Gestures and Multimodal Signaling in Bonobos

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Introduction

Studies on bonobos have come a long way in the last several decades. Our understanding of this remarkable ape's ecology, sexual behavior, dominance style, and conservation issues is constantly evolving. We know a great deal about the bonobo's vocal repertoire, as described by de Waal (1988), Hohmann and Fruth (1994), and Bermejo and Omedes (1999). Facial expressions have not been studied nearly as fully, perhaps because doing so requires close observation. For this and other forms of visual communication, captive studies remain invaluable. They allow for the observation of detailed social behavior at close range, as well as the observation of complex social interactions in their entirety.

One of the most interesting and least studied forms of social communication in apes is gesture. We see all four species of great ape – bonobo, chimpanzee, gorilla, and orangutan – using their hands to communicate, but gestures, as with facial expressions, are very difficult to study in the wild. Most studies of gesture concern human-trained ones, such as American Sign Language taught to a handful of individuals (Patterson 1979, Gardner et al. 1989, Miles 1990). Additionally, we know next to nothing about how natural gestures work in concert with other communicative signals.

Although there have been some advances, we still know relatively little about the evolutionary history of language (Christiansen and Kirby 2003). An understanding of this complex issue must be grounded in a range of disciplines, including linguistics,

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psychology, neuroscience, philosophy, archaeology, and primatology. An important way to further our knowledge is through the comparative study of closely related primate species (Marler 1976, Cheney and Seyfarth 1990). Though nonhuman primate vocalizations have long been the focus of language evolution theories, gesture also has much to contribute.

We will first review the general tenets of the gestural origins of language theory, after which we will briefly summarize the aspects of human gesture that relate to its probable evolution. We will also review what is known about ape gestures and how they may or may not fit the theory of gestural origins of language (Corballis 2002). We will then provide detailed descriptions of bonobo gestures, emphasizing their flexibility relative to other communicative signals. We will review multimodal communication and describe how gestures function within a multimodal scheme in bonobos. The flexible nature of gestures as compared to other communicative signals will provide food for thought for the role that gestural communication may have played in the evolution of human language (Corballis 2002).

We observed four groups of captive apes: one bonobo group at the San Diego Zoo and one at the San Diego Wild Animal Park, both in California, and two separate chimpanzee groups at the Yerkes National Primate Research Center in Lawrenceville, Georgia. All of these apes live in social groups in primarily outdoor settings, and each group contained a mix of sexes and ages. We recorded data onto videotape, which we used for subsequent analysis (with the exception of a small subset of focal data), and considered only social interactions that were initiated by a communicative signal (Pollick 2006, Pollick and de Waal 2007).

Gestural Origins of Language Theory

Historically, primate communication research has focused on the vocal modality, usually with the exclusion of other forms of communicative signals. This focus is probably a reflection of prevalent theories of language evolution at the time, emphasizing the vocal trajectory as the evolutionary origin of language (Marler 1965, Cheney and Seyfarth 1990). Though theories of human communication have long underscored the interplay of different modalities, it is only recently that theoretical debates about the evolutionary history of language have opened up to the possibility that other communicative behaviors conceivably evolved along with or perhaps even earlier than spoken language. Several decades ago, Hewes (1973) proposed a gestural origin of language theory, which Corballis (1999, 2002, 2003) has further developed. Corballis argues that there are several convincing pieces of evidence for why gesture may have been the original medium for evolving language in our hominid ancestors, which can be summarized as follows: 1) the advantage of manual communication in the hunting-and-gathering phase in early hominid society (silent communication to coordinate hunts); 2) paleoarchaeological evidence suggesting that the early hominid brain was "language ready" before the vocal apparatus was ready to produce complex speech; 3) the observation that apes use manual gestures in a more controlled manner than they do their voices; and 4) the fact that gesture use is lateralized in the Broca's area homologue in great apes.

Corballis thus argues that all of these elements add up to a plausible scenario in which gesture assumed the burden for the burgeoning linguistic capacity that was spilling from our fast developing neocortex, until the vocal tract further developed and human society came to rely predominantly on speech as its means of language. The theory has not been fully embraced by human gesture and linguistic researchers, who doubt the strength of the evidence Corballis calls upon (Jackendoff 2002, Pollick and de Waal 2004, McNeill et al. 2005). The importance of this theory, however, may not lay so much in prioritizing gesture over speech, but in the attention called to their co-evolution. A compromise that seems reasonable is that gestures and vocalizations may have been incorporated into a multimodal communication strategy. While we rely heavily on speech to convey the majority of linguistic information, this multimodal communication strategy is nevertheless evident in humans today.

