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Simone Pika

First Language 2008 28: 116

DOI: 10.1177/0142723707080966

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Gestures of apes and pre-linguistic human children: Similar or different?

Simone Pika, *University of Manchester*

ABSTRACT

The majority of studies on animal communication provide evidence that gestural signalling plays an important role in the communication of non-human primates and resembles that of pre-linguistic and just-linguistic human infants in some important ways. However, ape gestures also differ from the gestures of human infants in some important ways, and these differences might provide crucial clues for answering the question of how human language – at least in its cognitive and social-cognitive aspects – evolved from the gestural communication of our ape-like ancestors. This article provides an overview on the gestural signalling of monkeys and apes to enable a comparison with gestures in pre- or just-linguistic children. Implications for the evolution of language are discussed.

KEYWORDS

Apes; development; evolution of language; gestures; human children; learning

Language in humans (*Homo sapiens*) is traditionally described as communication by word of mouth. One of the puzzling questions about language is how it came to be the province of the oral modality, and recent genetic evidence has suggested that our hominid ancestors probably lacked some of the key capacities for normal speech production, perhaps until as little as 200,000 years ago (Enard et al., 2002). These findings indicate that many of the cognitive building blocks required for language processing must be substantially older, having evolved in the primate

lineage long before the advent of speech in modern humans. One important approach is therefore the comparative approach, which, with regard to language evolution, pinpoints similarities and differences between human language and the communication systems evolved in our closest living relatives, the nonhuman-primates (hereafter primates) (e.g., Hauser & Konishi, 1999; Snowdon, Brown & Petersen, 1982).

The primate lineage or the order primates consists of prosimians, monkeys, apes and humans. Humans, together with the five great ape species – chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*), gibbons (genus *Hylobates*), gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus*) – belong to the superfamily *Hominoidea* (following the taxonomy of Fleagle, 1999). Humans are most closely related to bonobos and chimpanzees, with whom they share around 95% of the same DNA (Britten, 2002). The Hominoids split off from the other primates (Old World monkeys, New World monkeys, and prosimians) an estimated 23 million years ago, and the human/chimpanzee divergence occurred approximately 5 million years ago (Kumar, Filipski, Swarna, Walker & Hedges, 2006).

Studies on the communicative skills of primates have mainly focused on vocalizations (e.g., Marler, 1977; Seyfarth, 1987; Snowdon, 1988; Zuberbühler, 2003). In the 1960s Struhsaker (1967) made the discovery that vervet monkeys (*Cercopithecus aethiops*) utter different, distinct alarm calls in response to different predators. The additional finding that vervet monkeys also use the information encoded for different escape responses, such as hiding in bushes and climbing a tree (Seyfarth, Cheney & Marler, 1980), raised the possibility that some primates, like humans, also use vocalizations to make reference to outside entities (Cheney & Seyfarth, 1990).

Referential signals have been reported from various monkey species in their natural habitats (e.g., Zuberbühler, 2000). But it has been found that alarm calls of this type are a common phenomenon in species that must also organize different escape responses for different predators, for instance prairie dogs and domestic chickens (for an overview, see Owings & Morton, 1998). Importantly, there is currently no evidence that any species of ape has developed such referent specific alarm calls. In addition, studies focusing on the referential use of other vocalizations of apes, e.g., long-distance calls, provided mixed results (e.g., Clark & Wrangham, 1993, 1994; Crockford & Boesch, 2003; Marler & Hobbett, 1975; Mitani & Brandt, 1994; Mitani, Hasegawa, Gros-Louis, Marler & Byrne, 1992; Slocombe & Zuberbühler, 2005). Furthermore, the majority of studies on primate vocalizations revealed that call morphology and call usage seem to have only limited flexibility (Corballis, 2002; Liebermann, 1998). Recent data on some primate species in their natural habitats have provided evidence for audience effects of vocalizations (Caine, Addington & Windfelder, 1995; Cheney & Seyfarth, 1985; Mitani & Nishida, 1993), categorical perception of vocalizations (Masataka, 1983), acoustic 'rules' regulating vocal exchange (Sugiura, 1993), flexibility of vocal production (Sugiura, 1998), the ability to combine calls into higher-order sequences that have a particular meaning (Arnold & Zuberbühler, 2006) and vocal learning (Crockford, Herbinger, Vigilant & Boesch, 2004; Mitani et al., 1992), but the comparative approach has not proved very successful. It mainly revealed that the two sorts of communication are so different that a comparison between them provides little insight about their common ancestry.

In addition to the acoustic modality, however, human speech embodies another means of communication: movements of the arms and hands, termed gestures (McNeill, 1985). The study of gestures has received tremendous research attention in recent years (e.g., Goldin-Meadow & Mylander, 1998; Iverson & Goldin-Meadow, 1998; Kendon, 1975; McNeill, 1992; Morris, Collett, Marsh & O'Shaughnessy, 1979; Pika, Nicoladis & Marentette, 2006), which might be partly due to the fact that many evolutionary stories involve an initial stage in which language was carried out in gesture (Arbib, 2002; Armstrong, Stokoe & Wilcox, 1995; Condillac, 1971; Corballis, 2002; Hewes, 1973; Hockett, 1978). In addition, it is thought that gestures form a single, integrated system with speech (McNeill, 1985), and can provide insight into an individual's mental representations and cognitive skills (e.g., Goldin-Meadow, Nusbaum, Kelly & Wagner, 2001; Iverson & Goldin-Meadow, 1998; McNeill, 1992; Nicoladis, Mayberry & Genesee, 1999). Moreover, within deaf cultures where the oral modality is not accessible, full-fledged sign languages have evolved in the manual modality and function without any use of speech at all (Klima & Bellugi, 1979). Interestingly, to some extent human-reared great apes are able to master gestural or ideographic communication systems (e.g., Gardner, Gardner & Van Cantford, 1989; Savage-Rumbaugh, Murphy, Sevcic, Brakke, Williams & Rumbaugh, 1993). Though by no means 'language', these projects provided evidence for the intentional, referential use of numerous gestures and ideograms (Savage-Rumbaugh, McDonald, Sevcic, Hopkins & Rupert, 1986), as well as understanding of human speech (Gardner et al., 1989; Savage-Rumbaugh et al., 1993). Great apes, therefore, seem to be able to use crucial aspects of language, given that the vocal-auditory channel can be by-passed.

In addition, primates also routinely use gestures in their natural communication, and the present article aims to provide an overview of the state of the art, beginning with primate gestural communication in general. In 1935 Ladygina-Kohts published a detailed comparison of the expressive behavior of a juvenile chimpanzee and of her own child, followed by modern ethological analyses of primate facial and gestural communication in the 1960s (e.g., Van Hooff 1967; Van Lawick-Goodall, 1968). Two decades later Tomasello and colleagues (e.g., 1985, 1994, 1997a, 1997b) introduced a new approach, which was inspired by the study of gestural communication in human children and focused on the underlying processes of social cognition, including learning mechanisms and flexibility of gesture. The majority of the resulting studies investigated common chimpanzees (*Pan troglodytes*), but more recently the work was expanded to cover other ape species (e.g., Liebal, Call & Tomasello, 2004b; Liebal, Pika & Tomasello, 2006; Pika, Liebal, Call & Tomasello, 2005a; Pika, Liebal & Tomasello, 2003, 2005b).¹ I will therefore focus mainly on these and related studies by addressing the following aspects:

- gestural repertoire;
- the development of gestures;
- the learning of gestures;
- the referential use of gestures;
- similarities and differences between the gestures of apes and pre- or just-linguistic human infants.

I will concentrate on studies that might be of most interest to researchers investigating human gestural communication.

PRIMATE GESTURAL COMMUNICATION

To date, studies investigating the gestural communication of primates are very unevenly distributed among species (for an overview, see Tomasello & Call, 2007) and concern mainly apes. There are only a few reports on the use of gestures in monkeys.

Monkeys

Kummer (1968) described *notifying behavior* in Hamadryas baboons (*Papio hamadryas*). This behaviour consists of approaching another animal and looking directly into her face and occurs mainly when an individual leaves others in a troop. One possible explanation of this behaviour is that the signaller wants to make sure that the recipient is attending before engaging in certain activities. In addition, Kummer & Kurt (1965) described an auditory² gesture, the so called *ground-slap* that seems to serve as an attention-getter and a kind of teasing behaviour during play. Furthermore, Maestriperi (1997, 1999, 2005) provided a very detailed insight in the gestural behaviour of macaques, focusing on three different species in captivity (*Macaca arctoides*, *M. nemestrina*, *M. mulatta*). His data showed that rhesus macaques (*M. mulatta*) have a relatively limited gestural repertoire, pigtail macaques (*M. nemestrina*) possess conspicuous signals of affiliation and bonding, and stump-tail macaques (*M. arctoides*) have the richest repertoire of assertive and submissive signals. Most similarities among species were found in signals of dominance and submission, and most differences in affiliative gestures and bonding patterns. These results therefore indicate that characteristics of a social structure, such as reduced influence of dominance and kinship, may select along with group size for a wider gestural repertoire in a given species. In addition, Maestriperi (1996) observed a very interesting behaviour between pigtail macaque mothers and their infants: when the infant does not want to follow the mother, the mother sometimes returns and stares in the infant's face (or even pokes the infant).

