

The gestural communication of apes

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Gestural communication of nonhuman primates may allow insight into the evolutionary scenario of human communication given the flexible use and learning of gestures as opposed to vocalizations. This paper provides an overview of the work on the gestural communication of apes with the focus on their repertoire, learning mechanisms, and the flexibility of gesture use during interactions with conspecifics. Although there is a variation between the species in the types and numbers of gestures performed, the influence of ecology, social structure and cognitive skills on their gestural repertoires is relatively restricted. As opposed to humans, apes do not use their gestures referentially nor do their gestures show the symbolic or conventionalized features of human gestural communication. However, since the gestural repertoires of apes are characterized by a high degree of individual variability and flexibility of use as opposed to their vocalizations it seems plausible that the gestures were the modality within which symbolic communication first evolved.

Keywords: gestural communication, apes, repertoire, learning, flexibility, audience effects

Human communication is unique in the animal kingdom in any number of ways. Most importantly, of course, human communication depends crucially on linguistic symbols, which, to our knowledge, are not used by any other species in their natural environment. Although there is no universally agreed upon definition of linguistic symbols, many theorists would agree that they are, in their essence, individually learned and intersubjectively shared social conventions used to direct the attentional and mental states of others to outside entities referentially.

In looking for the evolutionary roots of human language, researchers quite naturally looked first at primate vocalizations. The dramatic discovery that vervet monkeys use different alarm calls in association with different predators (leading to different escape responses in receivers) raised the possibility that some nonhuman species may, like humans, use vocalizations to make reference to outside entities (Cheney & Seyfarth, 1990). But it has turned out since then that alarm calls of this type have arisen numerous times in evolution in species that also must organize different escape responses for different predators, including most prominently prairie dogs and domestic chickens (Owings & Morton, 1998). It is also the case that primate vocalizations in general are unlearned and show very little flexibility of use: Infants reared in social isolation still produce basically all of their species-typical call types from soon after birth (see Snowdon et al., 1997, for a review), and rearing individuals within the social context of another primate species produces no significant changes in the vocal repertoire (Owren et al., 1992). And importantly, there is currently no evidence that any species of ape has such referent specific alarm calls or any other vocalizations that appear to be referential (Cheney & Wrangham, 1987; see Crockford & Boesch, 2003, for some interesting new observations) — which means that it is highly unlikely that vervet monkey alarm calls could be the direct precursor of human language — unless at some point apes used similar calls and have now lost them.

But human communication is also unique in the way it employs manual and other bodily gestures. For example, to our knowledge only human beings point to things deictically for conspecifics — the basic form of gestural reference.¹ And humans use other kinds of symbolic gestures as well, ranging from waving goodbye to signaling “OK” to conventionalized obscenities — which, to our knowledge, are also unique to the species. In general, one might say that human gestures are used functionally in ways very similar to language (e.g., symbolically, referentially, based on intersubjectively learned and shared social conventions) and many of the aspects of human linguistic communication that make it so different from primate vocalizations are also present in human gestures. The question thus arises: what is the nature of the gestural communication of nonhuman primates, and how do they relate to human gestures and language? This question has received surprisingly little research attention, that is, outside our own research group and a few others.

Our research group has been studying the gestural communication of non-human primates for about two decades. We have focused on their natural communication with one another, not with their communication with humans (for

interesting work of this type see Gomez, 1990; Leavens & Hopkins, 1998). The vast majority of our earlier work focused on chimpanzees, one of humans' two closest primate relatives, but more recently we have expanded our work to cover other ape species. In the current paper, we provide a summary of that work — beginning with primate gestural communication in general, based mainly on our extensive work with chimpanzees. We then briefly summarize our more recent work with other ape species. In all of this we focus especially on those aspects that might be of greatest interest to researchers investigating human gestural communication.