Gesturing as an Integral Part of Human Communication

Human gesture has been studied for over 60 years (Efron 1941, Kendon 1972, 1980, McNeill 1992, Goldin-Meadow and Wagner 2005), and we know some of the ways in which gesture facilitates and enhances vocal communication as well as cognitive and symbolic processes. Gesture produced while speaking can enhance information transfer and supplement the meaning of the linguistic signal (McNeill 1992). Though not normally produced without speech in hearing people, gesture can assume linguistic properties when users are prevented from talking (Goldin-Meadow 2001), even in children raised in linguistically poor environments (Goldin-Meadow and Mylander 1984). When a person is having trouble expressing a thought through speech, simultaneous gesturing may facilitate lexical retrieval (Morrel-Samuels and Krauss 1992), and even provide a kind of cognitive arena in which to think when speech does not provide the appropriate means of expression (Goldin-Meadow et al. 2001).

While some specific human gestures are universal, many are culture-specific. But we also show so-called "beat" gestures, which simply emphasize the flow of speech (McNeill 1992). We habitually gesture in the presence of speech, often in precise synchrony with speech (McNeill 1985). We even gesture in the absence of a visible audience, as we do when talking on the phone (Morris 1977, 1994), or communicating with blind individuals (Iverson and Goldin-Meadow 1998). The fact that gestures accompany speech even in situations in which its communicative value seems null, emphasizes its automaticity and encourages investigation into the possible evolution of this ubiquitous behavior.

What is even more remarkable is that some human gestures occur without learning from others. The ethologist Eibl-Eibesfeldt, who followed the expressive behavior of a congenitally deaf and blind girl named Sabine, observed her stretching her hand and pushing it back, palms facing outwards, in a gesture of rejection (Eibl-Eibesfeldt 1973), without her ever having observed such a gesture. Comparative theorists who view the difference between human language and other forms of communication as one of degree only argue that human linguistic capacity expanded from abilities already present in other animals, particularly closely related species. If this hypothesis is correct, and if gesturing is integral to human communication, we should expect to find certain precursors of this communication strategy in nonhuman primates.

Ape Gesturing

As pointed out by de Waal (2003), free hand gestures are virtually limited to the Hominoidea. This is not a mere quantitative difference with monkeys, but a qualitative one. Facial expressions and vocalizations are common means of communication in all primates and many other animals, but with the exception of a single gesture in a single species, monkeys lack ritualized hand gestures. Macaques may slap the ground with a hand when threatening another, or reach back to their partner during a sexual mount, but these are the limits of their manual communication. Contacts with a substrate or partner function as a signal, but involve more than the hand. In contrast, bonobos wave at each other, shake their wrists when impatient,

Fig. 4.1 Bonobo reaching out his arm in a gesture (Photograph by Frans B.M. de Waal.).

beg for food with an open hand held out, flex their fingers towards themselves when inviting contact, move an arm over a subordinate in a dominance-gesture, and so on. They even gesture with their feet (de Waal 1988).

Like facial expressions, many free hand gestures of apes are ritualized, that is, they are stereotypical, exaggerated, and tied to specific contexts. The begging gesture, which is also universal in humans, most likely derives from a cupped hand held under the mouth of a food possessor. The origin of this gesture is visible in the only known ritualized monkey gesture, which is hand-cupping by capuchins (*Cebus apella*). If one monkey possesses food, another will reach out a hand and hold it under the possessor's chin so as to catch dropping morsels. This seems an instrumental act, but the same gesture can also be given from a distance – for example, when two capuchins are separated by mesh and one is consuming food (de Waal 1997). In those instances, the gesture is used as a distant signal, divorced from its instrumental function, similar to the way all of the great apes use gestures. An important difference remains, however, in that apes have generalized the meaning of the begging gesture to apply to a variety of situations, whereas in capuchins, the gesture appears to be entirely food-specific.

Apes and humans gesture more with the right hand than the left hand (Annett 1985, Hopkins and Morris 1993, Hopkins and de Waal 1995). Since the right hand is left-brain controlled, this means that ape gestures share the same lateralization as human language. The highly flexible use of ritualized hand gestures, their recent appearance on the evolutionary scene (compared with other means of communication), and their culture-dependency in both humans and apes have implications for the role that gestural communication may have played in the evolution of human language (e.g. Corballis 2002).

There has been a resurgence of interest in natural gestural behavior in various ape species. The great apes use their hands extensively in daily life: in play, sharing food, getting one's attention, and grooming (Goodall 1968, van Hooff 1973, de Waal 1988, Kano 1992, Tanner and Byrne 1999, Tanner 2004). Studies of ape behavior in the wild included some attention to gestures (Goodall 1968, Kuroda, 1984, Kano 1992, Veà and Sabater-Pi 1998), but more abundant are observational studies of naturally occurring gestures in captive chimpanzees (Ladygina-Kohts 1935, van Hooff 1973, Plooij 1978, 1984, Tomasello et al. 1985, 1989, 1994, 1997), bonobos (Savage-Rumbaugh et al. 1977, de Waal 1988, Pika et al. 2005) and gorillas (Tanner and Byrne 1996, 1999, Pika et al. 2003, Tanner 2004).

