

“Hands-on communication”: Use of gestures in apes and humans

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Abstract: This paper presents an overview of gestural communication in apes with focus on flexibility and adjustment of gesture use depending on the behavior of the recipient. The different species vary in the number and types of gestures they produce as a result of varying social structure, ecological conditions and cognitive skills. As opposed to humans, the majority of ape gestures is not characterized by symbolic or conventionalized features; nor are they used in triadic interactions to refer to outside entities. However, since the use of gestures in apes shows a high degree of individual variability and flexibility, which is opposed to their vocalizations, gestural communication of nonhuman primates may shed light onto the evolutionary scenario of human communication, assuming that gestures represent the modality within which symbolic communication may have evolved first.

Key-Words: *Gestural communication, flexibility, referential gestures, pre-linguistic children, apes*

Human communication depends on the use of linguistic symbols. These symbols can be utilized referentially in the sense that they are used to direct the attention of others to particular aspects of the environment. In other words, they can be deployed to direct the attentional and mental states of others to outside entities. The unique symbolic and referential functions of human communication seem to differentiate humans from other animals and are not only found in human speech, but also in human manual gestures (Pika et al., 2005b). For example, humans seem to be the only species pointing to things for declarative purposes representing the basic form of a referential gesture use. Humans also perform a wide range of symbolic gestures, such as *thumbs up*, *waving goodbye* and *"OK"* indicating that speech and gesture represent a multimodal system (Mc Neill, 2000). In contrast to speech, gestural systems can be found in our closest phylogenetic relatives, the nonhuman primates. Careful study of primate gestures might therefore allow a comparative analysis of communication systems in related species, giving insight into their shared and unique features. As a matter of fact, there is an increasing interest in the nature of gestural communication in nonhuman primates. Species investigated include several macaques species (Maestriperi, 1997, 1999), gibbons or small apes (Liebal et al., 2004a), and great apes (Goodall, 1986; de Waal, 1988; Tomasello et al., 1994; Pika et al., 2003, 2005a; Liebal et al., 2006; Tanner & Byrne, 1999). These studies show that nonhuman primates use gestures to achieve a certain social goal within a variety of functional contexts, such as grooming, play, mating and nursing. Gestures such as *leaf clipping* (Nishida, 1980) and the *grooming hand clasp* (McGrew & Tutin, 1978) provide evidence for the existence of population-specific differences in gestural repertoires of wild chimpanzees, and Goodall (1986) described instances of “newly invented” gestures. In addition, great apes are also able to produce and comprehend human gestural or ideographic

'languages' (e.g., Fouts & Budd, 1979; Gardner & Gardner, 1969; Rumbaugh, 1977; Savage-Rumbaugh et al., 1986; Savage-Rumbaugh et al., 1985) if raised in a human environment and after the corresponding intense training.

The questions arising are to what extent the communicative systems of human and nonhuman primates are comparable in regard to the gestural repertoire, its function and its use in social interactions with conspecifics (Liebal et al., 2005), and whether gestural communication of apes may allow insight into the evolutionary roots of human language and proto-linguistic communication systems (Armstrong et al., 1995; Arbib, 2005; Corballis, 2002; Hewes, 1973). The goal of this paper is to present an overview of comparative studies that focus on the gestural communication of captive apes – including siamangs, as a representative of small apes or gibbons, and all four great ape species – followed by a comparison of gestural communication in human and nonhuman primates. Firstly, three studies are summarized, including the comparison of gesture use in different ape species (1.1.), the use of gesture sequences in chimpanzees (1.2.1.), and the adjustment of communicative patterns depending on the behavior of others in great apes (1.2.2.). Secondly, a comparison of gestural communication in nonhuman and human primates, with a focus on the direction and type of gesture use, is provided.

The focus was on intentionally used gestures, which are defined as expressive movements of limbs or head and body postures representing different modalities: Tactile gestures, involving physical contact between the interacting individuals, were distinguished from visual gestures, which were distant signals and represented movements of different body parts or specific body postures not involving body contact. Auditory gestures involved any sound not produced with the vocal cords. Communicative behaviors were considered “intentional gestures” if they served to reach a recurrent social goal; were directed at a particular recipient indicated via body orientation, eye gaze or physical contact with the sender; and expected a response, as evidenced by looking at the recipient, waiting for a response, or persisting in the communicative interaction (Sarimski, 2002). In addition, intentional gestures were characterized by flexibility of use (“means-end dissociation” (Bruner, 1981)) and varied as a function of the recipient’s behavior (“audience effect”. “Means-end dissociation” characterizes the use of a particular gesture in different functional contexts and/or diverse gestures for one functional context. “Audience effects” refer to the sender's sensitivity to the presence/absence of a potential recipient (Tomasello & Call, 1997) and the adjustment of communicative means to the attentional behavior and/or previous interactions with a particular recipient.

