Emerging Language: Cognition and Gestural Communication in Wild and Language-Trained Chimpanzees (*Pan troglodytes*)

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Declaration

I declare that the work undertaken and reported within this Ph.D. thesis is my own and has not been submitted in consideration of any degree or award.

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Abstract

An important element in understanding the evolutionary origin of human language is to explore homologous traits in cognition and communication between primates and humans (Burling, 1993, Hewes, 1973). One proposed modality of language evolution is that of gestural communication, defined as communicative movements of hands without using or touching objects (de Waal, 2003). While homologies between primate calls and language have been relatively well explored, we still have a limited understanding of how cognitive abilities may have shaped the characteristics of primate gestures (Corballis, 2003). Chimpanzees (*Pan troglodytes*) are our closest living relatives and display some complex cognitive skills in various aspects of their gestural behaviour in captivity (de Waal, 2003, Pollick and de Waal, 2007). However, it is not yet currently clear to what extent these abilities seen in captive apes are typical of chimpanzees in general and to what extent cognitive capacities observed in captive chimpanzees have been enhanced by the socio-cultural environment of captivity such as language training.

In this Ph.D. research, I investigated the cognitive skills underlying gestural communication in both wild and language trained chimpanzees, with a special focus on the repertoire and the intentionality of production and comprehension. The study of cognitive skills underlying the production of the repertoire and the role of intentionality is important because these skills are cognitively demanding and are a prerequisite in human infants for their ability to acquire language (Baldwin, 1995, Olson, 1993). My research suggests that chimpanzee gestural communication is cognitively complex and may be homologous with the cognitive skills evident in pre-verbal infants on the cusp of language acquisition. Chimpanzees display a multifaceted and complex signal repertoire of manual gestures. These gestures are the prototypes, within which there is variation, and between which the boundaries are not clear-cut, but there is gradation apparent along several morphological components. Both wild and language trained chimpanzees communicate intentionally about their perceived desires and the actions that they want the recipients to undertake. They do not just express their emotions, but they communicate flexibly by adjusting their communicative tactics in response to the comprehension states of the recipient. Whilst chimpanzees communicate their intentions flexibly, the messages conveyed are specific. However, recipients comprehend gestures flexibly in light of the signaller's overall intentions.

Whilst wild and language trained chimpanzee gestural communication revealed similar cognitive characteristics, language trained chimpanzees outperformed wild apes in that they had ability to use signals which made distinctions that human deictic words can make. Whilst these differences between wild and language trained chimpanzees may be due to the different methodological approaches used, it is conceivable that language training may have influenced captive ape cognitive skills in the representational domain. These results from wild and language trained chimpanzees indicate that chimpanzees possess some form of cognitive skills necessary for language development and that cognitive skills underlying repertoire and use in chimpanzees are a shared capacity between humans, other apes and a common ancestor. These findings render theories of the gestural origins of language more plausible.

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Table of Contents

Chapter 1: General introduction

RATIONALE

An important element in understanding the evolutionary origins of human language is to understand the features of cognition and communication in our closest living relatives (Burling, 1993, Hewes, 1973). Understanding homologous traits in cognition and communication between primates and humans is important because it allows us to explore fundamental questions about the evolutionary transition from pre-linguistic to linguistic communication, and how cognitive abilities may have shaped the form and function of communicative behaviour in our common ancestors (Burling, 1993, Hauser et al., 2002b, Fitch et al., 2005b, Hewes, 1973, Corballis, 2003). One proposed modality of language evolution is that of vocal communication, which is defined as the interaction of at least two individuals within a species, where production of auditory signal made by the vocal tract is perceived by and changes the behaviour of another individual (Bradbury and Vehrencamp, 1998).Vocalisations are important in investigating human language evolution because the primary modality of human language is vocal and vocalisations possess certain features homologous with human language such as functionally referential usage (Fitch, 2005).