Researchers have used gesture in apes as an experimental tool with which to ask questions about imitation (Custance et al. 1995), intentionality and perspective taking (Hopkins and Leavens 1998), linguistic ability (Gardner et al. 1989), and laterality (Cantalupo and Hopkins 2001). In these cases, gestures were usually either taught as part of an artificial system or generated using food or other desirable objects. While these experiments have been able to explore questions about theory of mind and intentionality, no current research truly asks questions about how gesture is used to mediate social life in a naturalistic environment.

A Word About Definitions

In reviewing the literature on gestural communication in primates, it soon becomes obvious that researchers use the term gesture in different ways. Prior behavioral studies (Goodall 1986, Plooij 1978), and none of the studies by Tomasello and colleagues, comprehensively defined gesture: investigators selected the contents of their ethograms on broadly described gestures. Some studies included facial expressions, body postures, or even locomotion patterns in their gesture definitions, e.g., back offer, belly offer, lip-lock, genital offer, spit-at, or swagger (Tomasello et al. 1997). Researchers who took care to define gesture, such as Savage-Rumbaugh et al. (1977), restricted the definition to movements of the hands or upper forelimbs, and generally did not include body postures or general body movement, even if directed at another individual. Tanner and Byrne's (1999) working definition is the most precise, and served as the model for our own studies: they defined gesture as all discrete, nonlocomotor limb and head movements that appear to be communicative, and the movement should be intentionally directed toward another individual. For a tactile interaction to be considered a gesture, it needs to involve a transformation of purposive behavior, so that it is no longer mechanically effective and communicates a specific desire, intent, or feeling (Bretherton and Bates 1979, Goldin-Meadow and Mylander 1984, Gomez 1990). Pollick (2006) provided an extensive working definition of gesture.

It is crucial that the study of gestures in apes is restricted to the limbs. This is not only so in relation to theories about the evolution of language, but also because the detection of manual activity in monkeys has been shown to be neurologically distinct from general body movements (Perrett et al. 1985). In humans, the neural space that houses language (Broca's area) is also active during the observance and performance of manual gestures, but not other body movements (Rizzolatti et al. 1996). Hence, a sharp distinction needs to be drawn between brachiomanual gestures and any other nonvocal bodily-based forms of communication.

Manual Gestures in Bonobos

Given the above restriction to the study of gestures in apes, we were able to finely discriminate against many different kinds of manual gestures in the San Diego Zoo and Wild Animal Park bonobos (Table 4.1).

For example, when stretching the arm and hand out in a gesture, the palm can face upwards, downwards, or to the side (a distinction made for chimpanzees by van Hooff 1972). However, we did not observe the three being used interchangeably with respect to social context: the reach out side gesture was more often made in food contexts, reach out up was made typically when requesting a grooming session, and reach out down was often produced in play. Of 32 different manual gestures observed, the bent wrist gesture was rarely produced, and when it was, it

Table 4.1 Gesture usage in bonobos and chimpanzees

BONOBOS		CHIMPANZEES	
Gesture	Percentage of Total gestures	Gesture	Percentage of total gestures
gentle touch	40.4	gentle touch	25.9
reach out down	10.2	bent wrist	11.1
reach out up	9	arm raise	9.7
arm raise	6.8	throw aimed	9.2
hard touch	5.2	reach out down	7.9
Pat	5.1	throw hold	5.8
foot/leg	3.1	hard touch	3.9
Dab	3	beg hand	3.4
reach out side	2.9	reach out up	3.4
slap ground	2.9	dab	2.2
poke	1.4	reach out side	2.2
shake wrist	1.4	rap knuckles	2.1
swing	1.3	slap ground	1.8
hunchover	1	shake wrist	1.6
rap knuckles	1	foot/leg	1
clap	0.8	pat	1
flap	0.7	armwave	0.9
bent wrist	0.5	hand/mouth	0.9
slapstomp	0.5	swing	0.9
throw aimed	0.5	flap	0.7
armwave	0.4	poke	0.7
beg hand	0.4	beckon	0.6
hand to hand	0.4	flail	0.6
beckon	0.1	hunchover	0.6
finger/mouth	0.1	clap	0.4
flail	0.1	finger flex	0.3
hand lead	0.1	point	0.3
point	0.1	slapstomp	0.3
stomp	0.1	stomp	0.3
		clasp self	0.1

Total number of gestures: 763 Total number of gestures: 673.
Both bonobos and chimpanzees used the *gentle touch* gesture more than any other, but contextual usage varied (see Pollick 2006).

was never in an agonistic situation. This is in stark contrast with chimpanzees, which often use this gesture to ask for or provide appeasement (Goodall 1968; Figure 4.2).