Apes

The gestural communication of apes has received much more research attention, with the majority of studies focusing on common chimpanzees. Following an ethological approach, Van Lawick-Goodall (1968) and Van Hoof (1973) published the first chimpanzee behavioural repertoires (so-called ethograms). These also included detailed descriptions of communicative and non-communicative behaviours and therefore also many of the communicative gestures that have been observed in later studies in the wild and in captivity. Nishida, Kano, Goodall, McGrew & Nakamura (1999) published the most complete chimpanzee ethogram to date, which includes a comparison with previous ethograms, particularly those developed by Goodall (1986a, 1986b; Van Lawick-Goodall, 1968). In addition, it also includes a comparison with the behaviour of the closest related congener of the chimpanzee, the bonobo (*Pan paniscus*). Various communicative behaviours of bonobos are mentioned in studies on wild populations at Lomako and Wamba in the Democratic

Republic of Congo (e.g., Badrian & Badrian, 1984; Ingmanson, 1996; Kano, 1980; Kuroda, 1980, 1984), but only researchers studying captive individuals addressed the use of gestures in more detail (Savage-Rumbaugh & Wilkerson, 1978; Savage-Rumbaugh, Wilkerson & Bakeman, 1977). Savage-Rumbaugh and colleagues, for instance, described the use of 20 different gestures in the sexual context, and de Waal (1988) provided a comparison of the gestural signalling of bonobos and chimpanzees. Like many of its predecessors, this comparison had its roots in the ethological tradition of cataloguing the different units of behaviour into comprehensive repertoires.

The first ethograms of the behaviour of mountain gorillas were also conducted in the second half of the last century (Fossey, 1974; Schaller, 1963, 1965). They contained mainly communicative signals, such as species-typical displays (Fossey, 1974; Schaller, 1963, 1965). In their compilation of gorilla ethograms, Ogden & Schildkraut (1991) mentioned a variety of auditory, tactile and visual gestures, and Parnell & Buchanan-Smith (2001) described a specific gesture, the *splash display*, for wild western lowland gorillas to intimidate other silverbacks. Fay (1989) observed *hand-clapping* behaviour in gorilla females, but the most detailed overview of gestures in captive gorillas was provided by Tanner & Byrne (1996, 1999). In addition, Tanner (2004) also described gesture-phrases and sequences between two individuals in captivity.

In contrast to the African great ape species, substantially less is known about the gestural communication of the Asian apes. MacKinnon (1974; but see also, Rijksen, 1978) provided a repertoire of tactile and visual gestures of wild Bornean (*Pongo pygmaeus*) and Sumatran orangutans (*P. abelii*). Chivers (1974), Ellefson (1967, 1974) and Palombit (1992) compared the communicative behavior of wild siamangs (*Symphalangus syndactylus*) and white-handed gibbons (*Hylobates lar*). In addition, Fox (1977) and Orgeldinger (1999) reported a number of different tactile and visual gestures³ in captive siamangs and concluded that the siamang's repertoire is generally limited in comparison to that of great apes.

GESTURAL REPERTOIRES

Gestures can be organized as a function of their main sensory modalities: auditory, tactile and visual. Auditory gestures rely mainly on sound production (although they also have an important visual component), tactile gestures depend mainly on establishing physical contact with the recipient, and visual gestures rely solely on visual information.

Bonobos

Pika and colleagues (Pika, 2007a; Pika et al., 2005b) studied the communicative behaviour of subadult bonobos ($N = 7$) in two different groups in two zoos in Europe and found that they used 20 different distinct gestures (see Fig. 1). Visual gestures represented the most common sensory modality in bonobos (11 visual, 1 auditory, 8 tactile).

Chimpanzees

Tomasello and colleagues (1985, 1989, 1994, 1997b) studied two groups of captive chimpanzees at the Yerkes Primate Research Center, Atlanta (USA) and found that subadult individuals used between 25 and 30 gestures depending on the study period (see also Liebal et al., 2004a). Combining all gestures from all studies produced a total of 38 gestures (20 visual, 4 auditory, 14 tactile; see Fig. 1).

Gorillas

Pika and colleagues (Pika, 2007b; Pika et al., 2003) described the use of 33 different distinct gestures (16 visual, 6 auditory, 11 tactile) used by subadult gorillas ($N = 13$) living in two groups in two different zoos in Europe (see Fig. 1).

Orangutans

Liebal and colleagues (Liebal, 2007a; Liebal et al., 2006) focused on the performance of gestures in two orangutan groups in two different zoos in Europe and found that subadults ($N = 7$) used 26 different distinct gestures, with visual gestures being the most common sensual modality (12 tactile, 14 visual; see Fig. 1).

Siamangs

Liebal and colleagues (Liebal, 2007b; Liebal et al., 2004b) investigated the use of gestures in three family groups of siamangs in two different zoos in Europe and reported that subadult siamangs ($N = 7$) use a gestural repertoire of 17 different distinct gestures, consisting only of tactile (10) and visual (7) signals; see Fig. 1).

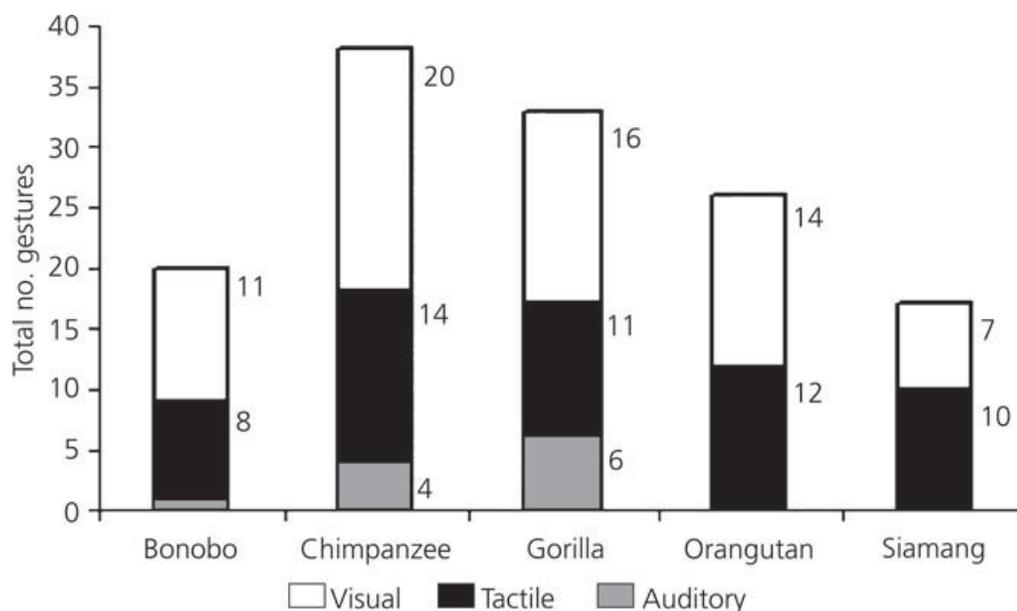


Figure 1 Total number of gestures used by different apes, divided into the three main signal categories

DEVELOPMENT OF GESTURES

To investigate the development of communicatory signals in apes and to decide whether they qualify as intentional acts, researchers have used the developmental Piagetian and the preverbal communication perspective. Plooiij (1978, 1979) was the first researcher to study the ontogeny of communicatory signals in chimpanzees in the wild, using Speech Acts Theory (see Austin, 1962; Bates, Camaioni & Volterra, 1975). He observed mother-infant dyads of chimpanzees in Gombe, Tanzania, and argued that, although the mother begins interpreting the baby's behaviour at birth, the neonatal chimpanzee does not perform any acts with a social-communicatory intention. At the age of 3–11 months, the chimpanzee infant starts to contribute to interactions with its mother by responding appropriately to her behaviours. However, only between the age of 9 and 12½ months does the chimpanzee infant start to initiate interactions with its mother by intentionally directing signals to her, e.g., by using gestures, such as *initiating tickling*, *grooming* and *approach*. In addition, only at this age does the chimpanzee infant start to understand its mother and conspecifics as social agents. This developmental stage therefore marks the onset of the use of protoimperative or imperative gestures (Bates et al., 1975; see definition on p. 126) and the developmental shift from perlocutionary to illocutionary acts. In perlocutionary acts the communication occurs only because the receiver is adept at interpreting the behaviour of the signaller, while in illocutionary acts the signaller directs its behaviour toward a recipient (Bates et al., 1975).

Tomasello et al. (1997b) investigated the development of the gestural repertoire in chimpanzees in captivity and found that the overall repertoire of one-year-old chimpanzees consisted of 12 different gestures and reached a peak of 19 gestures at 3 years of age. From this point on, the number of gestures remained stable, and some gestures were replaced by others, e.g., gestures for nursing disappeared, while gestures used for agonistic and sexual purposes became more prominent. Concerning gesture sequences of chimpanzees, Liebal et al. (2004a) showed that the length of the sequences decreased with age, with adults producing the shortest sequences and juveniles the longest sequences.

Focusing on the development of gestures in gorillas, Pika et al. (2003) found an increase in the mean number of gestures from 18.5 at the age of 3 to 24 at 4, whereas the number of gestures decreased to 20.6 gestures at the age of 5–6. This difference was not significant and Pika and colleagues argued that, due to the shortest infancy and juvenile stages of all apes (Bogin, 1999), gorillas develop certain aspects of physical maturity and intellectual development at a younger age (e.g., Antinucci, 1990; Parker, Mitchell & Lyn Miles, 1999; Redshaw, 1978; Spinozzi & Natale, 1989).

Bard (1992) studied the communicative abilities of orangutan infants in the food-sharing context, focusing on a different aspect of development: the transition from bifocal behaviour to behavioural sequences. Bard (1992) distinguished between 'intentional behaviour' (bifocal behavioural sequences involving either objects or social agents; Case, 1985) and 'intentional communication' (behavioural sequences involving coordination between social agents and objects; e.g., Bretherton, McNew & Beeghly-Smith, 1981). She showed that orangutans at the

age of 1–6 months used intentional behaviours, whereas intentional communication was observed in older orangutans only, ranging from 2½ to 5 years of age. In intentional behaviour, individuals directed their action to the food, for instance, with a *grasp* coordinated with eating, or they directed their behaviour to the mother, for instance, by performing a *pull* on the mother's body and subsequently eating. In intentional communication, on the other hand, individuals solicited food from the mother by using one open, cupped hand, palm up, held underneath, but not necessarily touching, the mother's chin. In addition, Liebal (2007a) showed that the median number of gestures increased from 9 to 17 in one infant orangutan and from 9 to 16 in juvenile and subadult orangutans, and decreased in adults to 12 gestures.