On the other hand, primate gestures such as communicative movements of the head, limbs, bodily postures and locomotory gaits are more cognitively complex than vocalisations and display several characteristics, which are more similar to human language, such as flexible use and cultural transmission (Tomasello and Zuberbühler, 2002, Tomasello and Call, 2007, Whiten et al., 1999, McGrew et al., 2001). In particular, manual gestures such as communicative movements of hands without using or touching objects are important (de Waal, 2003). Manual gestures are neurologically distinct from other types of gestural communication because only the brain structures underlying manual gestures are homologous with those areas responsible for human language (Rizzolatti et al., 1996a, Rizzolatti et al., 1996b, Perrett et al., 1985). While many primate species commonly communicate with calls, facial expressions or bodily movements, only apes and humans frequently communicate with hands (de Waal, 2003, Pollick and de Waal, 2007). While the homologies between primate calls and language have been relatively well explored, we have a relatively limited understanding of how cognitive abilities may have shaped characteristics of primate gestures (Corballis, 2003). However, it is important to investigate how features of cognition and gestural communication in our primate relatives compare with the characteristics of cognition and communication evident in human language. Gestural communication operates in a complementary fashion with a vocal mode of communication (Kendon, 2004) and may involve complex cognitive processes because signallers use gestures intentionally which implies that they may make informed choices which may be based on mental representations (Tomasello and Zuberbühler, 2002).

Wild East African chimpanzees (*Pan troglodytes schweinfurthii*) are among our closest living relatives (Olson and Varki, 2003) and display complex cognitive skills in various aspects of their social behaviour in captivity such as ability to understand that others are intentional beings with perspective states which may differ from one's own but which can be altered by communicative behaviour (Hare et al., 2001, Hare et al., 2000, Kaminski et al., 2008). However, the extent to which these abilities seen in captive apes are acquired via contact with humans or are typical of chimpanzees in general remains unclear (Call and Tomasello, 1996, Boesch, 2008, Tomasello and Call, 2008, Boesch, 2007). Therefore, it is also important to investigate cognitive capacities in wild ape populations, because their social and ecological environment may shape their cognition in a manner that is more characteristic of the social and ecological environment of the last common ancestor when compared with that of captive populations.

Additionally, the extent to which the cognitive capacities and communicative behaviours observed in captive chimpanzees have been enhanced by socio-cultural environment of captivity, or how these may vary with different degrees of enculturation, remains unclear (Call and Tomasello, 1996). In particular investigating cognitive skills underlying communicative behaviour in language trained chimpanzees could provide an important insight into chimpanzee communication (Call and Tomasello, 1994). This is because language-training represents the most intense form of enculturation and linguistic interaction may play a causal role in understanding that others have beliefs and intentions (Garfield et al., 2001). Thus, examining the cognitive skills underlying gestural communication in language trained chimpanzees may illuminate how social and cultural pressures may have shaped the cognitive abilities of our hominid ancestors, and perhaps also indicate how these pressures could have led hominids to acquiring symbolic capacities of language.

In this Ph.D. thesis I aim to explore homologous traits in the cognition underlying chimpanzee gestural communication and human language. Specifically, I attempt to explore the repertoire of manual gestures and the underlying role of intentionality in gesture use in wild and language trained chimpanzees. While prior research on the repertoire of manual gestures has provided a descriptive repertoire of gestures in chimpanzees primarily reared in captivity, very little is known about manual gestures in wild chimpanzees and the structural analysis of repertoire in both contexts is missing. Moreover, prior research on the intentions underlying gestural communication in captive chimpanzees has suggested that they display sensitivity to the visual awareness of the recipient. However, little is known about understanding intentions in wild chimpanzees and whether intentionality underlying gesture use can be seen in both signaller and recipient behaviour. Moreover, there is currently limited insight into how understanding of intentionality would compare in wild chimpanzees and chimpanzees exposed to language training.