Nonhuman primate gestural communication

Nonhuman primates communicate using manual and bodily gestures mainly in relative intimate social contexts such as play, grooming, nursing, and during sexual and agonistic encounters. These are in general less evolutionarily urgent functions than those signaled by acts of vocal communication (e.g., avoiding predators, defending against aggressors, traveling as a group, discovering food), and perhaps as a result primates tend to use their gestures more flexibly than their vocalizations (Tomasello & Zuberbühler, 2002). Thus, unlike the case of vocal signals, there is good evidence that many primate gestures, especially those of the great apes, are individually learned and used quite flexibly. The individuals of some ape species may even on occasion invent new gestural signals (Goodall, 1986; Tomasello et al., 1985), and apes raised by humans sometimes learn some human-like gestures (Tomasello & Camaioni, 1997). However, the gestural communication of nonhuman primates still shows few signs of referentiality or symbolicity, and so the questions arise: What is the nature of non-human primate gestures? How are they learned and used?

Our work over the last 20 years has focused mainly on chimpanzees. Based on a number of lines of evidence, both naturalistic and experimental, it seems clear that chimpanzees most often learn their gestural signals not via imitation but rather via a process of ontogenetic ritualization (Tomasello, 1996). In ontogenetic ritualization two organisms essentially shape one another's behavior in repeated instances of a social interaction. The general form of this type of learning is:

- Individual A performs behavior X;
- Individual B reacts consistently with behavior Y;

- Subsequently B anticipates A's performance of X, on the basis of its initial step, by performing Y; and
- Subsequently, A anticipates B's anticipation and produces the initial step in a ritualized form (waiting for a response) *in order to* elicit Y.

For example, play hitting is an important part of the rough-and-tumble play of chimpanzees, and so many individuals come to use a stylized 'arm-raise' to indicate that they are about to hit the other and thus initiate play (Goodall, 1986). An example from human infants is when they raise their arms to be picked up, which is not learned by imitating other infants but rather is ritualized from the picking up process itself (Lock, 1978). The main point in ritualization is that a behavior that was not at first a communicative signal becomes one by virtue of the anticipations of the interactants over time. There is no evidence that any primate species acquires the majority of its gestural signals by means of imitative learning (Tomasello & Call, 1997), which is normally required for the forming of a true communicative convention — although there may be some exceptions in the case of individual gestures (see below).

In addition, we have also investigated whether chimpanzees, like human infants, use their gestures "intentionally" and flexibly (Piaget, 1952; Bates, 1976; Bruner, 1981). The criterion most often used with human infants concern means-ends dissociation, characterized by the flexible relation of signaling behavior to the recipient and goal, for example, an individual uses a single gesture for several goals (*touch* for nursing and riding) or different gestures for the same goal (*slap ground* and *bodybeat* for play). With regard to such flexibility of use, Tomasello et al. (1994, 1997) found that many chimpanzee gestures were used in multiple contexts, sometimes across widely divergent behavioral domains. Also, sometimes different gestures were used in the same context interchangeably toward the same end — and individuals sometimes performed these in rapid succession in the same context (e.g., initiating play first with a 'poke-at' followed by an 'arm-raise'). In some instances both monkeys and apes have been observed to use some gestures in a way that suggests 'tactical deception', which — regardless of the appropriateness of this appellation — at least indicates that the human observer observed the use of a gesture outside its ordinary context of use (Whiten & Byrne, 1988).

Another important issue concerning flexibility of use its so-called audience effects, that is, differential use of gestures or other communicative signals as a function of the psychological states of the recipient. Tomasello et al. (1994, 1997) found that chimpanzee juveniles only give a visual signal to solicit play (e.g., 'arm-raise') when the recipient is already oriented appropriately, but they

use their most insistent attention-getter, a physical 'poke-at', most often when the recipient is socially engaged with others. Tanner and Byrne (1993) reported that a female gorilla repeatedly used her hands to hide her playface from a potential partner, indicating some flexible control of the otherwise involuntary grimace — as well as a possible understanding of the role of visual attention in the process of gestural communication. In an experimental setting, Call and Tomasello (1994) found that at least some orangutans also were sensitive to the gaze direction of their communicative partner, choosing not to communicate when the partner was not oriented to them. Kummer (1968) reported that before they set off foraging, male hamadryas baboons engage in "notifying behavior" in which they approach another individual and look directly into their face, presumably to make sure that the other is looking before the trek begins. Overall, audience effects are very clear in primate gestural communication, but these all concern whether others can or cannot see the gesture — i.e., are bodily oriented toward the gesturer — not the particular knowledge states of others (as is common in human communication).