Investigating the development of gestures in siamangs, Liebal et al. (2004b) reported that the gestural repertoire of siamang infants consisted of 8.5 gestures and reached a peak at the age of 4–5 years (11 gestures). From this point on, the number of gestures also seemed to remain quite stable, and some gestures were replaced by others.

LEARNING OF GESTURES

Focusing on learning processes, scientists distinguish between social and individual learning. Social learning can be defined as 'a group of learning mechanisms in which observation of other individuals facilitates or enables the acquisition of a novel behavior' (Call, 1999: 317). Researchers tend to discriminate at least four main phenomena: social facilitation, local and stimulus enhancement, emulation, and imitation (for an overview see, e.g., Heyes, 1994; Whiten & Ham, 1992; Zentall, 2001). In contrast, in 'individual learning' two or more individuals independently acquire the same behaviour through encountering and being shaped by similar learning environments (Whiten & Ham, 1992).

Observations of wild chimpanzee populations provide evidence for the existence of cultural variation among chimpanzee communities or unit-groups (Whiten et al., 2001). Nishida (1980), for instance, reported the use of the gesture *leaf clipping* in the Mahale K group, in Tanzania. In this gesture an individual takes 1–5 very stiff, dried leaves and strips them in its mouth, making a distinctive and fairly loud noise. The gesture was used in the sexual context, during play or frustration and was later also recorded in the chimpanzee community of Bossou, Guinea (Sugiyama, 1981), and in the chimpanzee community of Tai, Ivory Coast (Boesch, 1995). Interestingly, the individuals at Bossou use it mainly in the context of frustration or during play, whereas the males at Tai use it mainly as part of a drumming display. Another group-specific gesture used by chimpanzees in the wild is the *grooming hand clasp*. In this gesture two chimpanzees clasp both their right or both their left hands overhead, while parallel grooming each other with the other hand (McGrew & Tutin, 1978). This gesture has been observed at the study sites Tai, Ivory Coast, Lopé in Gabon, Mahale in Tanzania, and Kibale in Uganda (for an overview, see Whiten et al., 2001), and also recently in bonobos at the study site Lui Kotal, DRC (Fruth et al., 2006).

In both these cases, social learning is likely to be involved – for instance, by local enhancement as individuals watch others groom under the armpits of receivers or

watch others clip leaves and receive attention. Further evidence for the possibility of some form of social learning or imitation in the genesis of gestures has been provided by studies on captive apes (e.g., Pika et al., 2005b). Focusing on gorillas, Pika et al. (2003) described the use of the gestures *armshake* and *chuck-up*, which were used by multiple individuals within a particular group but were not used by the individuals in any other group.

Tomasello et al. (1994), studying the acquisition of gestures in chimpanzees in captivity, found no evidence for a social learning process. They suggested that the main learning process involved in the acquisition of gestures is an individual learning process called 'ontogenetic ritualization'. In ontogenetic ritualization, a communicatory signal is created by two individuals shaping each others' behaviour in repeated instances of an interaction (Tomasello & Call, 1997).

The general form of this type of learning is:

- individual A performs behaviour X;
- individual B reacts consistently with behaviour 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.

This means that a behaviour which was not at first a communicative signal becomes one by virtue of the anticipations of the interactants over time (Tomasello & Call, 1997). For example, *touching* is an important part of mother-infant interactions in gorillas to request drinking, and many individuals come to use a stylized *reach-arm* to indicate that they are about to touch the mother and drink (Pika et al., 2003). In orangutans, infants suck on the mother's lips while she is eating to obtain food pieces from her (Bard, 1990). Not until later, at an age of about 2.5 years (Bard, 1990), do they start to produce gestures, such as approaching the mother's face to beg for food without actually touching her mouth (Liebal et al., 2006).

Another important comparison for understanding the processes involved in learning is the degree of commonality of the individuals within a single social group and between social groups, who have never been in contact with one another. High levels of concordance of gestural repertoires within a group and group-specific gestures would provide evidence for the existence of a social learning process, whereas individual differences that overshadow group differences (i.e., a lack of systematic group differences, idiosyncratic gestures) imply that an individual learning process is mainly involved. To assess the degree of commonality in the performance of gestures between and within groups of apes, Pika et al. (2005a) used Cohen's Kappa statistics, with an individual either agreeing or disagreeing on the performance of each gesture as compared with each other individual (cf. Tomasello et al., 1997b). Interestingly, the within-group and between-group variability of all five ape species 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 was provided by the fact that all great ape groups had multiple individuals who used idiosyncratic gestures – used by single individuals only – presumably not learned from any other individual (but the

siamangs had no idiosyncratic gestures). These gestures involved recurrent events in the ape's life (e.g., food, play), they were accompanied by the signaller's expectation to receive a response (indicated by response waiting), and they most often received a response in the form of an action or a responding gesture. These results imply that the idiosyncratic gestures resembled a relatively stable part of a particular youngster's gestural repertoire and were understood by receivers (Pika et al., 2003; Pika et al., 2005a).

Furthermore, great apes seem to be able to copy gestures based on facilitation of pre-existing repertoire (Byrne & Tanner, 2006). The first report stems from an experiment with a single home-reared chimpanzee (Hayes & Hayes, 1952), using a so-called 'do-as-I-do' design: the individual is first trained to copy gestures that are demonstrated to her by the experimenter; then 'arbitrary gestures', not previously demonstrated, are introduced as a test of the ability to imitate. Custance et al. (1995) replicated the experiments with two nursery-reared chimpanzees and confirmed the basic phenomenon. In the report of Hayes & Hayes (1952), sparse documentation of the results had made interpretation problematic, but Custance et al. (1995) asked two independent, naïve observers to judge after each demonstration which of 48 possible actions the behaviour of the chimpanzee most resembled. They found significant matching, although the chimpanzees' copy was often imperfect. In addition, the same set of stimuli were used with another ape species, a language-trained orangutan (Miles, 1986). The orangutan received spoken commands in English and showed detectable but imperfect copying (Call, 2001). More recently, Byrne & Tanner (2006) reported a version of the do-as-I-do procedure with a nursery-reared gorilla. However, whereas previous experiments used reinforcement techniques to teach the procedure to the apes, the gorilla was not rewarded and copied the gestures spontaneously. This gorilla's gestural performance was very similar to that of the other great apes. However, note that none of the apes was raised by its natural mother, suggesting that a high orientation of behaviour towards humans may be essential to elicit this ability (Byrne & Tanner, 2006).

Overall, the reviewed data therefore suggest that individual learning is the main learning process involved in the acquisition of gestures. But the possibility of some form of social learning in the genesis of special gestures cannot be denied.

REFERENTIAL USE OF GESTURES

So far we have looked at gestures in terms of gestural repertoires, development, commonalities and individual differences. One other important question is whether apes use gestures referentially, i.e., that they use them to attract the attention of others to some outside entity, for example, an event or an object. This aspect is of special importance because the recipient must infer the signaller's intended meaning, which might indicate some important skills in the ability to share attention with others (Camaioni, 1993; Tomasello, 1995).

Referential gestures are always triadic, because they include a signaller, a recipient and a third entity or event. Although this 'third entity' mainly denotes an

outside entity (Bates, 1976), it can also include an inside entity, e.g., referring to one's own nose. In addition, Bates et al. (1975) differentiated between protoimperative and protodeclaratives. Protoimperatives are defined as the child's preverbal intentional use of the listener as an agent or tool in achieving some end (e.g., to request an object). Protodeclaratives are defined as the child's preverbal effort to direct the adult's attention to some event or object in the world. This approach suggests continuity between preverbal and later verbal communication and is useful when focusing on human children whose gestures precede speech (Bates et al., 1979). However, it is not coherent to use the term 'proto-' imperatives or declaratives in species who will never exhibit symbolic communication (Leavens, 2004; Leavens & Hopkins, 1998). I will therefore use the term imperative to refer to gestures being used to get another individual to help in attaining a physical goal, such as getting an object, playing, etc., and the term declarative to characterize those gestures which are used to attain a non-physical goal, namely to draw another's attention to an object or entity merely for the sake of sharing attention.

Referential gestures, such as imperative pointing, have been reported for captive chimpanzees interacting with their human experimenters (Leavens, Hopkins & Bard, 1996; Leavens, Hopkins & Thomas, 2004). This ability was discovered by accident while testing a chimpanzee on a matching-to-sample task, in which correct responses resulted in the delivery of a food reward by a feeder to a tube connected to the cage mesh (Leavens et al., 1996). Occasionally, a food reward would overshoot the pipe and land on the floor outside the cage. One day, the chimpanzee Clint was observed to repetitively vocalize, point with his index finger (sticking his index finger through the cage mesh), and alternate his gaze between a fallen food reward and the experimenter. This observation led to controlled experiments, which clearly showed that chimpanzees use intentionally-produced pointing gestures to request food (e.g., Leavens & Hopkins, 1999). Further evidence for imperative pointing has been provided by human-raised individuals, who were first trained in some kind of communication with humans that involved close-range pointing (e.g., Call & Tomasello, 1994; Gardner & Gardner, 1969; Krause & Fouts, 1997; Miles, 1990; Patterson, 1978a; Savage-Rumbaugh et al., 1986; Woodruff & Premack, 1979). In all cases, however, the apes then began spontaneously to point for humans in more flexible ways, e.g. to more distant objects they wished to have or to locations that they wished to visit, or even in a declarative way to share attention (see Miles, 1990, 1999).

