the actions of others when they point (for a review see Tomasello, Carpenter, & Liszkowski, 2007).

Pointing has gained prominence in debates about what makes humans different from apes (e.g., Tomasello, 2006), with some authors strongly claiming that apes do not point (Povinelli, Bering, & Giambrone, 2003). In response to these claims, Leavens, Hopkins and their colleagues conducted a large number of studies with captive chimpanzees specifically to elicit pointing (Leavens, Hopkins & Bard, 1996, 2005; Leavens, 2004). In a range of studies, Leavens and Hopkins have demonstrated that captive apes will indicate distal objects to human experimenters by extending an arm or finger toward the object. There has been some disagreement about whether the form of the gesture in apes (usually a whole hand extension) constituted pointing, but most researchers currently agree that captive apes can deictically indicate objects to humans when given the right environment. The focus then shifted to the motivation behind the act of pointing itself: whether the motivation of the gesturer is to change the behavior of the other individual (imperative pointing) or the contents of the other's mind (declarative pointing). Some have claimed that imperative gestures do not constitute intentional communication because they are not produced to change the knowledge state of another (Baron-Cohen, 1999).

Tomasello and colleagues argue that apes may point to request objects, but they do not point to share interest or to inform others (Tomasello, Carpenter, & Liszkowski, 2007). Tomasello and colleagues contend that such declarative pointing arises from and helps to foster the collaborative culture-rich environment in which humans are reared. Children point to share attention, to indicate novel things, and to inform or help. These abilities are all associated with human culture and are central to human social cognition. It is possible that captive apes do not possess the same cognitive abilities for social intelligence as humans and, therefore, lack the understanding and ability to perform declarative gestures (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007). Others argue, however, that the ability is present in apes, but differences in the rearing environment lead to a lack of motivation for declarative gesturing (Lyn, Russell, & Hopkins, 2010).

Enculturation

The advantage of being raised from birth in the enriched environment of a human culture may provide the motivation behind many communicative and cognitive abilities demonstrated by very young children and absent in captive apes. Apes reared in human enriched environments have opportunities to develop skills and motivations (e.g., desires to share attention or cooperate) absent in the natural rearing environments of great apes. Abilities such as theory of mind, shared intentionality, declarative communication, and displaced reference might develop during ontogeny only under ideal circumstances (i.e., our own), and only then with the encouragement and support of proficient adult tutors. This might help to explain why language-trained apes (and human-reared apes, in general) exhibit many cognitive skills that naturally reared apes do not (Leavens, Hopkins, & Bard, 2005; Lyn, Russell, & Hopkins, 2010). These human-reared culturally-enriched apes are often referred to as “enculturated,” and have demonstrated abilities both in comprehending and producing declarative pointing (Lyn et al., 2010).

Studies with enculturated apes show that apes have the capacity to acquire complex cognitive and communicative abilities when reared in the “right” way. These results shift the question from “Why do apes lack these abilities?” to “Why don't apes develop these abilities outside human-constructed contexts?” It is clear that the early rearing environment has an enormous effect on the development of the cognitive skills and motivations necessary for complex communication. The role of the developmental environment in different species and during evolutionary history must, therefore, be called on to help reconcile differences between the abilities and common practices of a species' communication.

Monkeys, apes, and humans all mature slowly and have an extremely long period of maternal dependence compared to most other mammals (Harvey & Clutton-Brock, 1985). It is likely that this period is needed to allow the acquisition and development of social and material skills needed to survive in primates' complex environments. Moreover, the slow rate of maturation in primates provides a period of time during which the brain continues to grow, and the infants' environment during this period can shape both brain structure and brain function, including the development of cognitive skills.

Social Environment

p. 187 Arguably, the complex social environments in which many primates live present the greatest cognitive challenges to the developing individual. It is likely that even the development of material and technological skills in primates requires the use of complex social skills, because many are acquired through observation of knowledgeable individuals. Mastering the complexity of a primate society requires a great deal of learning, and this need for learning was likely an important evolutionary force in the extension of the human developmental period (Dunbar, 1995; Flinn et al., 2005).

Social complexity is positively correlated with neocortex size in primates (Dunbar, 1995, chapter 6 of this volume; Reader & Laland, 2002). This evolutionary increase in the part of the brain associated with executive function is most likely driven by the need to understand social dynamics, forge alliances, and manage relationships with other individuals over many years. Longer juvenile periods are also associated with increased brain size and social complexity and all three likely co-evolved (Joffe, 1997). Bjorklund and colleagues have argued that these three factors form the foundation from which human intelligence evolved (Bjorklund & Bering, 2003; Bjorklund & Rosenberg, 2005).

Primates have a wide range of skills and relationships they must learn before they reach adult competency. All primates must be proficient learners; however, it is unclear whether the primary or only cognitive specialization of humans and other primates is an amazing ability to learn, or whether they are pre-adapted for learning, reasoning, and understanding in some particular domains. We argue that primates have evolved many specific cognitive specializations in the social domain and that some of these cognitive adaptations are apparent in the way primates communicate with others.