Chimpanzees employ basically two types of intentional gesture. First are "incipient actions" that have become ritualized into gestures (see Tinbergen, 1951, on "intention-movements"). For example, as noted above, many juveniles come to use a stylized 'arm-raise' to initiate play, ritualized from actual acts of play hitting in the context of rough-and-tumble play. Many youngsters also ritualize signals for asking their mother to lower her back so they can climb on, for example, a brief touch on the top of the rear end, ritualized from occasions on which they pushed her rear end down mechanically. Infants often do something similar, such as a light touch on the arm (ritualized from actually pulling the arm), to ask their mothers to move it so as to allow nursing. Interestingly, Tanner and Byrne (1996) described a number of gorilla gestures that they interpret as iconic. That is, an adult male gorilla often seemed to indicate to a female playmate iconically, using his arms or whole body, the direction in which he wanted her to move, the location he wanted her to go to, or the action he wanted her to perform. However, these might simply be normal ritualized incipient actions with the iconicity being in the eyes of the human only; in fact, a role for iconicity in gorillas' and other apes' comprehension of gestures has not at this point been demonstrated (Tomasello & Call, 1997).

The second type of intentional gestures are "attractors" (or attention-getters) aimed at getting others to look at the self. For example, a well-known behavior from the wild is the 'leaf-clipping' of adult males, which serves to make a noise that attracts the attention of females to their sexual arousal (Nishida,

1980). Similarly, when youngsters want to initiate play they often attract the attention of a partner to themselves by slapping the ground in front of, poking at, or throwing things at the desired partner (Tomasello, Gust, & Frost, 1989). Because their function is limited to attracting the attention of others, attractors most often attain their specific communicative goal from their combination with seemingly involuntary displays. That is, the specific desire to play or mate is communicated by the ‘play-face’ or penile erection, with the attractor serving only to gain attention to it.

On the surface, attractors would seem to bear some relation to deictics that simply point out things in the environment, and incipient actions would seem at least somewhat similar to lexical symbols that have relatively context-dependent semantic content. But the primate versions are obviously different from the human versions as well, most especially because the primate versions are dyadic and not referential. Attractors are thus really most similar not to deictics, which are referential, but to human attention-getters like “Hey!” that simply serve to make sure that a communicative channel is open, or else emphasizes a gesture. Incipient actions are most similar to certain kinds of ritualized performatives — for example, greetings and some imperatives — that serve to regulate social interactions, not refer to or comment upon anything external. It is also interesting that systematic observations of chimpanzee gesture combinations reveal no evidence of a strategy in which they first use an attractor to make sure the other is looking followed by an incipient action containing specific semantic content (vaguely analogous to topic-comment structure; Liebal, Call, & Tomasello, 2004). One would think that if chimpanzees understood the different communicative functions of these two types of gesture, this kind of combination would be relatively frequent.²

Importantly in the current context, virtually all of the intentional gestures used by chimpanzees share two important characteristics that make them crucially different from human deictic and symbolic gestures. First of all, they are almost invariably used in dyadic contexts (the one major exception is noted below). That is, attractors are used to attract the attention of others to the self, not triadically, to attract the attention of others to some outside entity. Likewise, incipient-movement gestures are used dyadically to request some behavior of another toward the self (e.g., play, grooming, sex), not to request behavior directed to some entity in the external environment. This almost exclusive dyadic use is different from the behavior of human infants who gesture triadically — that is, they gesture for persons to external entities — from their very first attempts at gestural communication before language (Carpenter, Nagell, & Tomasello, 1998).