Focusing on the use of pointing gestures of individuals in populations in the wild, anecdotal observations indicate that chimpanzees of the Bossou community in Guinea, where animals use stones in a hammer and anvil fashion to crack oil-palm nuts, have been observed to point to a stone (once) and to nuts (nine times) (Inoue-Nakamura & Matsuzawa, 1997). Interestingly, a report by Veà & Sabater-Pi (1998) provided the only anecdotal evidence for the use of a declarative pointing gesture by a bonobo male in the wild: he was sitting in a tree and pointed to the position of two groups of human observers, who tried to hide in nearby undergrowth. He alternated his gaze between his group members and the humans then repeated the pointing gesture twice while emitting vocalizations. Considerable debate continues about whether apes point in a referential way, and it remains unclear whether pointing represents a natural communication ability or is simply a by-product of living in a human encultured environment (Tomasello & Call, 1997).

Patterson (1978b), Savage-Rumbaugh (1988) and Savage-Rumbaugh, Rumbaugh & McDonald (1985) described the use of a declarative gesture: the gesture 'showing' in one human-raised gorilla, and in one human-raised bonobo. It should be noted, however, that in all cases interpretation is an issue and that the declarativeness might only exist in the eyes of the human beholder. In addition, Savage-Rumbaugh and colleagues (Savage & Bakeman, 1978; Savage-Rumbaugh et al., 1977) and Tanner & Byrne (1996) reported the use of several gestures that they consider iconic uses of gestures. Iconic gestures are related to their referent by virtue of some actual physical resemblance between the two (Bates, Benigni, Bretherton, Camaioni & Volterra, 1979), such as a desired motion in space or the form of an action. One male bonobo and one male gorilla seemed to signal with their hand, arm or head to a playmate the direction in which he wanted her to move, the action he wanted her to perform, or the position he wanted her to take. Roth (1995) and Pika et al. (2003) tried to find evidence to support these findings by studying three groups of bonobos and two groups of gorillas in captivity, but did not observe any instances of the iconic use of gestures. There might be several explanations: (a) the iconicity existed in the eyes of the human observers only (Tomasello & Call, 1997) and did not fulfil a function for the sender and the recipient; (b) the analyses of Roth (1995) and Pika et al. (2003) did not focus in sufficient detail on the receiver's response to detect gestures of an iconic nature; or (c) gesturing of an iconic nature represents a developmental phenomenon and appears only at adolescence, promoted by special social and physical conditions (Tanner & Byrne, 1999).

In a recent paper, Pika & Mitani (2006) describe the first observation of a widespread use of an indicative gesture by chimpanzees in the wild. The so-called *directed scratch* gesture was observed between adult males of the Ngogo community, Kibale National Park, Uganda. It involved one male chimpanzee making a relatively loud and/or exaggerated scratching movement on a part of his body, which could be seen by his grooming partner (see Fig. 2). In the majority of the observed cases the grooming individual immediately stopped grooming and started to groom the indicated spot.

Pika & Mitani (2006) therefore suggest that: (1) the gesture may be used communicatively to indicate a precise spot on the body and to depict a desired future action, namely grooming, and (2) the recipient of the signal has an understanding of the intended meaning of the gesture. They concluded that *directed scratches* therefore may qualify as referential.

In sum, the evidence provided shows that apes use referential gestures, such as imperative pointing, or declarative gestures with human experimenters or caretakers. In addition, apes use imperative, referential gestures in their natural communication with conspecifics.

SIMILARITIES AND DIFFERENCES BETWEEN THE GESTURES OF APES AND PRE- OR JUST-LINGUISTIC HUMAN INFANTS

The studies reviewed above provide evidence that apes develop multifaceted gestural repertoires and, similar to human children, they use their gestures as intentional acts. The majority of their intentional gestures are dyadic, i.e., used to attract

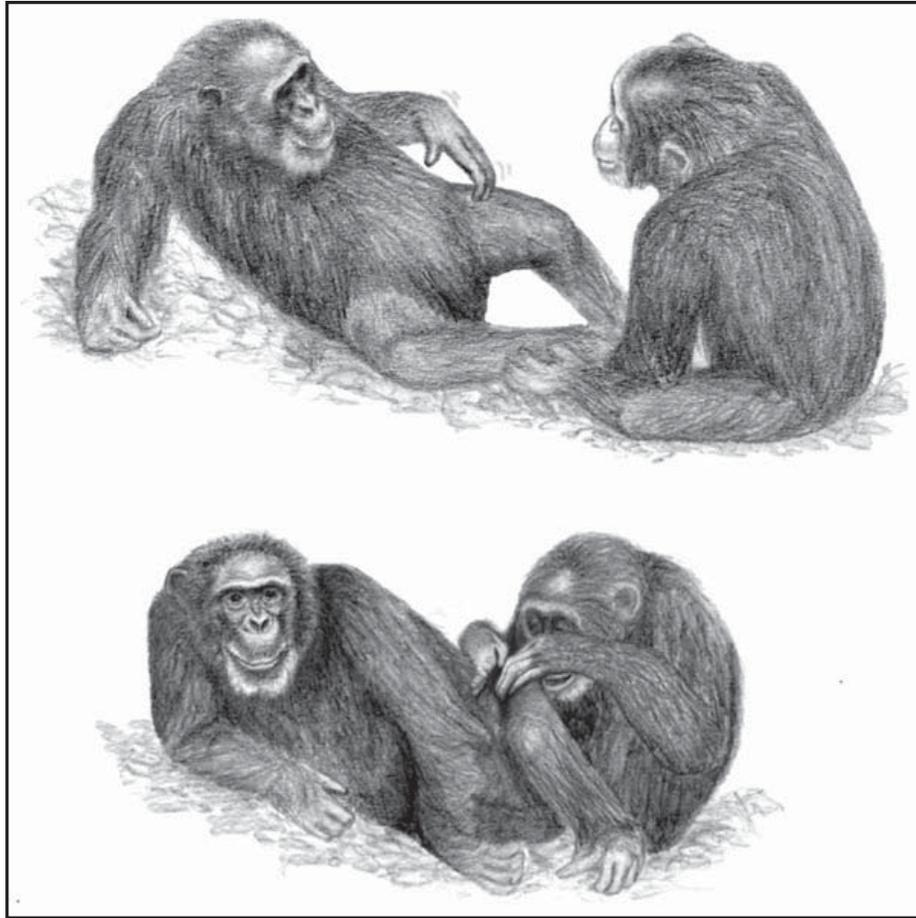


Figure 2 The *directed scratch* (© Dorothee Classen)

the attention of others to the self, not triadic, to attract the attention of others to some outside entity. Exceptions are the gestures *directed scratch* (Pika & Mitani, 2006), *food begging* (i.e., an animal holds out the hand, palm up to obtain food from another; for chimpanzees, see Tomasello et al., 1994; for orangutans, see Bard, 1992), *food offer* (an animal offers food placed on her arm to another one; Liebal et al., 2006) and *pointing*. These gestures are clearly triadic – a request to another for grooming or food, or an offer of food to another.

Human children, however, gesture from their very first attempts at gestural communication before language, using both dyadic and triadic gestures (Carpenter et al., 1998), but a quantitative comparison between the gestural performance of apes and pre-linguistic children has not yet been made. Such an approach could clarify in much more detail the role different types of gestures play in the communication of apes and of pre-linguistic children.

Concerning the type of gestures produced, researchers of pre-linguistic communication distinguish between ritualizations, deictics and symbolic gestures (Lock, 1978; for more detailed categorization, see also: Acredelo & Goodwyn, 1988; Iverson, Capirci & Caselli, 1994; Pizzuto, Cameracann, Corazza & Volterra, 1994). Apes perform ritualizations, in which the signaller uses an effective behaviour for a request.

For instance, apes often use a stylized *arm-raise* to initiate play, ritualized from actual acts of play hitting in the context of rough-and-tumble play. In addition, many youngsters ritualize signals for asking the mother to lower her back so that 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. Human children often use similar gestures, such as raising their arms to be picked up. Ontogenetic ritualization seems to be the learning process involved, which does not involve understanding of communicative intentions or cultural (imitative) learning of any sort. Thus, it does not create a shared communicative symbol (Tomasello, 2003).

The second type of gestures, deictics, involves a signaller, a recipient and some outside entity, and typically begins in human children around the age of 10 months. Although a third entity is involved, the use of deictics does not automatically imply that the human infant is using them in order to share attention with the adult on that third entity. For example, Moore & D'Etremont (2001) showed that many infants use arm and index finger extension to orient their own attention to things. Thus, pointing is for some infants just another ritualization and they produce the signal although they still do not understand the function of it (Carpenter et al., 1998; Franco & Butterworth, 1996). The reverse dissociation also exists in which infants visually follow adult pointing but do not themselves produce the gesture (Carpenter et al., 1998; Franco & Butterworth, 1996). Therefore, infants who learn to point via ritualization understand their pointing simply as a procedure to achieve a certain goal and not as a mutually understood communicative symbol to share attention. However, if infants learn to point via imitation, they are learning by understanding an adult's communicative intention in using the gesture first and then engaging in role reversal imitation to use the gesture her/himself when s/he has 'the same' communicative intention. To date, there has been no systematic research investigating which learning process is involved in the acquisition of deictics or if infants use individual learning strategies.

Substantially more studies have been made on the motives of pointing. Researchers differentiate three main motivations:

1. Pointing for imperative purposes, e.g., to request an object which is out of reach; Bates et al., 1975.
2. Pointing for declarative purposes, e.g., holding up an object and showing it; Bates et al., 1975.
3. Pointing to inform another person, e.g., of the location of an object; Liszkowski, 2005.

Imperative pointing requires only conceiving the other person as an animate 'agent' of action and is used simply to influence the other's behaviour. Declarative pointing, on the other hand, has been defined as a means to obtain adult's attention ('laughter, comment, smiles and eye contact – which we have termed "attention"'); Bates et al., 1975: 216). However, note that the most recent formulations of imperative and declarative communication define these modes of communication by reference to underlying psychological processes, or mental states (Liszkowski, Carpenter, Henning, Striano & Tomasello, 2004; Tomasello, 1995; Tomasello, Carpenter & Liszkowski, 2007).