Another contrast with chimpanzees lay in the tactile nature of some gestures: bonobos use more gestures that involve touching (albeit not forcefully), such as gentle touch and pat: tactile gestures comprised 55.8% of the all observed gestures in bonobos and 34.6% of those observed in chimpanzees. Perhaps bonobos, being generally less aggressive and dominance-oriented, are more tolerant of communicative touching than chimpanzees (Table 4.2).

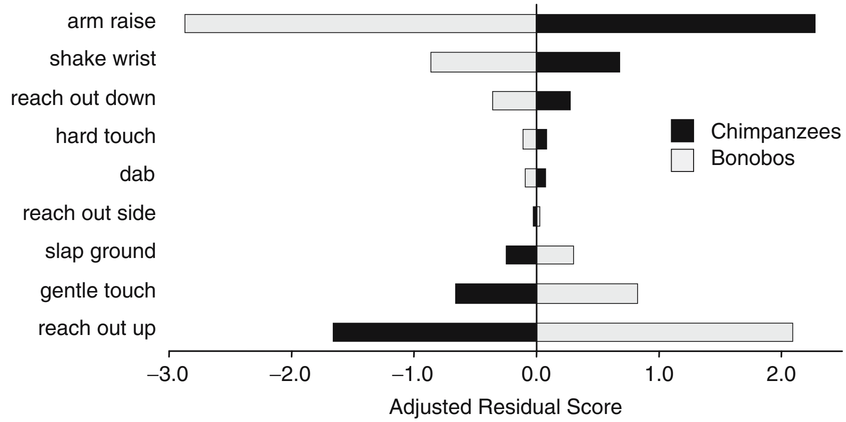

Fig. 4.2 Some manual gestures compared between bonobos and chimpanzees.

Table 4.2 Gestures observed in bonobos and chimpanzees

Gesture	Description
arm raise	one or both arms raised, which initially hang more or less down, forwards with usually a quick, jerky movement; fingers are flexed slightly and palm of hand may be oriented towards the other individual and upwards, or away from the other individual and downwards; arms stop rising at horizontal position, and hand may swing further upwards; recipient is never struck
armwave	rising to a bipedal position while facing another individual and either swinging arms in front of torso or raising one or both arms rapidly into the air (not as part of a swagger/bluff display)
beckon	one or both arms raised forward and upward sweepingly and stiffly with the elbows more extended than in the arm raise; hands are hanging down limply with finger flexes usually; movement is held at end of upward swing while individual stares at recipient
beg with hand	placing one or both hands around or under lips, or chin and lips, of recipient that has food in mouth; or touching the hand by the mouth of individual containing the food
bent wrist	flexing the wrist while holding the back or side of hand out towards another individual; contact possible
clap hands/feet*	flat palms of hands are brought into contact with each other either in vertical or horizontal position; can be repetitive
clasp self*	arms are crossed in front of torso, with hands curled and usually slapped on individual's arms, repeated two or three times in succession
dab	touching approaching or stationery individual with back of flexed fingers where after touching hand is withdrawn immediately; sequence can be repeated a number of times in quick succession
finger flex	palm can be up or down, and wrist is not bent; fingers move rapidly back and forth

(continued)

Table 4.2 (continued)

Gesture	Description
finger/hand in mouth	putting a finger or hand into another individual's mouth
flail*	arms and hands are completely raised above head and are shaken in rapid succession (usually in tantrum or approach); repetitive
flap	one arm and hand raised and makes a downward slapping movement of the hand in direction of another individual – no forceful contact with substrate (ground, wall, etc.)
foot/leg gesture	any extension of leg or foot towards another individual
gentle touch	any sort of contact made with hand (front or back) or fingertips with another individual, without appreciable force
hand lead	taking the hand of another individual and bringing it into contact with his own body, but without sufficient force to move recipient's entire body
hard touch	any sort of contact made with hand (front or back) or fingertips with another individual, without appreciable force, but the actual contact itself is more forceful than a simple laying of the hand on another's body
hunchover*	one arm is swept over back of another individual, but there is no hugging or extended contact (less than two seconds)
pat	rapidly repeatedly contacting another individual with flattened palm surface of hand; not in play; repetitive
point*	either whole hand or one or more digits directed to recipient, another individual, or object
poke	pushing one more fingertips with sudden movement onto body part of another individual; repetitive
rap knuckles*	knuckles of one or both hands are rapped on ground or wall or object while looking at recipient; repetitive
reach out down∧	holding a hand toward another individual by extending the arm, wrist, and hand in more or less horizontal position, and stretching the fingers while palm is facing downwards; other individual is not touched
reach out side	same as reach out down except the palm of the hand is directed sideways
reach out up∧	same as reach out down except that the palm of the hand is directed upwards
shake wrist	shaking the hand vigorously with flexible wrist towards another individual; repetitive
slap ground*	flattened palm of hand is forcefully brought into contact with ground in front of self or on an inanimate fixture such as a wall or net
slapstomp	simultaneous slap ground and stomp
stomp∧	hitting an object or ground with sole(s) of foot (feet); can be done with both feet in quick alternation
swing	arm is swung in an underhanded arch; can involve contact
throw aimed	over or underarm throw of object, including loose dirt, in forward direction while looking at target; not in play
throw hold	arm is raised above head, as if in a throw, but movement not carried out for at least two seconds (if at all)