Second and relatedly, chimpanzee gestures, both attractors and incipient-movements, seem to be used exclusively for imperative purposes to request actions from others. They do not seem to be used declaratively to direct the attention of others to an outside object or event, simply for the sake of sharing interest in it or commenting on it. Most clearly, chimpanzees in their natural habitats have not been observed to draw attention to objects in the typically human ways of pointing to them or holding them up for showing to others (Tomasello & Call, 1994). Again this is as opposed to human infants who produce gestures for both imperative and declarative purposes from early in their communicative development. Overall, the almost exclusive use of dyadic gestures for imperative purposes is consistent with the view that chimpanzees mostly do not use their gestures symbolically, that is, in intersubjective acts of reference.

The one major exception to this pattern of chimpanzee gestures as dyadic and imperative (and mainly produced in close physical proximity) is food-begging, in which youngsters attempt to obtain food from adults. Infants beg for food by a number of related means, some of which do not involve communicative signals, such as: directly grabbing the food, staring at the food or into the eyes of the adult from very close range, sucking on the lower lip of the adult, rubbing the adult's chin as she is chewing the food, and so forth. In addition, however, infants sometimes hold out their hand, palm up, under the mother's chin (see Bard, 1992, for a similar behavior in infant orangutans). This 'palm-up' gesture is clearly triadic — it is a request to another for food — and it is somewhat distal since the signaler is not touching the recipient. It should be noted, however, that food begging happens in very close physical proximity, with much touching, and that the 'palm-up' gesture is likely ritualized from the rubbing of the chin. And it is still an imperative gesture, of course, since the goal of obtaining food is clear. Nevertheless, this 'food-beg' gesture demonstrates that in some circumstances chimpanzees can ritualize some triadic and moderately distal gestures for purposes of obtaining things from others.

Overall, chimpanzee and other primate gestural communication clearly shows more flexibility of use than primate vocal communication, perhaps because it concerns less evolutionarily urgent activities than those associated with vocalizations. Apes in particular create new gestures routinely, and in general use many of their gestures for multiple communicative ends. Audience effects are also integral to ape gestural communication and concern more than simple presence-absence of others — but only in the sense of whether others are in a position to see the gesture. Overall, then, we have much evidence that nonhuman primates use their gestures much more flexibly than their vocal signals.

But we still have very little evidence that they use any of their gestures symbolically or referentially.

A comparison of apes

Most of the general description just given was based on work with chimpanzees, with only a minority of observations from other nonhuman primate species. Recently our research group has focused systematically on the gestural communication of the other three great ape species, along with one species of small ape, respectively: bonobos (*Pan paniscus*; Pika & Tomasello, 2005), gorillas (*Gorilla gorilla*; Pika et al., 2003), orangutans (*Pongo pygmaeus*; Liebal et al., submitted), and siamangs (*Symphalangus syndactylus* — one of approximately a dozen species of gibbon; Liebal et al., 2004). For current purposes, our main question is whether the chimpanzee pattern is also characteristic of these species.

This is certainly not a foregone conclusion as there have been a number of proposals to the effect that the nature of the communication of different species should be a function of (1) the ecology of the species, (2) the social structure of the species, and (3) the cognitive skills of the species. These apes vary from one another greatly in all of these dimensions. For example, in terms of ecology it has been proposed that vocal communication predominates in arboreal species, when visual access to conspecifics is poor, whereas gestural communication predominates in more terrestrial species (Marler, 1965). In the apes, the orangutans and siamangs are almost totally arboreal, bonobos and chimpanzees divide their time between the ground and the trees, and gorillas are mainly terrestrial. In terms of social structure, it has been proposed that species with a more despotic social structure in which the outcome of most social interactions is, in a sense, predetermined should have a smaller repertoire of gestural signals, whereas species with a more egalitarian social structure involving more complex and negotiated social interactions should have a larger repertoire of gestural signals (Maestripieri, 1997). In the apes, gorillas perhaps tend toward the more despotic, whereas bonobos are more egalitarian. In terms of cognitive skills, we really do not have enough information to know if apes differ from one another in ways relevant for communication.