Vocal Communication

In terms of vocal communication, nonhuman primates possess no extraordinary production skills. Their vocal repertoires are highly fixed and it is almost impossible for them to acquire new calls, even when cross-fostered by other species (including humans) (Gardner & Gardner, 1969; Owren, Dieter, Seyfarth, & Cheney, 1992). It is clear that primates' extended period of development is not used to acquire a large repertoire of calls. In contrast, species that display remarkable vocal learning, such as songbirds or parrots, devote a considerable amount of time during development to the acquisition and practice of complex songs. The breadth and accuracy of the acquired repertoire has direct fitness benefits in many species of birds: females may prefer males with more complex songs, and territorial disputes may be won by the individual with the largest repertoire of songs (e.g., Mountjoy & Lemon, 1996; Searcy, 1992; for a review see Catchpole & Slater, 2003).

Instead of learning to produce new calls during development, monkeys and apes mainly learn how to interpret them. Primates may learn to narrow down the contexts in which they give a particular call so that they call only in response to a particular type of stimulus (Seyfarth & Cheney, 1986), but the underlying motivation to call and the types of calls used appear to be mainly innate. It is the receivers (rather than the senders) who have the most to learn in primate vocal communication (Seyfarth & Cheney, 2003). Primates must learn how to respond to specific calls—pairing particular sounds with external events and learning to react appropriately in each case. However, the structures of many types of calls seem designed to elicit immediate physiological responses in others (e.g., alarm calls and fear; see Rendall et al., 2009) and much of the learning that does occur can be accomplished in large part by behavioral conditioning (Seyfarth et al., 2010).

Great apes have slower and more extended periods of development and maturation than monkeys. They also use manual gestures to communicate to a much greater extent than monkeys do. As we discussed earlier, there is no evidence that ape gestures are socially learned from others. However, the flexibility with which apes use gestures in different contexts and in response to different aspects of the social environment likely requires considerable developmental learning and experience. If gestures develop through a process of ontogenetic ritualization, it would require many exposures to and opportunities to perform a particular action before it became a gesture. Infants would begin by attempting to manipulate their partners directly, and as their partners began to anticipate their desires, the infants would slowly learn that only part of the movement was necessary to elicit the desired response. This ritualization process would allow an ape to learn which movements are effective indicators of desired actions, and also when these different gestures are effective. If the forms of gestures are largely innate, then a period of learning when different gestures are likely to be effective (e.g., use the visual modality only when visible) would be required. Much like vervet monkey infants must learn which species deserve alarm calls and which should be ignored (Seyfarth & Cheney, 1986), infant apes would learn which contexts and social variables were important in determining how and when to gesture. We propose that primates, and especially great apes, have evolved cognitive specializations to attend to and learn to use social variables (such as the identity, visual attention, and dominance of communication partners) during communication, and particularly during gesture.

Comparative Development: The Future of the Field?

The importance of development in shaping primate communication has been investigated in only a limited number of studies, and most of them have focused on vocal communication (e.g., Hauser, 1996; Pistorio, Vintch, & Wang, 2006; Seyfarth & Cheney, 1997, but see Tomasello et al., 1994). Additionally, little is known about the relationships between socio-cognitive abilities (such as understanding visual attention, gaze following, and recognizing individuals) and the structure and use of communication systems in nonhuman primates. In humans, language develops alongside a whole range of cognitive abilities, building upon some and providing the foundation for others. The relationship between the emergence of language and other cognitive abilities is well studied in humans; similar work is needed to understand the relationship between communication and cognition in nonhuman primates.

Comparative developmental studies are needed to understand whether and how the development of one ability (e.g., understanding social hierarchies) affects or is affected by the development of communicative behaviors (e.g., using different strategies when communicating with a dominant versus a subordinate individual). Within this framework, developmental studies of gesture acquisition and experimental studies of gesture use in animals of different ages have the potential to shed new light on the socio-cognitive specializations of great apes and their relationship to communicative structures.

Our own evolutionary history was marked by qualitative changes, not only in the types of cognitive abilities that human infants develop, but also in the nature of the developmental period and rearing environment itself. Primates raised in human environments filled with cooperation, tool use, symbolic communication, and teaching develop abilities that they do not naturally exhibit in the wild. We are only beginning to explore the role of the social environment in shaping the development of socio-cognitive and communicative abilities in primates. We must also ask what external environmental pressures led to *rearing* environments that could shape and develop these abilities. Comparative studies of both ontogeny and rearing hold great promise to provide insight into the relationships between the physical and social environment and the development of cognitive and communicative abilities. Cross-species studies comparing ontogenetic environments and the development of cognitive and communicative abilities are essential to understand the unique combination of environmental, social, and ontogenetic factors that led to the capacity for culture and language in the human lineage.

Future Directions

1. What features of the rearing environment influence the development of communicative and cognitive complexity?
2. What aspects of ape gesture systems (if any) are learned?
3. Do nonhuman primates process gesture and vocalization in similar ways?
4. Why do nonhuman primates so rarely synchronize vocal and gestural modalities given that it is so common in human communication?

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