In informative pointing, the providing of information is not to engage mutually about an event or referent but, instead, mainly to benefit the other person (Liszkowski, Carpenter, Striano & Tomasello, 2006). Informative pointing therefore reflects sensitivity to others as agents with informational states (Liszkowski, Carpenter & Tomasello et al., 2007).

Some gestures of great apes such as *pointing* are clearly deictic, and some gestures such as *food offer*, *food-begging* and *directed scratches* seem to bear some resemblance to deictics: *food offer* and *food-begging* are clearly triadic, somehow distal (because the signaller is not touching the recipient) and are used to point out something specific. In addition, the gesture *directed scratch* clearly involves some form of reference, but this reference is, in contrast to the other examples, self-directed. Overall, however, all these gestures are used as effective procedures to achieve a certain goal, but examples of apes using declarative or informative deictics in their natural communication are so far unknown.

The third gesture type are symbolic gestures that are either associated with a referent metonymically (the gesture refers to an element or attribute of something to mean the thing itself) or iconically (Acredelo & Goodwyn, 1988; Pizzuto & Volterra, 2000). Examples for human children are sniffing for a flower, panting for a dog, holding arms out for an airplane, raising arms for big things, and blowing for hot things. There is no research so far investigating whether symbolic gestures are acquired via ritualization or via imitation (Lock, 1978). However, it seems much more likely that in most cases infants are learning these symbolic gestures via imitative learning.

On the surface there seems to be no example of apes' gestures that bear some resemblance to symbolic gestures. Nevertheless, group specific gestures such as leaf clipping (Nishida, 1980), the grooming hand clasp (McGrew & Tutin, 1978), somersault (Pika et al., 2005b) and armshake (Pika et al., 2003) suggest that social learning, in the form of some kind of group-specific cultural transmission is involved. Furthermore, directed scratches used by chimpanzees in the wild provide evidence that (a) chimpanzees have an understanding of the intended meaning of the gestures, and (b) signallers might be able to signal the action they want a receiver to do. It is therefore possible that they constitute the first step towards symbolic gestures.

Interestingly, although the most recent studies on gestural communication in apes were inspired by the study of gestural communication in human children, there is one intriguing difference in approaches to this topic: researchers investigating gestural signals in apes include those gestures which incorporate the use of objects, for instance, *move* (Pika et al., 2003), *object shake* (Liebal, 2007a; Liebal, 2007b; Pika et al., 2003), *present object* (Liebal, 2007a), *straw wave* (Pika et al., 2003), *wave object* (Pika et al., 2005b; Tomasello et al., 1985). Moreover, some of the gestures described, incorporate repeated movements on objects or on the ape's own body, such as the gestures *chest beat*, *body beat*, *slap ground* and *object drum* (Pika et al., 2003). In contrast, researchers working on gestures of human children focus mainly on gestures that are performed in space (Bates et al., 1975; Capirci, Montanari & Volterra, 1998; Nicoladis et al., 1999) and may only in specific cases include touching an object (e.g., pointing by touching the referent; Iverson et al., 1994). Research on gestures in human children is therefore biased towards so-called 'empty-handed'

gestures (Petitto, 1988). Many studies exclude gestures that are performed on objects or gestures with an object-referent in hand, denoting them as functional object use play or meaningful action (e.g., Acredolo & Goodwyn, 1988; Goldin-Meadow & Morford, 1990; Guidetti, 2002; Iverson & Goldin-Meadow, 2005). However, Iverson et al. (1994) correctly noted that this exclusion procedure leads to an underestimation of the production of gestures. They suggest that in order to employ comparable criteria for communicative gestures, gestures incorporating objects should be included if they appear to be truly communicative (which means they have to be accompanied by eye contact, vocalization, or other clear evidence of an effort to direct the attention of another person present in the room; Thal & Tobias, 1992). Similarly, Capirci, Contaldo, Caselli & Volterra (2005: 162) note that 'actions and gestures produced in a communicative context are not clearly separate categories. Rather they should be considered a continuum and even adults can produce gestures with an object in hand for communicative purposes.'

Overall, the crucial difference between gestures of apes and of pre- and just-linguistic human children seems to be the obvious focusing on the *function* of gestures. In their natural communication, apes mainly use imperative gestures to communicate with their conspecifics, while all examples of declarative gesturing are from apes interacting with their caretakers or from human-raised or language-trained individuals (see also Leavens et al., 2004). Human children gesture for imperative purposes but also, from very early on, for declarative purposes to direct the attention of others to some third entity, simply for the sake of sharing interest in it or commenting on it (Bates et al., 1975; Liskowski et al., 2004), and later for informative purposes (Liskowski, 2005). These abilities seem to be unique for human beings and might have triggered the onset of symbolic communication, i.e., language. It is therefore quite puzzling why only human beings comment on outside entities simply to share experiences. One possibility is that this behaviour is linked with the cognitive ability that enables humans to understand other persons as intentional agents with whom they may share experience (Tomasello, Carpenter, Call, Behne & Moll, 2005). This propensity derived from the need to create a new medium for social bonding triggered by an increase of group size, superseding grooming as a servicing tool for social relationships (Dunbar, 1996; Pika, in press). During grooming the social relationships of (mainly) two individuals can be established and serviced at the same time, but the medium of declarative gestures offers two key features, which make communication in larger groups more efficient. First, it is possible to gesture to several people at the same time, thereby increasing the rate at which signallers interact with recipients. Second, gesturing about third entities allows the exchange of information about evolutionary urgent (e.g., predators, food) and other relevant things in the world, thereby creating a wider network of individuals and relevant facts than is possible for monkeys and apes.

CONCLUSION

Many human gestures are used functionally in ways very similar to language. 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 (Pika et al., 2005a). Apes also gesture on a regular basis in their natural communication but use these communicative means mainly as effective procedures in dyadic interactions to request actions from others. However, many of these gestures are used intentionally and are clearly learned. Thus, this review provides further support for the hypothesis that the gestural modality of our closest living relatives might have been the crucial modality within which the evolutionary precursors of symbolic communication evolved. Future studies, comparing the communicative skills of humans and apes in natural settings and the cognitive capacities that are thus demonstrated will, it is hoped, shed further light on the skills that were available during the dawn of language.

ACKNOWLEDGEMENTS

I am grateful to J. Call, K. Liebal and M. Tomasello, who shared their data with me. I am indebted to Dorothee Classen, who let me use her drawing of the directed scratch. For comments on an earlier draft and lively discussions, I would like to thank Michèle Guidetti and two anonymous reviewers. I was also inspired by valuable discussions with participants of the Cradle of Language Conference in Stellenbosch, South Africa.

NOTES

1. See also the website for the Primate Gesture Center: <http://www.primate-gesture-center.eu>
2. Auditory gestures generate sound while performed.
3. Defined in the next paragraph.

REFERENCES

- Acredelo, L. P. & Goodwyn, S. W. (1988). Symbolic gesturing in normal infants. *Child Development*, 59, 450–466.
- Antinucci, F. (1990). The comparative study of cognitive ontogeny in four primate species. In K. R. Gibson & S. T. Parker (Eds), *“Language” and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 157–171). New York: Cambridge University Press.
- Arbib, M. A. (2002). The mirror system, imitation, and the evolution of language. In K. Dautenhahn & C. L. Nehaniv (Eds), *Imitation in animals and artifacts. Complex adaptive systems* (pp. 229–280). Cambridge, MA: MIT Press.
- Armstrong, D. F., Stokoe, W. C. & Wilcox, S. E. (1995). *Gesture and the nature of language*. Cambridge: Cambridge University Press.
- Arnold, K. & Zuberbühler, K. (2006). Semantic combinations in primate calls. *Nature*, 441, 303.
- Austin, J. L. (1962). *How to do things with words*. New York: Oxford University Press.
- Badrian, A. & Badrian, N. (1984). Social organization of *Pan paniscus* in the Lomako Forest, Zaire. In R. L. Susman (Ed.), *The pygmy chimpanzee: Evolutionary biology and behavior* (pp. 325–346). New York: Plenum Press.
- Bard, K. (1990). Social tool use by free-ranging orangutans: A Piagetian and developmental perspective on the manipulation of an animate object. In K. R. Gibson (Ed.), *Language*