The methods of observation and analysis used in our studies derive ultimately from the series of studies on chimpanzee gestural communication conducted by Tomasello and colleagues over a dozen year period (Tomasello et al.,

1985, 1989, 1994, 1997). We also conducted a follow-up study focused on the issue of gesture combinations (Liebal et al., 2004). The precise methods used evolved during this time period, and so the methods used in the recent studies are based most directly on the two studies from the 1990's and the follow-up study. Of special importance, only the follow-up study used focal animal sampling — observers watch a particular individual for a specific length of time no matter what it is doing — and so only it can be used to estimate absolute frequencies (the earlier studies used scan sampling in which observers simply looked for occurrences of target behaviors from anyone in the group). All of the studies summarized here used either focal animal sampling, or some combination of focal animal and scan sampling (see Call & Tomasello, in preparation, for details). To count in our observations, we had to observe an individual produce the same gesture on more than one occasion. In all five species, individuals from several different captive groups were observed.

Most of our observations and analyses have focused on three major issues. First is the goal-directed or intentional nature of particular gestures, operationalized as flexibility of use. We thus want to know such things as the variability in the gestural repertoires of different individuals, as an indication of the degree to which there is a fixed set in the species. Perhaps of most direct relevance to issues of flexibility, we want to identify gestures that are used by the same individual in multiple behavioral contexts, and also to identify contexts in which the same individual uses multiple gestures.

This second issue is how particular gestures are learned. In the absence of experimental interventions, we will again be interested in individual differences as an indication of whether gestures are learned or not learned — or perhaps even invented, as signals used by only one individual would seem to indicate individual invention. But most directly, we are concerned with whether particular gestures are ontogenetically ritualized in something like the manner outlined above, or whether, alternatively, they are socially learned from others using one or another form of imitation. In general, signals used by all or most members of one group, but not by the members of any other group of the same species, would seem to suggest some of type of social learning or imitation. Conversely, if the variability in individual gestural repertoires within a group is just as large as that between groups of the same species, then it is very unlikely that social learning or imitation is the major learning process — and much more likely that ontogenetic ritualization is what has occurred.

The third issue is adjustments for audience. As noted above, it is fairly common for primate species to produce particular gestural signals only when

certain types of individuals are present — and indeed such audience effects are also characteristic of the vocal signaling of some nonprimate species as well (e.g., domestic chickens; Evans, Evans, & Marler, 1993). But our more specific concern is with the question of whether an individual chooses a particular type of gesture depending on the attentional state of a particular recipient. For example, we are interested in whether individuals use visual gestures only when the potential recipient is visually oriented to them, and whether they use tactile signals preferentially when the potential recipient is not visually oriented to them. Such adjustments would seem to indicate that the signaler knows something about how its signal is being perceived by the recipient.

Repertoire and use

Perhaps the most basic comparative question is the relative sizes of the gesture repertoire of the different species. Our two nearest ape relatives, chimpanzees and bonobos, display between 20 and 30 gesture types across all groups studied, with particular individuals using, on average, about 10 gestures each from the species-wide pool. This pattern also holds for siamangs and indicates relative high individual variability. Gorillas and orangutans are at the high end of this repertoire size across groups (± 30), but individuals in the species are more similar to one another as their individual repertoire sizes are close to 20, roughly double the size of the two *Pan* species.

In terms of flexibility of use, we may look first from the perspective of functional contexts such as play, nursing, travelling, etc. Chimpanzees, bonobos, gorillas, and siamangs use an average of two to three gestures per functional context. Orangutans, on the other hand, use about five different gestures per functional context. Looking from the opposite perspective, we can ask in how many contexts each gesture is used. In this case, chimpanzees, orangutans, and siamangs, used between 1.5 and 2 gestures in more than a single context, whereas the bonobos and gorillas used more like three to four.

Overall, then, in terms of simple repertoire size and flexibility of use, there is variation among our five ape species, but not in any way that maps simply onto the ecology, social structure, or cognition of the different species.

Learning

Following Tomasello et al. (1994), we may compute concordances among the individual repertoires of different individuals of a species. For issues of social

learning, the important comparison is the degree of commonality of the individuals within a single social group versus the degree of commonality of individuals across social groups, who have never been in contact with one another. Using the Kappa statistic, we looked at both within-group and between-group variability across several social groups in each species. Interestingly and importantly, the within-group and between-group variability did not differ significantly in any species — suggesting that social learning, in the form of some kind of group-specific cultural transmission, is not the major learning process at work.