The following species comparison includes siamangs (Liebal et al., 2004a), orangutans (Liebal et al., 2006), gorillas (Pika et al., 2003), chimpanzees (Tomasello et al., 1985; Tomasello et al., 1989; Tomasello et al., 1994, Tomasello et al., 1997), and bonobos (Pika et al., 2005a).

1. Gestural communication of apes

1.1. Repertoire and use

A variety of distinct gestures was observed, ranging from 20 gestures in siamangs and bonobos, 29 in orangutans, 30 in chimpanzees to 33 gestures in gorillas. No individual performed the complete gestural repertoire observed in a given species, but the repertoires varied as a function of age, sex and group affiliation. A few gestures such as *pull*, *poke at* and *slap* were common in all apes, whereas other gestures were distinct for a certain species. For example, *throwback head* was a typical visual gesture of siamangs, whereas *chest beat* was

exclusively performed by gorillas. Differences between species were also obvious in the types of gestures used in relation to their degree of terrestriality. Thus, the repertoire of arboreal siamangs and orangutans consisted of a considerable number of tactile gestures, whereas the other, more terrestrial species performed a higher variety of visual gestures. This result is in concordance with a hypothesis stating that given restricted visibility in dense vegetation, arboreal species should use less visual gestures compared to more ground-dwelling, terrestrial species (Maestriperi, 1999; Marler, 1965). However, gorillas were outstanding in regards to the number of auditory gestures they used, which were not observed in siamangs and orangutans.

Social organization also seems to have an impact on the gestural repertoires of the different species. The highest degree of variability between group members was found in chimpanzees whereas the individual repertoires of orangutans showed a slightly lower degree of variability, which was similar to that of bonobos. In contrast, the individual repertoires of siamangs and gorillas were characterized by a higher degree of concordance. Thus, on the one hand, the egalitarian social structure of the siamang family groups lacking a hierarchy and the – although more despotic – cohesiveness of the gorilla social system seem to cause the uniform character of individual repertoires in these species (Pika, 2002). On the other hand, the high degree of variability in the fission–fusion societies of bonobos and chimpanzees (Nishida, 1979; Wrangham & Smuts, 1980; Thompson-Handler et al., 1984; Hohmann & Fruth, 2002) results in a variable and flexibly used communicative repertoire. Similarly, orangutans live in an individual-based fission-fusion system which varies over space and time (van Schaik, 1999) and therefore requires a variable and flexibly used gestural repertoire.

In regard to socio-cognitive skills, all species adjusted to the attentional state of the recipient and used their visually based gestures much more often when the recipient was visually oriented toward them bodily (80% to 90%) than when its back was turned (10% to 20%). On the other hand, tactile gestures were used more frequently (about 60%) when the recipient was not attending.

1.2. Flexibility of use

Intentional communication implies that the sender considers the recipient as a social agent and adjusts its communicative means by augmentation, addition or substitution of the signal until the social goal is obtained (Bard, 1992; Bates et al., 1979). Both the combination of gestures and the adjustment to audience effects therefore characterize the flexible use of gestures. In particular gesture combinations may represent a mean to increase the flexibility of a relatively limited gestural repertoire. Following, two studies, one investigating the task of flexibility in regard to the use of gesture sequences in chimpanzees (Liebal et al., 2004b) and the other investigating the kind of gestures great apes utilize depending on the recipient's attentional state (Liebal et al., 2004c), are presented.

1.2.1. Gesture combinations in chimpanzees

In communicating, the persistence to force a response of the recipient, and the substitution of signals until the sender's social goal is obtained, are both mechanisms underlying intentional communication in humans (Bruner, 1981; Bates et al., 1979; Bard, 1992). Chimpanzees are not only sensitive to audience effects and therefore modify their communicative behavior depending on the recipient's behavior (Povinelli and Theall, 2003), but also use particular gestures to attract the recipient's attention (Leavens et al., 2004; Tomasello et al 1994). Hostetter et al. (2001) found that chimpanzees modify their gestures and vocalizations according to the attentional state of a human experimenter, indicating that chimpanzees can