- and intelligence in monkeys and apes. *Comparative developmental perspectives* (pp. 356–378). New York: Cambridge University Press.
- Bard, K. A. (1992). Intentional behaviour and intentional communication in young free-ranging orangutans. *Child Development*, 63, 1186–1197.
- Baron-Cohen, S. (1991). Precursors to a theory of mind: Understanding attention in others. In A. Whiten (Ed.), *Natural theories of mind: Evolution, development and simulation of everyday mindreading* (pp. 233–251). Oxford: Blackwell.
- Bates, E. (1976). *Language and context: The acquisition of pragmatics*. New York: Academic Press.
- Bates, E., Benigni, L., Bretherton, I., Camaioni, L. & Volterra, V. (1979). *The emergence of symbols: Cognition and communication in infancy*. New York: Academic Press.
- Bates, E., Camaioni, L. & Volterra, V. (1975). The acquisition of performatives prior to speech. *Merrill-Palmer Quarterly*, 21, 205–226.
- Boesch, C. (1995). Innovation in wild chimpanzees. *Animal Behaviour*, 48, 653–667.
- Bogin, B. (1999). Evolutionary perspectives on human growth. *Annual Review of Anthropology*, 28, 17–25.
- Bretherton, I., McNew, S. & Beeghly-Smith, M. (1981). Early persons' knowledge as expressed in gestural and verbal communication: When do infants require a 'theory of mind'. In M. E. Lamb & L. R. Sherrod (Eds), *Infant social cognition: Empirical and theoretical considerations* (pp. 333–373). Hillsdale, NY: Erlbaum.
- Britten, R. J. (2002). Divergence between samples of chimpanzee and human DNA sequences is 5% counting indels. *Proceedings of the National Academy of Sciences of the United States of America*, 99, 13633–13635.
- Byrne, R. W. & Tanner, J. (2006). Gestural imitation by a gorilla: Evidence and nature of the capacity. *International Journal of Psychology and Psychological Therapy*, 6, 215–231.
- Caine, N. G., Addington, R. L. & Windfelder, T. L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour*, 50, 53–60.
- Call, J. (1999). Levels of imitation and cognitive mechanisms in orangutans. In S. T. Parker, R. W. Mitchell & H. L. Miles (Eds), *The mentalities of gorillas and orangutans* (pp. 316–341). Cambridge: Cambridge University Press.
- Call, J. (2001). Body imitation in an enculturated orangutan (*Pongo pygmaeus*). *Cybernetics and Systems: An International Journal*, 32, 97–119.
- Call, J. & Tomasello, M. (1994). Production and comprehension of referential pointing by orangutans. *Journal of Comparative Psychology*, 108, 307–317.
- Camaioni, L. (1993). The development of intentional communication: A re-analysis. In J. Nadel & L. Camaioni (Eds), *New perspectives in early communicative development* (pp. 82–96). London: Routledge.
- Capirci, O., Contaldo, A., Caselli, M. C. & Volterra, V. (2005). From action to language through gesture. *Gesture*, 5, 155–177.
- Capirci, O., Montanari, S. & Volterra, V. (1998). Gestures, signs, and words in early language development. In J. M. Iverson & S. Goldin-Meadow (Eds), *The nature and functions of gesture in children's communication. New directions for child development* (pp. 45–60). San Francisco: Jossey Bass.
- Carpenter, M., Nagell, K. & Tomasello, M. (1998). Social cognition, joint attention, and communicative competence from 9 to 15 months of age. *Monographs of the Society for Research in Child Development*, 36 (4, Serial No. 255).
- Case, R. (1985). *Intellectual development: Birth to adulthood*. New York: Academic Press.
- Cheney, D. & Seyfarth, R. (1985). Vervet monkey alarm calls: Manipulation through shared information? *Behavior*, 94, 150–166.
- Cheney, D. L. & Seyfarth, R. M. (1990). *How monkeys see the world*. Chicago and London: University of Chicago Press.

- Chivers, D. J. (1974). *The siamang in Malaya: A field study of a primate in tropical rain forest*. Basel: Karger.
- Clark, A. P. & Wrangham, R. W. (1993). Acoustic analysis of wild chimpanzee pant hoots: Do Kibale forest chimpanzees have an acoustically distinct food arrival pant hoot? *American Journal of Primatology*, 31, 99–109.
- Clark, A. P. & Wrangham, R. W. (1994). Chimpanzee arrival pant-hoots: Do they signify food or status? *International Journal of Primatology*, 15, 185–205.
- Condillac, E. B. de (1971). *An essay on the origin of human knowledge; being a supplement to Mr. Locke's Essay on the human understanding. A facsimile reproduction of the translation of Thomas Nugent*. Gainesville, FL: Scholars' Facsimiles and Reprints.
- Corballis, M. C. (2002). *From hand to mouth, the origins of language*. Princeton, NJ: Princeton University Press.
- Crockford, C. & Boesch, C. (2003). Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: Analysis of barks. *Animal Behaviour*, 66, 115–125.
- Crockford, C., Herbinger, I., Vigilant, L. & Boesch, C. (2004). Wild chimpanzees produce group-specific calls: A case for vocal learning? *Ethology*, 110, 221–243.
- Custance, D. M., Whiten, A. & Bard, K. A. (1995). Can young chimpanzees (*Pan troglodytes*) imitate arbitrary actions? Hayes & Hayes (1952) revisited. *Behaviour*, 132, 11–12.
- de Waal, F. B. M. (1988). The communicative repertoire of captive bonobos (*Pan paniscus*) compared to that of chimpanzees. *Behaviour*, 106, 183–251.
- Dunbar, R. (1996). *Grooming, gossip and the evolution of language*. London: Faber & Faber.
- Ellefson, J. O. (1967). *A natural history of gibbons in the Malay Peninsula*. Berkeley: University of California.
- Ellefson, J. O. (1974). A natural history of white-handed gibbons in the Malayan Peninsula. In D. S. Rumbaugh (Ed.), *Gibbon and siamang* (pp. 2–134). Basel: S. Karger.
- Enard, W., Przeworski, M., Fisher, S. E., Lai, C. S. L., Wiebe, V., Kitano, T., Monaco, A. P. & Paebo, S. (2002). Molecular evolution of FOXP2, a gene involved in speech and language. *Nature*, 418, 869–872.
- Fay, J. M. (1989). Hand-clapping in western lowland gorillas. *Mammalia*, 53, 457–458.
- Fleagle, J. G. (1999). *Primate adaptation and evolution*. New York: Academic Press.
- Fossey, D. (1974). Observations on the home range of one group of mountain gorillas (*Gorilla g. beringei*). *Animal Behaviour*, 22, 568–581.
- Fox, G. J. (1977). *Social dynamics in siamang*. Milwaukee: University of Wisconsin.
- Franco, F. & Butterworth, G. (1996). Pointing and social awareness: Declaring and requesting in the second year. *Journal of Child Language*, 23, 307–336.
- Fruth, B., Hohmann, G., Beuerlein, M. M. & McGrew, C. (2006). Grooming hand clasp by bonobos of Lui Kotal, Democratic Republic of Congo. *Pan African News*, 13, 6–8.
- Gardner, R. A. & Gardner, B. (1969). Teaching sign language to a chimpanzee. *Science*, 165, 664–672.
- Gardner, R. A., Gardner, B. & Van Cantford, T. E. (1989). *Teaching sign language to chimpanzees*. Albany: State University of New York Press.
- Goldin-Meadow, S. & Morford, M. (1990). Gesture in early child language. In C. J. Erting (Ed.), *From gesture to language in hearing and deaf children* (pp. 249–262). New York: Springer-Verlag.
- Goldin-Meadow, S. & Mylander, C. (1998). Spontaneous sign systems created by deaf children in two cultures. *Nature*, 391, 279–281.
- Goldin-Meadow, S., Nusbaum, H., Kelly, S. D. & Wagner, S. (2001). Explaining math: Gesturing lightens the load. *Psychological Science*, 12, 516–522.
- Goodall, J. (1986a). *The chimpanzees of Gomb: Patterns of behaviour*. Cambridge: The Belknap Press of Harvard University Press.

- Goodall, J. (1986b). A preliminary report on expressive movements and communication in the Gombe Stream chimpanzees. In P. Jay (Ed.), *Primate studies in adaptation and variability* (pp. 313–382). New York: Holt, Rinehart & Winston.
- Guidetti, M. (2002). The emergence of pragmatics: Forms and functions of conventional gestures in young French children. *First Language*, 22, 265–285.
- Hauser, M. D. & Konishi, M. (1999). *The design of animal communication*. Cambridge, MA: MIT Press.
- Hayes, K. J. & Hayes, C. (1952). Imitation in a home-raised chimpanzee. *Journal of Comparative and Physiological Psychology*, 45, 450–459.
- Hewes, G. W. (1973). Primate communication and the gestural origin of language. *Current Anthropology*, 12, 5–24.
- Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, 69, 207–231.
- Hockett, C. F. (1978). In search of Jove's brow. *American Speech*, 53, 243–313.
- Ingmanson, E. J. (1996). Tool-using behavior in wild *Pan paniscus*: Social and ecological considerations. In A. E. Russon & K. A. Bard (Eds), *Reaching into thought: The minds of the great apes* (pp. 190–210). Cambridge: Cambridge University Press.
- Inoue-Nakamura, N. & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 111, 159–173.
- Iverson, J. M., Capirci, O. & Caselli, M. C. (1994). From communication to language in two modalities. *Cognitive Development*, 9, 23–43.
- Iverson, J. M. & Goldin-Meadow, S. (1998). Why people gesture when they speak. *Nature*, 396, 228.
- Iverson, J. M. & Goldin-Meadow, S. (2005). Gesture paves the way for language development. *Psychological Science*, 16, 367–371.
- Kano, T. (1980). Social behaviour of wild pygmy chimpanzees (*Pan paniscus*) of Wamba: A preliminary report. *Journal of Human Evolution*, 9, 243–260.
- Kendon, A. (1975). Gesticulation, speech and the gesture theory of language origin. *Sign Language Studies*, 9, 349–373.
- Klima, E. & Bellugi, U. (1979). *The signs of language*. Cambridge, MA: Harvard University Press.
- Krause, M. A. & Fouts, R. S. (1997). Chimpanzee (*Pan troglodytes*) pointing: Hand shapes, accuracy, and the role of eye gaze. *Journal of Comparative Psychology*, 111, 330–336.
- Kumar, S., Filipowski, A., Swarna, V., Walker, A. & Hedges, S. B. (2006). Placing confidence limits on the molecular age of the human-chimpanzee divergence. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 18842–18847.
- Kummer, H. (1968). *Social organization of hamadryas baboons*. Chicago: University of Chicago Press.
- Kummer, H. & Kurt, F. (1965). A comparison of social behaviour in captive and wild hamadryas baboons. In H. Vagtberg (Ed.), *The baboon in medical research* (pp. 1–16). Texas: University of Texas Press.
- Kuroda, S. J. (1980). Social behavior of the pygmy chimpanzees. *Primates*, 21, 181–197.
- Kuroda, S. [J.] (1984). Rocking gesture as communicative behavior in the wild pygmy chimpanzee in Wamba, Central Zaire. *Journal of Ethology*, 2, 127–137.
- Ladygina-Kohts, N. N. (1935). *Infant chimpanzee and human child. A classic 1935 comparative study of ape emotions and intelligence*. New York: Oxford University Press.
- Leavens, D. (2004). Manual deixis in apes and humans. *Interaction Studies*, 5, 387–408.
- Leavens, D. A. & Hopkins, W. D. (1998). Intentional communication by chimpanzees: A cross-sectional study of the use of referential gestures. *Developmental Psychology*, 34, 813–822.
- Leavens, D. A. & Hopkins, W. D. (1999). The whole hand-point: The structure and function of pointing from a comparative perspective. *Journal of Comparative Psychology*, 113, 417–425.