This Ph.D. thesis is the first systematic analysis into gestural communication in wild East African chimpanzees and captive language-trained chimpanzees using a comparative approach. The comparative method constitutes a special, strategic tool with which to tackle the problem of language evolution because it allows us to explore fundamental questions about the evolutionary pressures that accompanied the transition from pre-linguistic to linguistic communication, and how these evolutionary pressures may have shaped our common ancestor's system of cognition and communication.

BACKGROUND

Studying human behaviour from an evolutionary perspective allows a unique understanding of the function of human behaviour, by providing insights into questions such as how behaviour influences the genetic fitness of the individual, and how this is subsequently expressed in the gene pool of the future generations (Dunbar and Barrett, 2007). To date, we have good evidence for how the behavioural strategies of our ancestors have been shaped to maximise their fitness. For instance, using paleontological remains we are able to deduce at what stage in human evolution humans manufactured complex tools, and developed rudimentary forms of art and religion (Barrett et al., 2002). Whilst we have relatively good insight into various aspects of life of our hominid ancestors, the evolution of language is still largely hypothetical. The lack of 'fossilisation' of language prior to the arrival of writing has made it difficult to draw inferences about the presence and form of language in our hominid ancestors (Fitch, 2005).

An important first step in examining the evolution of a faculty for language is to distinguish its various constituent properties (Hauser et al., 2002b). Viewed as a system of cognition and communication, the key areas of inquiry in language evolution are the definition of language, its fundamental function and its phylogenetic antecedents (Tinbergen, 1963). Hauser and colleagues (2002b) distinguish between two main mechanisms involved in language, i.e. broad and narrow language faculties. Broad language faculty defines any mechanisms involved in language in a broad sense (see Hockett and Altmann, 1968a for detailed description of design features of language), while mechanisms that are specific and unique to human language are a subset of broad language faculty and are defined as the narrow language faculty. Determining homologies between primate communication and the narrow language faculty is important because it allows research efforts to focus on those key innovations which characterised the transition from pre-linguistic to linguistic communication in humans. Additionally, determining those traits of communication that are different from the communicative system of our closest living relatives, but are analogous with traits in other more distant taxa, is a key issue because it allows us to determine which adaptive pressures selected for language, and how these pressures have shaped the form and function of human language faculty (Fitch, 2005).

When exploring language evolution it is important to focus on the narrow language faculty and to distinguish questions concerning language as a system of communication from those questions concerning the cognitive mechanisms underlying language (Hauser et al., 2002b). This is because the central cognitive capacities of language may have evolved due to non–communication related selective pressures, but were reshaped due to the constraints imposed by the communicative requirements of language. In terms of the narrow language faculty, the key components of this communicative system are speech, syntax and semantics (Fitch et al., 2005b). Speech is defined as the principal signalling modality of language, which relies on reconfigured vocal apparatus for the production of a range of sounds, and vocal imitation as a mode of acquisition. Syntax is understood as an open-ended system, which allows parsing and production of hierarchical structures within language to allow greater communicative flexibility. Finally, semantics is defined as encoding of an unlimited set of distinct propositional meanings in language which may involve both concrete and abstract meanings (see e.g. Fitch, 2005 , Hockett and Altmann, 1968a for more detailed information on these principle components of language).

Whilst we now understand relatively well that none of these narrow language characteristics such as speech, syntax and semantics are present in the natural communication systems of any great ape species, the presence or absence of the cognitive abilities underlying these communicative abilities is less clear (Tomasello and Zuberbühler, 2002). However it is important to investigate the cognitive processes underlying primate communication, rather than simply how they communicate. This is because language is inseparably bound up with human cognition and language is critically important for human thought and mental processing (Tomasello, 2008). Furthermore, whilst there may be limitations on the capacity to express cognitive abilities in one communicative modality, the cognitive abilities displayed by apes in other communicative modalities may indicate that a certain degree of continuity in language may be present in our closest living relatives (Burling, 1993, Hewes, 1973). That is, rather than asking whether primates have language, we should instead look for the component features that are the building blocks of the capacity for language, allowing us to evaluate whether these abilities are widespread across a range of species or more species specific (de Waal and Ferrari, 2010).