also distinguish a human's attentional state. When interacting with conspecifics, chimpanzees often attract the attention of others by *slapping the ground* in front of, *poking at*, or *throwing things* at the desired partner when they want to initiate play (Tomasello et al., 1989). In contrast, other gestures communicate more directly what specifically is desired and are more transparent in their meaning. For example, play hitting is an important part of play in chimpanzees, and often a stylized *arm-raise* is used to indicate that they are about to hit the other to initiate play. Because this *arm-raise* signal is ritualized from actual play hitting, its precise meaning is, unlike the case of attention-getters, transparent in context. Gesture sequences provide the opportunity to investigate whether chimpanzees manipulate the attentional state of conspecifics in the sense that they use an attention getting gesture first, before using visual gestures to assure that the recipient will perceive this signal. Gesture sequences are defined as situations in which an individual uses more than one gesture, one after the other, for the same end, during a delimited period of time (Tomasello et al, 1994). Since chimpanzees use gestures of several modalities (visual, auditory, tactile) this provides a number of possibilities of combination and may result in an increase of flexibility in regard to the usage of a limited number of gestures.

About one-third of the gestures observed in one group of captive chimpanzees were part of a gesture sequence. Almost two-thirds comprised two gestures only, which most often represented tactile gestures. Close to 40 % of the gesture sequences were repetitions of the same gesture, and more than half of all sequences occurred in the context of play. No significant differences were found with respect to use of gesture sequences compared to single gestures across the different functional contexts. Gesture sequences were also not utilized to create new meaning, and were not performed in functional contexts other than when performed singly. With respect to the question of how gesture sequences emerge it was obvious that gesture sequences resulted most frequently from situations in which the first element of the sequence failed to get a response. This suggests that chimpanzee gesture sequences may not be premeditated constructions, but rather *post hoc* responses to an unresponsive recipient. This would also explain the high number of repetitions (instead of choosing another more efficient gesture as the second element) even if the recipient was unresponsive to the initial gesture. Although the chimpanzees were sensitive to the attentional state of the recipient and therefore used visually based gestures mostly when others were visually attending, they did not use particular attention-getting gestures to combine with a second visually based gesture first, in case the recipient was not attending. Instead, they used other interesting strategies to make sure that the recipient is attending before the sender started to produce visual gestures. The sender either frontally approached the potential recipient before starting to gesture or walked around a non-attending recipient to position itself into its visual field before producing a visual gesture.

In conclusion, this observational study suggested that when faced with a partner with its back turned, chimpanzees tend to move around to the front of a non-attending partner and then gesture - rather than gesturing once to attract attention and then again to convey a specific intent. Thus, chimpanzees do not seem to use gestures to manipulate the attention of others with respect to the subsequent gesture, but rather use other strategies to make sure that the recipient sees the sender performing visual gestures. These findings suggest that the goal of chimpanzee communicative signals is to manipulate the behavior, and not necessarily the attentional or mental states, of others.

1.2.2. Great apes' adjustment to the attentional states of humans

In contrast to the observational study of gesture use described under 1.2.1., several experiments have shown that not only chimpanzees (Hostetter et al., 2001), but also gorillas

and orangutans (Poss et al., 2006) use particular gestures to attract the attention of a human experimenter, when begging for food. This is strengthened by Leavens et al. (2004), who found that chimpanzees adjust their communicative behavior according to the attentional orientation of a human experimenter. Thus, the behavioral sequences of a chimpanzee to beg for food were unimodal (visual-visual) or bimodal (visual-vocalization), respectively, if the human's attention was directed towards this particular chimpanzee, but changed to auditory-auditory sequences if the human's attention was focused at another chimpanzee in an adjacent cage.

In contrast, Povinelli and Eddy (1996) reported that although chimpanzees gestured preferentially to humans whose body was oriented toward them rather than away from them, in more complex situations chimpanzees did not seem to show sensitivity to the attentional state of the human. Furthermore, Theall and Povinelli (1999) found that although chimpanzees frequently produced attention-getting behavior, they did not use those gestures significantly more often if the human experimenter was not visually attending, since the frequency and temporal patterning of the chimpanzee's communicative behavior was not affected by the degree to which the human was visually attending to them. Theall and Povinelli (1999) concluded, therefore, that chimpanzees' attention getting behaviors are deployed without being mediated by an explicit understanding of the internal attentional state of the recipient, and that their knowledge is largely governed by the general posture of others, in particular the orientation of the face. However, Kaminski et al. (2004) argued that the study of Povinelli and Eddy (1996) confounded two factors: the human's bodily orientation, which indicates her ability to obtain and give the chimpanzee the food, and perceptual orientation, which indicates her ability to perceive the signal. Contrary to the findings of Theall and Povinelli (1999), the results of this experiment showed that orangutans, chimpanzees and bonobos were sensitive to the body and face orientation of the experimenter separately. Specifically, apes gestured more to the human when her face was oriented toward them than when it was oriented away, but only if her body was in a position to deliver the food. Kaminski et al. (2004) therefore concluded that body and face orientation signal two different types of information: face orientation indicates the human's perceptual access to the signal, whereas body orientation indicates the human's ability and disposition to provide food.