- Leavens, D. A., Hopkins, W. D. & Bard, K. A. (1996). Indexical and referential pointing in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 110, 346–353.
- Leavens, D. A., Hopkins, W. D. & Thomas, R. K. (2004). Referential communication by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 118, 48–57.
- Liebal, K. (2007a). The gestural communication of orangutans. In J. Call (Ed.), *The gestural communication of monkeys and apes* (pp. 69–98). Mahwah, NJ: Erlbaum.
- Liebal, K. (2007b). The gestural communication of siamangs. In J. Call (Ed.), *The gestural communication of monkeys and apes* (pp. 131–158). Mahwah, NJ: Erlbaum.
- Liebal, K., Call, J. & Tomasello, M. (2004a). Chimpanzee gesture sequences. *Primates*, 64, 377–396.
- Liebal, K., Pika, S. & Tomasello, M. (2004b). Social communication in siamangs (*Symphalangus syndactylus*): Use of gestures and facial expression. *Primates*, 45, 41–57.
- Liebal, K., Pika, S. & Tomasello, M. (2006). Gestural communication of orangutans (*Pongo pygmaeus*). *Gesture*, 6, 1–38.
- Liebermann, P. (1998). *Eve spoke: Human language and human evolution*. New York: W. W. Norton & Co.
- Liszkowski, U. (2005). Human twelve-month-olds point cooperatively to share interest with and provide information for a communicative partner. *Gesture*, 5, 135–154.
- Liszkowski, U., Carpenter, M., Henning, A., Striano, T. & Tomasello, M. (2004). Twelve-month-olds point to share attention and interest. *Developmental Science*, 7, 297–307.
- Liszkowski, U., Carpenter, M., Striano, T. & Tomasello, M. (2006). Twelve- and 18-month-olds point to provide information for others. *Journal of Cognition and Development*, 7, 173–187.
- Liszkowski, U., Carpenter, M. & Tomasello, M. (2007). Reference and attitude in infant pointing. *Journal of Child Language*, 34, 1–20.
- Lock, A. (1978). *Action, gesture and symbol: The emergence of language*. New York: Academic Press.
- MacKinnon, J. R. (1974). Behaviour and ecology of Orang Utans. *Animal Behaviour*, 22, 3–74.
- Maestriperieri, D. (1996). Maternal encouragement of infant locomotion in pigtail macaques (*Macaca nemestrina*). *Animal Behaviour*, 51, 603–610.
- Maestriperieri, D. (1997). Gestural communication in macaques. *Evolution of Communication*, 1, 193–222.
- Maestriperieri, D. (1999). Primate social organization, gestural repertoire size, and communication dynamics. In B. J. King (Ed.), *The origins of language: What nonhuman primates can tell* (pp. 55–77). Santa Fe: School of American Research Press.
- Maestriperieri, D. (2005). Gestural communication in three species of macaques (*Macaca mulatta*, *M. nemestrina*, *M. arctoides*). *Gesture*, 5, 57–73.
- Marler, P. (1977). The evolution of communication. In T. A. Sebeok (Ed.), *How animals communicate* (pp. 45–70). Bloomington: Indiana University Press.
- Marler, P. & Hobbett, L. (1975). Individuality in a long-range vocalization of wild chimpanzees. *Zeitschrift für Tierpsychologie*, 38, 97–109.
- Masataka, N. (1983). Categorical responses to natural and synthesized alarm calls in Goeldi's monkeys (*Callimico goeldii*). *Primates*, 24, 40–51.
- McGrew, W. C. & Tutin, C. E. G. (1978). Evidence for a social custom in wild chimpanzees? *Man*, 13, 234–251.
- McNeill, D. (1985). So you think gestures are nonverbal? *Psychological Review*, 92, 350–371.
- McNeill, D. (1992). *Hand and mind*. Chicago: The University of Chicago Press.
- Miles, H. L. (1986). Cognitive development in a signing orangutan. *Primate Report*, 14, 179–180.
- Miles, H. L. (1990). The cognitive foundations for reference in a signing orangutan. In S. T. Parker & K. R. Gibson (Eds), *Language and intelligence in monkeys and apes* (pp. 511–539). Cambridge: Cambridge University Press.

- Miles, H. L. (1999). Symbolic communication with and by great apes. In S. Taylor Parker, R. W. Mitchell & H. L. Miles (Eds), *The mentalities of gorillas and orangutans: Comparative perspectives* (pp. 197–210). Cambridge: Cambridge University Press.
- Mitani, J. C. & Brandt, K. L. (1994). Social factors influence the acoustic variability in the long-distance calls of male chimpanzees. *Ethology*, *96*, 233–252.
- Mitani, J. C., Hasegawa, T., Gros-Louis, J., Marler, P. & Byrne, R. W. (1992). Dialects in wild chimpanzees? *American Journal of Primatology*, *27*, 233–243.
- Mitani, J. C. & Nishida, T. (1993). Contexts and social correlates of long-distance calling by male chimpanzees. *Animal Behaviour*, *45*, 735–746.
- Moore, C. & D'Entremont, B. (2001). Developmental changes in pointing as a function of parent's attentional focus. *Journal of Cognition and Development*, *2*, 109–129.
- Morris, D., Collett, P., Marsh, P. & O'Shaughnessy, M. (1979). *Gestures, their origins and distribution*. New York: Stein & Day.
- Nicoladis, E., Mayberry, R. I. & Genesee, F. (1999). Gesture and early bilingual development. *Developmental Psychology*, *35*, 514–526.
- Nishida, T. (1980). The leaf-clipping display: A newly-discovered expressive gesture in wild chimpanzees. *Journal of Human Evolution*, *9*, 117–128.
- Nishida, T., Kano, T., Goodall, J., McGrew, W. C. & Nakamura, M. (1999). Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science*, *107*, 141–188.
- Ogden, J. & Schildkraut, D. (1991). *Compilation of gorilla ethograms*. Atlanta: Gorilla Behavior Advisory Group.
- Orgeldinger, M. (1999). *Paarbeziehungen beim Siamang-Gibbon (Hylobates syndactylus) im Zoo: Untersuchungen über den Einfluß von Jungtieren auf die Paarbindung*. Münster: Schöningh Verlag.
- Owings, D. H. & Morton, D. S. (1998). *Animal vocal communication: A new approach*. Cambridge: Cambridge University Press.
- Palombit, R. A. (1992). Pair bonds and monogamy in wild siamang (*Hylobates syndactylus*) and white-handed gibbon (*Hylobates lar*). Davis: University of California.
- Parker, S. T., Mitchell, R. W. & Lyn Miles, H. (1999). *The mentalities of gorillas and orangutans*. Cambridge: Cambridge University Press.
- Parnell, R. J. & Buchanan-Smith, H. M. (2001). Animal behaviour: An unusual social display by gorillas. *Nature*, *412*, 294.
- Patterson, F. (1978a). Conversations with a gorilla. *National Geographic*, *134*, 438–465.
- Patterson, F. (1978b). Linguistic capabilities of a lowland gorilla. In F. C. C. Peng (Ed.), *Sign Language and Language Acquisition in Man and Ape* (pp. 161–201). Boulder, CO: Westview Press.
- Petitto, L. A. (1988). 'Language' in the prelinguistic child. In F. S. Kessel (Ed.), *The development of language and language researchers: Essays in honor of Roger Brown* (pp. 187–221). Hillsdale, NY: Erlbaum.
- Pika, S. (2007a). The gestural communication of bonobos. In J. Call (Ed.), *The gestural communication of monkeys and apes* (pp. 41–67). Mahwah, NJ: Erlbaum.
- Pika, S. (2007b). The gestural communication of gorillas. In J. Call (Ed.), *The gestural communication of monkeys and apes* (pp. 99–130). Mahwah, NJ: Erlbaum.
- Pika, S. (in press). What is the nature of the gestural communication of great apes? In J. Zlatev, T. Racine, C. Sinha & E. Itkonen (Eds), *The shared mind*.
- Pika, S., Liebal, K., Call, J. & Tomasello, M. (2005a). The gestural communication of apes. *Gesture*, *5*, 41–56.
- Pika, S., Liebal, K. & Tomasello, M. (2003). Gestural communication in young gorillas (*Gorilla gorilla*): Gestural repertoire, learning and use. *American Journal of Primatology*, *60*, 95–111.