Further support for this view is supplied by the fact that 4 of the 5 species had multiple individuals who used idiosyncratic gestures, presumably not learned from any other individual (the siamangs had no idiosyncratic gestures). Nevertheless, in contrast to the general pattern, there were several gestures used by multiple individuals within a particular group that were not used by the individuals in any other group (again the siamangs had none). These suggest the possibility of some form of social learning or imitation in the genesis of the gesture. For example, we found that three of four bonobos in a small captive group initiated play by somersaulting into one another, whereas no bonobo individuals in the other two groups we observed ever did this (Pika et al., 2005)

It is noteworthy in terms of species differences that the major quantitative difference observed was that the overall concordance rate was lowest among chimpanzees and bonobos, reflecting more individual differences (and so perhaps more learning), and highest among gorillas, reflecting more homogeneity among individuals of the species both within and between groups. This might perhaps be related to the “fission-fusion” social structure of the two *Pan* species, in which individuals separate and reunite with one another regularly, often on a daily basis.

Adjustments for audience

Across species tactile and visual gestures were most common, each comprising from one-third to one-half of the repertoires of each species. The major differences in this regard, was that gorillas used more auditory gestures (close to one-fifth of their repertoire), including the famous chest-beat; chimpanzees used a fair number of auditory gestures (close to one-tenth of their repertoire), including such things as ground-slap; whereas orangutans used no auditory gestures.

All five species used their visually based gestures much more often when the recipient was oriented toward them bodily (80% to 90%) than when its back was turned (10% to 20%). On the other hand, tactile gestures were used somewhat more often (about 60%) when the recipient's back was turned. It is clear that all five species understand something about how the recipient must be situated in order to receive their gesture effectively — perhaps based on understanding of what others can and cannot see (see Call & Tomasello, in preparation). This may suggest that the basic social cognitive skills underlying the gesture use of the five different species are in fact quite similar.

Conclusions

The gestural modality provides a rich source of information about the nature of human and nonhuman primate communication. Many researchers agree that in the vocal modality, humans use linguistic symbols whereas other primate species do not — certainly not in their natural environments. Although there is no widely agreed upon definition of linguistic symbols, at the very least they are intersubjectively shared communicative devices used to direct attention triadically and referentially, sometimes for declarative purposes. This mode of communication clearly depends on a deep understanding of the intentional states of others, and a deep motivation to share intentional states with others as well — which seems to be especially characteristic of the human species (Tomasello et al., 2005).

Interestingly, we can see a very similar contrast across humans and other primates in the gestural modality. Many human deictic and symbolic gestures are also used to intersubjectively direct the attention of others referentially and for declarative purposes. Nonhuman primates do not seem to use gestures in this same way. (Even apes learning language-like signs use them almost exclusively for imperative, not declarative, purposes.) However, because many of their gestures — in contrast to their vocalizations — are clearly learned and used quite flexibly, with adjustments for the attentional state of the recipient, it would seem plausible that the gestural modality of our nearest primate relatives was the modality within which symbolic communication first evolved. The research we have reported here demonstrates interesting variability among closely related ape species in a variety of dimensions, but none of the species seems to be using either gestural or vocal symbols of the human kind — and no species stands out as doing something wildly different from the others, nor

does ecology, social structure or cognition seem to make huge differences. Future research will hopefully discover potential evolutionary mechanisms by which the vocal and gestural signals of apes transformed into the linguistic and gestural symbols of human beings.

Notes

1. Apes raised in contact with humans sometimes learn to point for humans (e.g., Leavens & Hopkins, 1998), but the nature of what they are doing still seems qualitatively different from what human infants do — for example, they only point when they want something (imperatives) not when they just want to share attention (declaratives; see Tomasello & Camaioni, 1997, for a direct comparison).
2. What chimpanzees and other apes seem to do instead is to actively move around in front of the recipient before giving a visual signal (Liebal et al., 2004).

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