All labels and descriptions, except where noted, are based on Plooij (1984).

Those marked with * are descriptions based on personal observations and are similarly described in Nishida et al. (1999).

Those marked with ∧ are based on Plooij's (1984) descriptions but are labeled differently.

Gestures as a Suitable Candidate for Language Evolution

Characteristics that we share with apes but not monkeys likely evolved recently. Hence, they may have provided a basis for the development of even more unique patterns found only in humans (de Waal 2003). In this context, the difference in gesture usage between apes and monkeys is highly relevant, and becomes even more intriguing if we consider that apes appear to possess greater control over the production of gestures versus other signals (Preuschoft and Chivers 1993, Wiesendanger 1999). This hypothesis is supported by several observations, and the case of cultural transmission of gestures is one example. Just as there are cultural variations of gestures in humans, population-specific communicative behaviors are also known to exist in chimpanzees, such as leaf-clipping (Nishida 1980) and handclasp grooming (McGrew and Tutin 1978, de Waal and Seres 1997, Bonnie and de Waal 2005). In chimpanzees and all other great apes species, manual gestures are more culture-specific than facial expressions, which tend to be relatively invariant. The tendency of cultural communication patterns to be nonfacial and nonvocal is probably due to the ape's limited control over face and voice. In humans too, facial expressions seem universal (Ekman 1972), whereas many gestures vary by culture (Kendon 1995).

The fact that apes appear to have greater cortical control over limb movements than vocalizations, is further supported by observations that while efforts to teach chimpanzees to modify their vocalizations have failed dismally (Hayes 1952), apes can learn to employ American Sign Language in a referential manner (Gardner et al. 1989). In fact, each of the species of great ape has been taught to communicate using visual and manual signals. Both chimpanzees and bonobos have learned to use a keyboard containing symbols, which they point to in sequence to deliver messages. Kanzi, a bonobo, spontaneously added gestures to this repertoire (Savage-Rumbaugh et al., 1998).

Greater control over gestures than other signals is also suggested by observations of deception, in which apes may use their hands to modify a facial expression (de Waal, 1982) or a vocalization. Goodall (1986) reported how a chimpanzee attempted to muffle his excited pant-hoot, signaling the discovery of food, by covering his mouth with his hand, presumably in an attempt to keep the food to himself. Finally, monkeys also seem to have great difficulty producing vocal signals in the absence of a triggering situation (Goodall 1986). This is no doubt why in so-called ape language studies, the forelimbs have proven a more promising candidate for intentional communication.

These observations in conjunction with one another support the gestural hypothesis about human language evolution, which is further bolstered by the theory that the early human brain was capable of producing language before the vocal chords (Lieberman et al. 1972), the early appearance of gestural communication in human infants (Petitto and Marentette 1991), and the right-hand (hence left-brain) bias of both human and ape gestures.

Towards a More Flexible Communication Strategy: Contextually Defined Meaning

Whereas monkeys possess a rich repertoire of communicative signals, some with a demonstrable degree of referentiality (e.g., Seyfarth et al. 1980, Gouzoules et al. 1984, Zuberbühler 2000), they are by-and-large fixed signals with regards to emotional and/or social context. Ape gestures seem quite different: a single gesture may communicate entirely different needs or intentions depending on the social context in which it is used. Unlike the majority of facial expressions and vocalizations, manual gestures are more flexible (Tomasello et al. 1985, 1989, 1994, 1997) in the sense that they can be divorced from highly arousing contexts.

Because many gestures do not seem tied to a specific social situation, there is a great deal of equipotentiality in these communicative signals, and we don't really understand how they acquire meaning (in the absence of other discrete signals such as facial expressions and vocalizations). In the case of apes, for example, the begging gesture has absolutely no meaning unless one can deduce its referent from the context. For instance, a chimpanzee stretching out an open hand toward a third party during a fight signals a need for support, whereas the same gesture towards a possessor of food likely signals a desire for a share (de Waal and van Hooff 1981).