To summarize, although apes in these studies were sensitive to the attentional state of humans and deployed their gestures accordingly, the conclusions differ in regard to whether chimpanzees and other great apes use particular attention-getting behaviors to attract somebody's attention. However, as pointed out in 1.2.1, chimpanzees tended to move into the attentional field of the recipient, e.g. by walking in front of it, and then performed visual gestures there, rather than manipulating its attentional state. As opposed to this more natural situation, the apes tested under experimental conditions did not have the choice of altering their position in relation to the bodily orientation of the human experimenter. Therefore, Liebal et al. (2004c) presented a situation in which great apes could beg for food from a non-attending human; but unlike in previous studies, they were given the option to either move in front of the experimenter to gesture there, or to attract her attention by using auditory or tactile gestures behind her. All four great ape species (chimpanzees, bonobos, gorillas, orangutans) were tested under identical conditions to investigate, whether the strategies of chimpanzees described under 1.2.1. could be reproduced under experimental conditions.

The results showed that when she has her back turned to them the four nonhuman great ape species walked around a human experimenter to produce begging gestures in front of her, rather than calling attention behind her to make her turn around and then beg for food. All species gestured less and left the testing area more often in case the food was located at a

different location than the human. This result indicates that apes are less likely to beg for food if the human is not in a position to give it to them, confirming the findings of Kaminski et al. (2004). However, despite the overall similarities among species, an intriguing difference among genera emerged in the conditions in which the experimenter moved to an alternative location and left the food behind her. Chimpanzees and bonobos differed from gorillas and orangutans in both their movement patterns and the deployment of their visual signals. Chimpanzees and bonobos moved more often when the experimenter changed location (and the food remained in the same place) compared to when the food changed location (and the experimenter remained in the same place). This seems to indicate a special sensitivity for directing visual signals to a human with the appropriate body orientation. This is particularly remarkable because they had to leave the place where the food was and move to the location where the human (without food) was sitting. In contrast, gorillas and orangutans did not move differentially across these two conditions.

In regard to gesture use, chimpanzees and bonobos preferentially used visual gestures in front of the experimenter in all conditions, whereas orangutans and, especially gorillas, failed to do this in the condition in which the human turned around leaving the food next to the subject. This finding seems to indicate a greater sensitivity of the members of the genus *Pan* (chimpanzees and bonobos) to the orientation of humans when deploying visual gestures compared to the other two great ape genera. It may show that *Pan* has refined its social cognitive abilities after the split of the common ancestor between *Pan* and *Gorilla* indicating a possible difference in social cognition among the great apes.

2. Comparison of gestural communication of apes and humans

The comparison presented here mainly focuses on the use of gestures in apes as opposed to gestural communication of pre-linguistic children. Speech-accompanying gestures are therefore not included here. Gestures of children are generally differentiated in regard to the direction and type of gesture used (Bates, 1976). The direction of gestures includes both dyadic and triadic interactions. Dyadic gestures are exchanged between two individuals and serve to attract the recipient's attention towards the acting individual. Triadic gestures incorporate an external object or event into the interaction of two individuals and are used to attract the attention of the partner to this outside entity (Pika, in press). Therefore, triadic gestures function referentially. Since the recipient must infer the signaler's meaning, the use of these gestures has been linked with cognitive capacities such as mental state attribution (Camaioni, 1993; Tomasello, 1995) which appears in human children at the age of 12 months. The type of gesture includes both imperative and declarative gestures. Imperative gestures are used to get another individual to help in attaining a goal (Bates, 1976), whereas declarative gestures are used to draw another's attention to an outside entity to share attention (Bates, 1976). Therefore, declarative gestures are triadic and function referentially.