“Cognition, broadly defined, includes perception, learning, memory and decision making, in short all the ways in which animals take in information about the world through the senses, process, retain and decide to act on it” (page 278, Shettleworth, 2001). Behaviour which involves complex cognitive processing is different from other behaviours, which include simple associations and reflexes that are tied to particular emotions, because the former are underpinned by an ability to voluntarily control one's behaviour and this allows greater behavioural flexibility. The ability to manipulate others behaviour and mental states in response to the perception of particular goal states indicates cognitive complexity (Tomasello and Call, 1997). Cognitive abilities are particularly important in language use and acquisition. For instance, learning by imitation is a complex cognitive skill that is necessary for developing linguistic communication because language is based on an ability to generate and learn a large and open-ended lexicon of words (Fitch, 2005). Additionally, a cognitive ability to recognise and to act upon the behavioural or mental states of others is important in language use because language is a social tool primarily adapted to directing a recipient's attention and imagination, so that the recipient will do, know or feel what the signaller wants to convey (Tomasello, 2008).

To date, research in primate communication has primarily examined important aspects of cognitive abilities in relation to the vocal communication systems (Tomasello and Zuberbühler, 2002). The evidence suggests that primates may have certain representational abilities indicated by functionally referential calls in many primate species that can reliably provide recipients with information about the presence of predators or food in the environment (Zuberbühler, 2009). For instance, vervet monkeys use different alarm calls in association with different predators leading to different escape responses in recipients; perceiving the call or the predator itself elicits the same specific response (Seyfarth et al., 1980). Chimpanzees in captivity produce acoustically different food grunts in response to quality of the food eaten (Slocombe and Zuberbühler, 2006, Slocombe and Zuberbühler, 2005). Additionally, there is evidence in vocal communication for audience effects, where the signaller's vocal behaviour is affected by social characteristics (such as relative dominance or familiarity) or the presence or absence of conspecifics. For instance, Townsend and Zuberbühler (2009) have shown that East African chimpanzee females suppress production of copulation vocalisations in presence of other dominant females. Gouzoules and colleagues (1984) have shown that rhesus macaques produce acoustically different scream variants as a function of aggression severity, relatedness and the relative rank of the opponent.

On the other hand we also currently understand that certain skills of language cognition are absent in primate vocal systems. For instance, it has been shown that signals are not intentional from the sender's perspective; signallers do not attempt to inform others about presence of external referents but instead vocalisations just express their emotional states. For instance, vervet monkeys continue producing alarm calls when the response of the recipients relative to external referent has already been made (i.e. vervet monkeys have already escaped to safety, Seyfarth et al., 1980). Chimpanzees continue producing loud pant-hoot calls upon finding patches of food even if the whole community is already feeding on the food tree (Clark and Wrangham, 1994). This lack of complex cognitive skills underlying vocal behaviour is further supported by findings from vocal development in primates and demonstrates inability of primates to invent and acquire new sounds from other individuals. For instance, cross-fostering of Rhesus monkeys and Japanese monkeys produces no significant changes in the repertoire or structure of their species-typical vocalisations (Owren et al., 1992). Additionally, language-trained ape subjected to years of language instruction is unable to acquire any substantial vocabulary of words (Hayes and Hayes, 1951). This apparent lack of cognitive skills in the vocal domain of communication may not reflect overall limitations of primate cognition, but rather the difficulty of the communicative mechanism to control vocal output (Lieberman, 1968, Fitch, 2000). Whilst the basic vocal tract anatomy of primates would support production of language, neural connectivity responsible for detailed voluntary control of the vocalisations and the capacity to link auditory input to corresponding motor outputs are lacking in our primate relatives (Jurgens, 1998).