Given this distinction, we set out to test the hypothesis that gestures are less tightly tied to behavioral contexts than facial or vocal signals. Calculating the percentage that each communicative signal, be it gesture, facial expression, or vocalization, occurred in the context in which it was produced with the highest frequency, Pollick and de Waal (2007) found that, as a group, gestures showed far looser contextual associations than facial or vocal signals. Gestures also showed far greater contextual variation than facial and vocal displays both between bonobos and chimpanzees, and between groups within each species. Thus, knowing the usage of a facial/vocal display in one species allows one to predict how it will be used the other species, whereas knowing the usage of a gesture in one species does not allow one to predict how the other species uses it, and sometimes not even how other members of the same species use it in other groups. For example, the facial expression of silent bared teeth and the vocalization scream were almost always produced in agonistic contexts in both ape species, yet the arm raise gesture was used mostly in play in bonobos, but in chimpanzees it was used mostly to solicit grooming.

This suggests that the meaning of, for example, a gentle touch is informed by other signals as well as by the situation, and that individuals need to interpret these manual actions in light of the behavioral context (Goodall 1968, de Waal and van Hooff 1981). The flexibility of this class of signals suggests that gestural communication may have been one through which symbolic meaning was acquired in our hominid ancestors, alongside referential vocalizations (Corballis 2002, Pollick and de Waal 2004).

Multimodal Communication

The production and perception of communicative signals such as vocalizations, gestures, and facial expressions generally do not occur in isolation, but instead occur more often in combinations.

Different modes of communicative signals such as facial expression, gesture, body posture, head movement, touch, and vocalization often work together in a multimodal strategy that is common in humans and other animals. It may be that gestures combined with other signals have different effects than either have on their own. Researchers are becoming increasingly aware that a deeper understanding of the evolution of communication must be based on comparative studies of vocal as well as other communicative abilities, but also of how the signals work in concert to convey information. Multimodal communication may have been the springboard for the evolution of the almost infinite flexibility of human language (Rizzolatti and Arbib 1998, Corballis 2002).

Although the bulk of the animal signaling data concentrates on signals sent via a single sensory modality, multimodal signaling is quite common. Researchers have long understood the importance of multimodal signals (Møller and Pomiankowski 1993, Johnstone and Grafen 1993, Partan and Marler 1999), and the majority of the data has been collected just over the past decade or so. Multimodal signaling occurs across taxa, from snapping shrimp to spiders to birds, and in many different contexts, though ones involving courtship and mating are the best documented (Pollick 2003).

There are many ways to characterize multimodal signaling, from simply documenting which modalities are involved, to describing intricate temporal patterns of the signals. Of course, bonobos employ a battery of communicative signals, including head movement, posture, and gaze, among others. Here, we talk only about three of the more distinguishable and easily observed signals: manual gestures, facial expressions, and vocalizations. How the patterns differ from those of chimpanzees serves as interesting contrast.

Both facial and vocal signals were equally likely to occur in the bonobo combinations, whereas vocalizations were much more prevalent in chimpanzee combinations: 50% of bonobos and 66% of chimpanzees. Chimpanzees aren't necessarily more vocal than bonobos; the discrepancy is likely the result of more combinations in agonistic situations in chimpanzees, which usually involve much vocalizing. Within a combination, the facial or vocal signal tended to occur first, just before the gesture, which was also true of chimpanzees (cf. van Hooff 1973). It may be that the facial/vocal signals are more uninhibited, highly arousing, and tied to specific contexts, and perhaps the subsequent gesture informs or emphasizes the meaning of the first signal in a more cognitive or deliberate manner.

A multimodal signaling strategy can serve a variety of functions, including redundancy, amplification, and modulation (Partan and Marler 1999). Whatever the exact function of multimodal communication, it is clear that ape gestural flexibility, combined with their graded facial/vocal signal system (Parr et al. 2005), may be

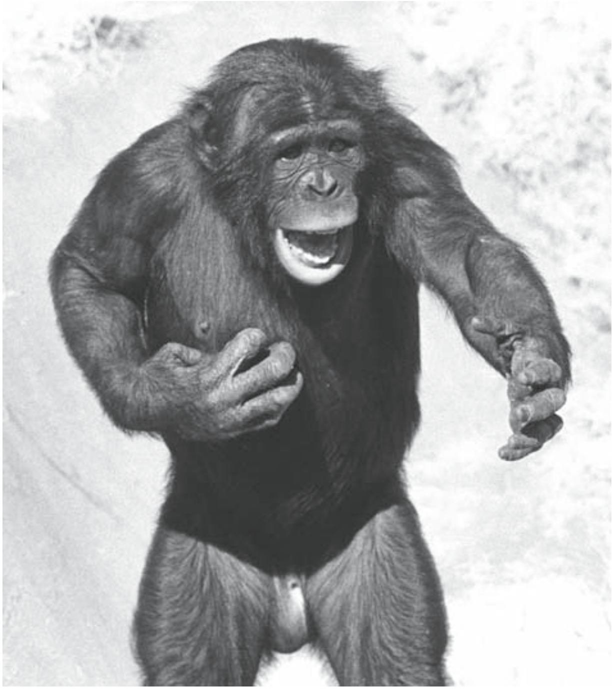

Fig. 4.3 Multimodal communication: a bonobo gestures and vocalizes simultaneously (Photograph by Frans B.M. de Waal).