As opposed to gestures of pre-linguistic human children, the majority of gestures used in interactions between great apes can be defined as dyadic. Thus, a sender directs a certain gesture, such as *poke at*, *arm raise* or *lip touch*, towards a particular recipient. The meaning of the gesture is often defined by the context in which this interaction occurs. For example, *presenting the anogenital region* of siamangs is usually used in sexual context to initiate mating, but it can also be deployed as a reassurance gesture in case of an agonistic encounter between two individuals (Liebal et al., 2004a). Gestures can also include the use of objects, such as *hitting with sticks*, *waving branches*, or *throwing stones*. However, they are not used to attract the recipient's attention towards this object, but are merely incorporated as tools into

the execution of a certain gesture. One of the few exceptions are gestures such as *food-begging*, (an animal holds out the hand, palm up to obtain food from another, see for orangutans, Bard, 1992; see for chimpanzee Tomasello et al., 1994), *offer arm with food pieces* (an animal offers food placed on her arm to another one, Liebal et al., 2006) or *present object* (an animal holds an object in front of another animal, Liebal et al., 2006). Since the execution of these gestures incorporates an object (food) or body part (hand) towards which the attention of the recipient is attracted, these gestures can be considered triadic (Pika, in press). Another triadic gesture, which has been reported for captive chimpanzees when interacting with human experimenters, is *pointing* (e.g., Leavens & Hopkins, 1998; Leavens et al., 2004; for human-raised and language trained apes e.g., Gardner and Gardner, 1969; Miles, 1990; Patterson, 1978a). For wild apes, there is only one study describing the use of pointing in one bonobo (Vea and Sabater-Pi, 1998). Thus, it is not clear yet whether pointing of captive apes is part of their natural communication abilities or whether it is a byproduct of living in a human encultured environment (Tomasello and Call, 1997). It is argued that the occurrence of pointing in captive apes is attributable to environmental influences on their communicative development, since both captive and wild chimpanzees share the same gene pool and therefore both should deploy this behavior (Leavens et al., 2005). This is supported by the fact that pointing in humans can also vary between different cultures and does not only include index finger pointing, but also other variations of pointing involving other body parts, such as lip pointing (Kita, 2003; Enfield, 2001). Leavens et al. (2005) therefore conclude that the variability of pointing in both apes and humans may be explained by their different rearing or cultural environments.

Concerning the type of gestures, the majority of gestures used in natural communication between apes are imperative gestures. There are reports about '*showing*' in one gorilla and one bonobo, but these observations refer to language-trained individuals (Patterson, 1978b; Savage-Rumbaugh, 1988; Savage-Rumbaugh et al., 1985). A "sub-type" of referential gestures are iconic gestures, which relate to their referent by some actual physical resemblance such as a desired motion in space or the form of an action (Bates et al., 1979), which have been reported from one gorilla and one bonobo. Thus, they seemed to signal to a playmate with their hand, arm, or head the direction in which they wanted her to move, the action they wanted her to perform, or the position they wanted her to take (Savage and Bakeman, 1978; Savage-Rumbaugh et al., 1977; Tanner and Byrne, 1996). These instances of iconic gestures are rare, and similar gestures were not observed in other studies focusing on gestural communication in gorillas and bonobos (Pika et al., 2003, 2005a). Interestingly, a recent study reports the use of a gesture in wild chimpanzees considered as referential and iconic gesture (Pika and Mitani, 2006). The '*directed scratch*' involves one chimpanzee making a loud, exaggerated scratching movement on a part of his body directed towards his grooming partner. Since in most of the observed instances the indicated spot was groomed directly by the recipient, it seems that the gesture may be used referentially in a sense that it refers to a precise spot on the chimpanzees' body, and iconically since it depicts a desired future action (grooming).

In conclusion, apes use their gestures flexibly across a number of different functional contexts and adjust their gestures depending on the recipient's behavior. These features are characteristics of intentional communication comprising the sender's adjustment of communicative means by augmentation, addition or substitution of the signal until the social goal is obtained (Bates et al., 1979). Although apes seem to have the cognitive potential to use referential gestures on a regular basis when interacting with humans (e.g., Leavens et al., 2005), the majority of their gestures performed in interactions with conspecifics is used dyadically for imperative purposes. Thus, the important difference between gestures of apes

and human children seems to become obvious in the type of gestures used: Apes mainly use their gestures imperatively, whereas human children gesture for declarative purposes as well as to direct the attention of others to an outside object or event (Bates et al., 1975; Liszkowski et al., 2004). The communication about outside entities might have triggered the use of linguistic symbols by humans and therefore might represent a crucial difference between the communication of apes and humans (Pika, in press), which is possibly linked with the cognitive ability to understand other persons as intentional agents with whom they may share experience (Tomasello et al., 2005).

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