Whilst we have a relatively good understanding of cognitive capacities underlying vocal behaviour in primates, such capacities in gestural domain are still poorly understood (Hewes, 1973, Corballis, 2003). However, it is important to understand what cognitive characteristics underlie gestural communication in primates. Whilst features of cognition make primate vocalisations an unlikely sole candidate for an evolutionary precursor to human language, it is possible that the cognitive skills underlying language evolution are present in the gestural modality of communication (Corballis, 2003, Hewes, 1973, Burling, 1993). This is because primates have a greater voluntary control over their limbs than their vocal output and more important similarities with human language can be observed in the gestural modality in many areas of cognition such as learning, symbolic communication and intentionality (Tomasello and Zuberbühler, 2002). For instance, whilst vocal cultures have not yet been shown among any of the primate species (Pollick and de Waal, 2007), gestural cultures in chimpanzees have been reported both in the wild (see e.g. hand clasp, leaf clipping and missile throw, McGrew and Tutin, 1978, McGrew et al., 2001, Whiten et al., 1999) and in captivity (Pika et al., 2005b, Pika et al., 2003). Additionally, whilst chimpanzees display an inability to learn vocal modifications, they have ability to acquire and use symbolically many gestures of American Sign Language, which they are then able to transmit culturally to their offspring (Gardner et al., 1989).

When elucidating the cognitive skills underlying gestural communication, manual gestures are particularly important, defined as communicative movements of hands without using or touching objects. This is because manual gestures are neurologically distinct from other types of gestural communication, such as bodily movements and locomotory gaits. Broca’s area is a region of the hominid brain with functions linked to speech production (Broca, 1861). The ape Brodmann’s area 44, which is homologous with humans’ Broca’s area, is enlarged in the left hemisphere (Cantalupo and Hopkins, 2001). In contrast to vocalisations, monkeys' Brodmann's area is activated during both the production and perception of manual movements (Rizzolatti et al., 1996a, Rizzolatti et al., 1996b, Perrett et al., 1985). These neural structures underlying manual gestures in the great apes, are homologous with the language areas in the human brain, suggesting an important link between language and primate manual gestures, but not primate calls or other primate bodily movements (Corballis, 2003). Additionally, while many primate species commonly communicate with calls, facial expressions or bodily movements, manual gestures are typical only in humans and other great apes (de Waal, 2003). This lack of homology between Hominoidea and all other primate species regarding manual gestures, indicates a shift towards a more flexible and intentional production for manual gestures in our pre-hominid ancestors prior to emergence of vocal language (Corballis, 2003).

Despite the importance of manual gestures to understanding of cognitive skills underlying human language evolution, to date, few studies have addressed the cognitive skills underlying manual gestures, such as repertoire and intentionality of production and comprehension. The study of a species' repertoire is an important prerequisite to understanding the cognitive processes underlying human language evolution because it helps us to understand the breadth of relevant traits of the communicative system, and which traits could be homologous with the human communicative repertoire (Altmann, 1967). The repertoire of communicative signals can be defined as a collection of actions or cues within a species which are used to initiate change in behaviour of a recipient (Bradbury and Vehrencamp, 1998). Analysis of the repertoire of communicative signals is an important first step in addressing questions about the phylogeny of communication and provides a basis for comparative investigations of function, ontogeny and adaptive significance of communicative signals (Altmann, 1967).

Additionally, the study of intentionality in communication also informs our understanding of the cognitive processes underlying language evolution. Intentionality is one of the most cognitively demanding features of human language and the emergence of communicative intentions is a foundational capacity required for the ability to acquire words in human infants (see e.g. Baldwin, 1995, Olson, 1993 for detailed discussion of why intentionality is important for development of language). Intentionality can be defined as such state of perception whereby interactants understand that others have goals and intentions different from one's own (Tomasello and Call, 1997). Intentionality in communication is a key prerequisite for human language because language is a form of social activity composed of linguistic conventions, with signal production motivated by the perception of a recipient's mental states, in terms of the desire of the signaller to request, inform or share social or other goals and beliefs (Tomasello, 2008).