advantageous over the more stereotyped signals of monkeys in that it allows for greater communicative complexity. One specific benefit of multimodal signaling may be its effectiveness in altering the recipient's behavior. Pollick and de Waal (2007) found that combinations of gestures and facial or vocal signals in bonobos were significantly more effective in getting the recipient to respond (defined as any change in overt behavior shown within 10 seconds of the signal). Although chimpanzees produce more combinations than bonobos, they seem to be less effective in getting the receiver to respond. Possibly, the relative scarcity of combinations in bonobos renders them more salient and more likely to affect behavior.

Directions for Future Research

We have given a broad overview of bonobo and chimpanzee gesturing, but much remains to be studied, starting with multimodal signaling. We discussed data on facial and vocal signals accompanying gestures, but there are other possible combinations; for example, a gesture could not only be accompanied by a vocalization, it could also be followed by a full-body bow or a head nod. These other kinesic movements have been shown to modulate meaning in humans (Kita 2003). It remains to be seen, however, if those signals are as meaningfully or consistently combined with gesture or other signals, in ways that affect receiver behavior.

Another way to expand on the data discussed here involves the nature of combinations during an interaction. There was a clear temporal pattern in the combinations data in this study, but the timing of combinations may be very different during an ongoing interaction, especially when repetitions or sequences are considered. The latter factors may have a different impact on the receiver's response and the nature of the entire interaction. We employed a narrow lens with which to view combinatorial signaling (looking only at signals which initiated an interaction), so alternate or more encompassing methods need to be tried. If signals during ongoing interactions are studied, alternate criteria for discerning responses would also be necessary. Perhaps instead of looking at the immediate behavior subsequent to the signal, the larger behavioral state change could be analyzed over a broader timeframe, such as 10 minutes following the signal.

Bonobos have individual, complex social relationships with one another, and their behavioral flexibility allows for very different ways of interacting with and signaling within particular dyads. For example, a high-ranking female may have a better chance of getting a male to react to her with a single gesture than a low-ranking female does with a combination, or an adolescent male is more likely to react to his mother than he is to an unrelated female. So it is not about the efficacy of the signals themselves so much as it may be about the relationship between the two participants, since so little of their gestural communication is stereotyped. Ideally, individual baseline rates of signaling and responding need to be established for every possible pair of social partners being studied, which would then be used to compare combinations in each dyad. This way, on an individual or dyadic basis, true differences in response can be determined.

Variations on what is considered effectiveness need to be explored. Because there were relatively few combinations on which to conduct analysis, all responses had to be pooled into a dichotomous "response/no response" category. These responses ranged from positive reactions, such as engaging in sex or sharing food, to negative ones, such as direct aggression or fleeing (or more broadly, appropriate versus inappropriate to context). These data can speak only to how responsive individuals are to different signal strategies, not necessarily how effective the strategies are at communicating a specific message. More data and analyses are needed on the quality of the response and how it varies as a function of the type of gesture and combination used; in this way, we will get closer to the issue of meaning.

Acoustic analysis comparing vocalizations produced alone and those produced in combinations might reveal other aspects of efficacy. Recent work on chimpanzee vocalizations (Slocombe and Zuberbühler 2005) has revealed a level of complexity and possible referentiality heretofore unexplored in apes, and much remains to be investigated in these signals within combinatorial strategies.

Finally, there is a great need for experimental work on the perception and classification of gesture. Description of how signals work behaviorally and how they visibly affect receivers' actions is a necessary component of our understanding of communication, but there is a growing awareness that animals may not perceive, and more importantly, may not categorize their signals the way we do (Evans 1997). Studies have shown that chimpanzees classify their own communicative signals (largely facial expressions) and can do so according to their emotional meaning (Parr 2001). It is completely unknown whether great apes categorize their gestures in the same way. It would also be interesting to see if they associate particular gestures with social contexts, such that if presented with a choice between a bent wrist and a reach out down after viewing a fight, would they always pick the bent wrist, or if supplementation with another signal affects that choice.