- Pika, S., Liebal, K. & Tomasello, M. (2005b). Gestural communication in subadult bonobos (*Pan paniscus*): Gestural repertoire and use. *American Journal of Primatology*, 65, 39–51.
- Pika, S. & Mitani, J. C. (2006). Referential gesturing in wild chimpanzees (*Pan troglodytes*). *Current Biology*, 16, 191–192.
- Pika, S., Nicoladis, M. & Marentette, P. F. (2006). A cross-cultural study on the use of gestures: Evidence for cross-linguistic transfer? *Bilingualism: Language and Cognition*, 9, 319–327.
- Pizzuto, E., Cameracann, E., Corazza, S. & Volterra, V. (1994). Terms for spatio-temporal relations in Italian sign language. In R. Simone (Ed.), *Iconicity in language* (pp. 238–256). Amsterdam & Philadelphia: John Benjamins.
- Pizzuto, E. & Volterra, V. (2000). Iconicity and transparency in sign languages: A cross-linguistic cross-cultural view. In K. Emmorey & H. Lane (Eds), *The signs of language revisited: An anthology to honor Ursula Bellugi* (pp. 261–286). New York: Erlbaum.
- Plooiij, F. X. (1978). Some basic traits of language in wild chimpanzees? In A. Lock (Ed.), *Action, gesture and symbol* (pp. 111–131). London: Academic Press.
- Plooiij, F. X. (1979). How wild chimpanzee babies trigger the onset of mother-infant play. In M. Bullova (Ed.), *Before speech* (pp. 223–243). Cambridge: Cambridge University Press.
- Redshaw, M. (1978). Cognitive development in human and gorilla infants. *Journal of Human Evolution*, 7, 133–141.
- Rijksen, H. D. (1978). *A field study on Sumatran orangutans*. Wageningen, Netherlands: Mededeelingen Landbouwhogeschool.
- Roth, R. R. (1995). A study of gestural communication during sexual behavior in bonobo (*Pan paniscus*, Schwartz). Unpublished PhD thesis, Department of Anthropology, University of Calgary.
- Savage, S. & Bakeman, R. (1978). Sexual morphology and behavior in *Pan paniscus*. In: *Proceedings of the Sixth International Congress of Primatology* (pp. 613–616). New York: Academic Press.
- Savage-Rumbaugh, E. S. (1988). A new look at ape language: Comprehension of vocal speech and syntax. Comparative perspectives in modern psychology. In D. W. Leger (Ed.), *Comparative Perspectives in Modern Psychology, Nebraska symposium on motivation* (pp. 201–256). Lincoln: University of Nebraska Press.
- Savage-Rumbaugh, E. S., McDonald, K., Sevcic, R. A., Hopkins, W. D. & Rupert, E. (1986). Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *Journal of Experimental Psychology: General*, 115, 211–235.
- Savage-Rumbaugh, E. [S.], Murphy, J., Sevcic, R. A., Brakke, K. E., Williams, S. L. & Rumbaugh, D. M. (1993). Language comprehension in ape and child. *Monographs of the Society for Research in Child Development*, 58 (3–4, Serial No. 233).
- Savage-Rumbaugh, E. S., Rumbaugh, D. M. & McDonald, K. (1985). Language learning in two species of apes. *Neurosciences and Biobehavioral Review*, 9, 653–656.
- Savage-Rumbaugh, E. S., Wilkerson, B. J. & Bakeman, R. (1977). Spontaneous gestural communication among conspecifics in the pygmy chimpanzee (*Pan paniscus*). In G. H. Bourne (Ed.), *Progress in ape research* (pp. 97–116). New York: Academic Press.
- Savage-Rumbaugh, S. & Wilkerson, B. (1978). Socio-sexual behavior in *Pan paniscus* and *Pan troglodytes*: A comparative study. *Journal for Human Evolution*, 7, 327–344.
- Schaller, G. B. (1963). *The mountain gorilla, ecology and behavior*. Chicago: University of Chicago Press.
- Schaller, G. [B.] (1965). The behaviour of the mountain gorilla. In I. de Vore (Ed.), *Primate behavior* (pp. 324–367). New York: Holt, Rinehart & Winston.
- Seyfarth, R. M. (1987). Vocal communication and its relation to language. In B. Smuts, D. L. Cheney, R. Seyfarth, R. Wrangham & T. Struhsaker (Eds), *Primate societies* (pp. 440–451). Chicago: University of Chicago Press.

- Seyfarth, R. M., Cheney, D. L. & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour*, 28, 1070–1094.
- Slocombe, K. E. & Zuberbühler, K. (2005). Functionally referential communication in a chimpanzee. *Current Biology*, 15, 1179–1784.
- Snowdon, C. (1988). A comparative approach to vocal communication. In D. L. Leger (Ed.), *Comparative perspectives in modern psychology, Nebraska symposium on motivation* (pp. 145–199). Lincoln: University of Nebraska Press.
- Snowdon, C. T., Brown, C. H. & Petersen, M. R. (1982). *Primate communication*. Cambridge: Cambridge University Press.
- Spinozzi, G. & Natale, F. (1989). Early sensorimotor development in gorilla. In F. Antinucci (Ed.), *Comparative cognition and neuroscience: Cognitive structure and development in nonhuman primates* (pp. 21–38). New York: Cambridge University Press.
- Struhsaker, T. T. (1967). Auditory communication among vervet monkeys (*Cercopithecus aethiops*). In S. A. Altmann (Ed.), *Social communication among primates* (pp. 281–324). Chicago: Chicago University Press.
- Sugiura, H. (1993). Temporal and acoustic correlates in vocal exchange of coo calls in Japanese macaques. *Behaviour*, 124, 207–225.
- Sugiura, H. (1998). Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. *Animal Behaviour*, 55, 673–687.
- Sugiyama, Y. (1981). Observations on the population dynamics and behavior of wild chimpanzees at Bossou, Guinea, 1979–1980. *Primates*, 22, 432–444.
- Tanner, J. E. (2004). Gestural phrases and gestural exchanges by a pair of zoo-living lowland gorillas. *Gesture*, 4, 25–42.
- Tanner, J. E. & Byrne, R. (1996). Representation of action through iconic gesture in a captive lowland gorilla. *Current Anthropology*, 37, 162–173.
- Tanner, J. E. & Byrne, R. (1999). The development of spontaneous gestural communication in a group of zoo-living lowland gorillas. In S. T. Parker, R. W. Mitchell & H. L. Miles (Eds), *The mentalities of gorillas and orangutans: Comparative perspectives* (pp. 211–239). Cambridge: Cambridge University Press.
- Thal, D. & Tobias, S. (1992). Communicative gestures in children with delayed onset of oral expressive vocabulary. *Journal of Speech & Hearing Research*, 35, 1281–1287.
- Tomasello, M. (1995). Joint attention as social cognition. In C. Moore & P. J. Dunham (Eds), *Joint attention: Its origin and role in development* (pp. 103–130). Hillsdale, NY: Erlbaum.
- Tomasello, M. (2003). *Constructing a language*. Harvard: Harvard University Press.
- Tomasello, M. & Call, J. (1997). *Primate cognition*. New York: Oxford University Press.
- Tomasello, M. & Call, J. (2007). *The gestural communication of monkeys and apes*. Mahwah, NJ: Erlbaum.
- Tomasello, M., Call, J., Nagell, K., Olguin, R. & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: A trans-generational study. *Primates*, 35, 137–154.
- Tomasello, M., Call, J., Warren, J., Frost, G. T., Carpenter, M. & Nagell, K. (1997a). The ontogeny of chimpanzee gestural signals: A comparison across groups and generations. *Evolution of Communication*, 1, 223–259.
- Tomasello, M., Call, J., Warren, J., Frost, T., Carpenter, M. & Nagell, K. (1997b). The ontogeny of chimpanzee gestural signals. In S. Wilcox, B. King & L. Steels (Eds), *Evolution of communication* (pp. 224–259). Amsterdam & Philadelphia: John Benjamins.
- Tomasello, M., Carpenter, M., Call, J., Behne, T. & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral & Brain Sciences*, 28, 1–17.
- Tomasello, M., Carpenter, M. & Liszkowski, U. (2007). A new look at infant pointing. *Child Development*, 78, 705–722.
- Tomasello, M., George, B. L., Kruger, A. C., Farrar, M. J. & Evans, A. (1985). The development of gestural communication in young chimpanzees. *Journal of Human Evolution*, 14, 175–186.

- Tomasello, M., Gust, D. & Frost, G. T. (1989). A longitudinal investigation of gestural communication in young chimpanzees. *Primates*, 30, 35–50.
- Van Hooff, J. A. R. A. M. (1967). The facial displays of the catarrhine monkeys and apes. In D. Morris (Ed.), *Primate Ethology* (pp. 7–68). London: Weidenfeld & Nicolson.
- Van Hooff, J. A. R. A. M. (1973). A structural analysis of the social behaviour of a semi-captive group of chimpanzees. In M. von Cranach & I. Vine (Eds), *Social communication and movement: Studies of interaction and expression in man and chimpanzee* (pp. 75–162). London & New York: Academic Press.
- Van Lawick-Goodall, J. (1968). A preliminary report on expressive movements and communication in the Gombe stream chimpanzees. In P. C. Jay (Ed.), *Primates. Studies in adaptation and variability* (pp. 313–374). New York: Holt, Rinehart & Winston.
- Vea, J. J. & Sabater-Pi, J. (1998). Spontaneous pointing behaviour in the wild pygmy chimpanzee (*Pan paniscus*). *Folia Primatologica*, 69, 289–290.
- Whiten, A., Goodall, A. G., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., et al. (2001). Charting cultural variation in chimpanzees. *Behaviour*, 138, 1489–1525.
- Whiten, A. & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. *Advances in the Study of Behaviour*, 21, 239–83.
- Woodruff, G. & Premack, D. (1979). Intentional communication in the chimpanzee: The development of deception. *Cognition*, 7, 333–352.
- Zentall, T. R. (2001). Imitation in animals: Evidence, function, and mechanisms. *Cybernetics and Systems: An International Journal*, 32, 53–96.
- Zuberbühler, K. (2000). Interspecific semantic communication in two forest monkeys. *Proceedings of the Royal Society*, 267, 713–718.
- Zuberbühler, K. (2003). Referential signalling in non-human primates: Cognitive precursors and limitations for the evolution of language. *Advances in the Study of Behavior*, 33, 265–307.

ADDRESS FOR CORRESPONDENCE

Dr Simone Pika
University of Manchester, School of Psychological Sciences,
Coupland 1 Building, Oxford Road, Manchester, M13 9PL, UK
E: simone.pika@manchester.ac.uk