Investigating the capacity for intentional communication in our primate relatives is important because it can provide key insights into the level of representations that the primates are able to maintain and therefore the complexity of their cognitive processing. For instance, primates may display cognitive abilities for primary, secondary or meta-representations. Primary representation relates to a direct, singular and current assessment of the world where individual acts through simple association between the current and preceding behaviours. On the other hand, secondary representations are more complex because these involve the ability to model hypothetical or nonexistent situations (e.g. the past and future) and entertain multiple models, such as attributing intentions or attentional states to another person (Perner 1991).This ability to form secondary representations gives rise to an understanding of a key characteristic of mind, which is 'aboutness', i.e. understanding of one's own goals and goal directed actions and importantly, that others have intentions and goals that can be different from one's own (Suddendorf and Whiten 2001). Additionally, an ability to form secondary representations allows an individual to mentally process the desired goal state; taking necessary steps to achieve that goal state, as evidenced by monitoring and amending of the goal-directed behaviour until the desired goal state is achieved (Piaget 1954; Bullock and Luetkenhaus 1988; Deloache et al. 1985). The study of repertoire and intentionality in primate manual gestures is thus important to understanding language evolution and provides vital insights into the cognitive underpinnings of communication in our closest primate relatives.

Most of our knowledge about chimpanzee gestural communication comes from studies of gestural behaviour in captivity (see e.g. Liebal et al., 2004a, Leavens et al., 1996, Leavens and Hopkins, 1998, Tomasello et al., 1984, Tomasello et al., 1985, Tomasello and Frost, 1989, Tomasello et al., 1994, Tomasello et al., 1997). Gestural communication in free-ranging chimpanzees has not been studied systematically and existing studies are primarily descriptive and based upon opportunistically sampled data on gestural repertoire. For instance, the gestural communication of the Kasakela group of Gombe (Tanzania) in East Africa, with a special focus on adults, was described by Goodall (see e.g. Goodall, 1986, van Lawick-Goodall, 1968). She found that gestures are used in variety of contexts, such as aggression, affiliation and courtship. These observations were later supplemented by observations on infants in the same group by Plooij (1979). McGrew and Tutin (1978) described grooming hand-clasp as a first case of a communicative behaviour described as a social custom in chimpanzees. Systematic cross-site comparisons also indicated that other gestures are population specific in wild chimpanzees, such as leaf clipping and missile throw (Whiten et al., 1999).

Moreover, the repertoire of manual gestural communication in chimpanzees both in captivity and in the wild has received limited research attention and has generally been reported within a broader framework, focusing on all communicative bodily movements and facial expressions. The catalogues of manual gestures in captivity were compiled in greatest detail by van Hooff (1971), Tomasello with colleagues (Tomasello et al., 1985, Tomasello and Frost, 1989, Tomasello and Camaioni, 1997, Tomasello et al., 1997, Tomasello et al., 1984), Liebal with colleagues (Liebal et al., 2004a) and Pollick and de Waal (2007). For instance, Pollick and de Waal (2007) reported 16 manual gesture types in captive chimpanzees, such as arm raise, reach out down and point. In terms of wild populations, the only reports of manual gestures come from same chimpanzee Kasakela group at Gombe (Tanzania) described by Plooij (1979) and van Lawick-Goodall (1968). For instance, van Lawick-Goodall (1968) reported 14 gesture types and Plooij (1979) reported 17 gesture types such as beckoning, begging with hand and arm high (see table 2.11 in Chapter 2 for more details on gestural repertoires described in these studies).