Conclusions

Manual gestures play a significant role in bonobo communication. The flexible nature of these gestures is highlighted by the fact that facial/vocal signals correlated to a much higher degree with regard to contextual usage than did gestures. This flexibility is all the more striking when we consider the fact that apes gesture and monkeys do not. Monkeys possess a rich repertoire of communicative signals, some of which have been demonstrated to contain the seeds of referentiality (Seyfarth et al. 1980, Zuberbühler 2000), but they are, generally, signals bound to specific emotional and/or social contexts (with the exception of deceptive use). Manual gestures, on the other hand, have been repeatedly shown to be flexible signals that can be divorced from highly arousing contexts. Thus, there is a great deal of equipotentiality in gestural signals, and how they acquire meaning (in the absence of other discrete signals such as facial expressions and vocalizations) remains to be investigated.

Few studies have attempted to observe multimodal signaling in ape communication, and the data discussed here examined how gestures are combined with facial and vocal signals. In this study, facial expressions and vocalizations constituted the other half of a combination at equal rates, while bonobos combined their gestures with vocalizations less often than with facial expressions than did chimpanzees. This may be due to the overall prevalence of vocal activity in chimpanzees (de Waal 1988), but it may also concern the issue of control. If bonobos can better regulate their vocal output and divorce them from highly arousing contexts, it is not necessarily the case that this will happen at the start of social interactions. We observed much vocal “chattering” among the bonobos, by which we mean vocalizing (to each other or to humans) to garner attention in the absence of excitement, low-intensity vocalizing in the presence of food, but not in a chorus-like manner the way chimpanzees do, low-intensity vocalizing when traveling, and dialogue-like vocalizing in alarm situations. This greatly contrasted with the vocal output of chimpanzees, which was mostly restricted to highly charged situations such as aggression or food anticipation. Thus, greater control over this modality may not necessarily translate to greater production in general or greater use in initiating social interactions.

When combinations occurred in both species, the two signals tended to overlap rather than occur separately in time. Combinations did occur in highly charged situations, such as fights and reconciliations, but this was not always the case. The overlap, therefore, was not necessarily due to lack of inhibition during emotionally charged situations. It may be that, as has been theorized for humans, there is a common cognitive underpinning for both signals (McNeill 1992). In humans, this underpinning, what McNeill calls the "growth point," represents the initial form of a thought that is eventually expressed in two modalities. The growth point's defining characteristic is the tight co-expression of gesture and speech. While this pattern was not consistently observed in the apes, there were several notable instances in which the strokes of a repetitive gesture were closely matched by pauses in the accompanying vocalization. This tight synchrony is possible evidence of a shared neural space from which symbolic communication evolved (Cantalupo and Hopkins 2001, Corballis 2002).

Across all signals and contexts, combinations of gestures and facial/vocal signals were more effective at eliciting a response than gestures alone. This supports the bulk of the multimodal signaling literature across animal taxa (Møller and Pomiankowski 1993, Partan 2002), in that multimodal signaling has a differential effect, whether that effect is simply a response at all, an enhanced response, or a compound response (Partan and Marler 1999). This was true only for the bonobos, however, and not the chimpanzees, which is interesting given that combinations occur less frequently in the bonobos. It may be that the relative scarcity of combinations renders them more salient and more likely to affect behavior, whereas the relative ubiquity of combinations in chimpanzees is associated with a lower rate of response. This held true even when combinations were broken down into specific contexts.

Environmental noise, however, can affect the efficacy of signaling, and it often exerts evolutionary pressure on the signals themselves (Brown and Waser 1988). For example, if a species typically lives in a heavily forested area and in a fission-fusion society, communication will evolve to overcome these barriers and rely more heavily on vocal rather than visual signals (Brown and Waser 1988). There are some differences in the wild habitats of bonobos and chimpanzees: bonobos live in more humid forest while chimpanzees occupy a drier forest (Kano 1992), but these differences do not seem to dramatically differ with respect to visual or vocal barriers. One intriguing difference, however, lies in the fact that chimpanzees spend considerably more time foraging for food than bonobos do (the latter species' environment is more abundant in fruit; Kano 1992), and thus may spend more time communicating about food. This greatly contrasts with how signals are used in captive apes, and remains an important difference in comparing wild and captive ape communication.

Kano (1992) suggested that the characteristics of bonobos are more original and closer to those of the common ancestor, having retained a larger number of ancestral genes due to a slower rate of selection. The habitat of bonobos likely resembles our shared ancestor's; thus, Kano suggests, we should look to them as a model of the physical and behavioral characteristics of the common ancestor of the African great apes and humans. From that perspective, the bonobos' more flexible gestural repertoire and greater responsiveness to combinatorial signaling may be characteristic of the communicative repertoire of the early hominoid lineage, and perhaps of our direct ancestors as well.

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