Whilst we know relatively little about manual gestures in chimpanzees in general, there is even less knowledge about how the repertoire of gestures could be structured in terms of distinctiveness of precise morphology across gesture types. Only the grooming hand-clasp has been studied in terms of precise morphology of gestural communication and how this might vary across populations. For instance, McGrew and others (2001) reported two types of grooming hand-clasp: palm to palm hand-clasp and non palm to palm. In the first type of grooming hand-clasp, two chimpanzees clasp each other’s hands and there is mutual palmar contact. In the second type, there is no palmar contact, wrists are flexed and one limb is resting on the other’s limb. McGrew and colleagues (2001) examined photographs and videos of these hand-clasp types across two chimpanzee communities, focusing on the precise morphological features of each hand clasp type. They reported that while K-group displayed both hand-clasp types, in M-group only non palm-to palm hand-clasp was found. In extension to this study Nakamura and Uehara (2004) examined gradation within hand-clasp types by measuring angles of the wrist and the elbow as well as palm contact. They found that a flexed type of grooming hand-clasp occurred only in M-group, and that individuals displayed consistent tendencies for wrist angles but not elbow angles. These findings are foundational to our understanding of how differences between populations emerge in communicative behaviour, because they explain how communicative behaviour could be acquired and transmitted across generations within populations and thus how ‘culture’ could be formed in the populations. To date, however, no other studies have attempted to identify specific morphological features characteristic of manual gestures, or explore whether such variation in features could be quantified statistically both within and between gesture types.

Moreover, whilst we know very little about repertoire and morphology of manual gestures in chimpanzees, this situation is exacerbated by a lack of any intentionality criteria applied when considering ethograms from wild populations. However, it is important to investigate whether the observed signal is voluntary because the distinction between simple behavioural actions, which may be used by others to infer intentions, and meaningful gestural communication lies in determining whether the action is used intentionally (Doherty-Sneddon, 2003, Leavens and Hopkins, 1999). For example, activities which regularly precede a particular event, such as those that indicate changes in activity state (i.e. between resting and locomotion), can become communicative to the receiver although this signal is unintentional from sender’s perspective (Tomasello and Call, 1997).

In human intentional communication, interactants understand one’s own and other’s goals, beliefs and intentions and act flexibly in terms of the means of directing a recipient’s attention and imagination so that the recipient will do, know or feel what the signaller wants to convey (Tomasello and Call, 1997). Using criteria operationalized for defining intentional behaviour in human pre-lingustic infants, studies in captivity have shown that great apes use their gestures socially, i.e. signallers display sensitivity to the presence of an audience when producing their gestures (Leavens et al., 2004). Signallers are sensitive to the recipient’s attentional state, gesturing more often when recipient is already looking at them (Tomasello and Camaioni, 1997), as well as using attention-getting behaviour in absence of visual attention from recipients (Krause and Fouts, 1997b). While these studies have shown flexible use of gestures in response to both the presence and visual attention of an audience, a more compelling set of supporting evidence for complex cognitive skills underlying gestural communication comes from reports of communicative persistence and elaboration. Persistence can be defined as the continued production of the same signal. Elaboration is defined as substitution of original signals, which have failed to communicate the goal, with different signal types used until the goal is obtained (Bates et al., 1979). The cognitive abilities underlying persistence and elaboration are important because they suggest that apes may be capable of secondary representation such as means-ends reasoning, i.e. that individuals recognise others desired goal state and understand which necessary steps need to be taken to achieve their goals (Perner, 1991). Moreover, the cognitive processing underlying persistence and elaboration in communication is demanding because individuals may be attributing mental states to their recipients when attempting to achieve their goals (Suddendorf and Whiten, 2001).

Despite the importance to understanding of cognitive skills underlying language evolution in humans, to date only a few studies have addressed the ability of great apes to persist in their communicative attempts in interactions between conspecifics. However, when interacting with humans, chimpanzees exhibit both persistence and elaboration in gestures and vocalisations when an experimenter fails to deliver the desired object (Leavens et al. (2005b). Cartmill and Byrne (2007b) observed that orangutans not only persist in their communicative attempts when faced with communicative failure, but also they modify their gestural communication flexibly to take into account recipient's state of comprehension when their goals are not met or only partially met. Although this previous research has contributed to our understanding of persistence and elaboration in great ape gestural communication, we still have only a limited understanding of whether great apes intentionally persist and elaborate in their communication. For instance, these studies did not make any assumption about whether these sequences of gestures were directed towards achieving a particular goal. However, without the assumption that the gestures were made towards specific goals and identifying what these goals were, inferences about the success or failure of communication cannot be made when examining intentional persistence in sequences of gestures (Golinkoff, 1986). Additionally, previous studies on persistence and elaboration in communicative attempts have included clearly stereotypical behaviours in their analysis, rather than focusing on gestures alone. However, stereotypical behaviours are not used purposefully to influence the behaviour of recipient to achieve desired goals by use of communication. Thus, the fundamental requirement of persistence, that signallers direct their communication at a recipient with a priori knowledge of the effect that the signal will have on the recipient (Bates et al., 1979, Bates et al., 1975) is not met in those analyses. Finally, none of the previous studies on elaboration and persistence have focused on manual gestures but instead all bodily movements were taken into account. However, it is important to examine manual gestures in particular because manual movements are neurologically distinct from other types of gestural communication and may be underlined by more complex cognitive processing than other gesture types.

Moreover, whilst we already have some insights into the signaller’s understanding of other’s goals and comprehension states and how signallers act flexibly to direct a recipient’s behaviour, almost nothing is known about the recipient’s understanding of the signaller’s intentions, or how recipients comprehend gesture meanings in light of a signaller’s ultimate goals and intentions. Such contextually defined comprehension of gestural signals requires that the recipient understands not only the semantic content of a gesture, but also takes the goals of the signaller into account when deciding how to respond, and infers the common cooperative goal of the signaller from the combination of gesture with context (Grice, 1975, Levinson, 1983). In most primate studies, contextually defined comprehension has been operationalised as the use of communicative signals, where one signal type is associated with variety of contexts and one context is associated with variety of gesture types, i.e. one to many rather than one to one relationship between gesture and context (Pollick and de Waal, 2007, de Waal, 2003, Pika and Tomasello, 2002). Using these criteria, to date studies across all captive species of great apes have demonstrated that gesture comprehension is contextually defined and thus concluded that gestures have no specific meanings; responses are determined by the recipient's perception of overall context. On the other hand, studies have also indicated that gesture comprehension could also be semantic because some gesture types reliably receive specific responses regardless of the context in which they are used (see e.g. Genty and Byrne, 2009).

This dichotomous view of the gesture comprehension system in primates suggests that relying on either the relationship between gesture type and context or receiver's response alone may not be an adequate criterion for determining contextually defined usage. This is because the context of gesture production alone cannot tell us if recipients take the signaller's goal into account in deciding how to respond to a gesture. Additionally, looking at recipients' responses without taking into account the ultimate goals of signaller is not particularly informative about the signaller's intentions and how recipients account for these in responding. However, it is important to address this question systematically because the cognitive abilities underlying contextually defined comprehension are complex and would suggest that individuals may be capable of shared intentionality and secondary representation, in contrast to semantic comprehension of gestures which could rely predominantly on automatic responses (Tomasello, 2008). To date however, no studies have addressed the issue of comprehension of gestures using a systematic approach and we therefore lack clear data on whether great apes possess skills of contextually defined gesture comprehension.

Finally, almost all of the studies to date concerning cognitive skills underlying gestural communication in great apes have been done in captivity. It therefore remains contentious whether the cognitive skills underlying communicative behaviour in great apes are an artefact of rearing conditions. For instance, Tomasello and Call (2004) claim that great apes raised in normal captive conditions (as opposed to intense language training rearing conditions) develop an understanding that other individuals have goals and comprehend the importance of others' visual perception in relation to knowledge states (i.e. that others are intentional beings). They attribute these cognitive capacities in captive apes to extensive contact with human interactants, especially during ontogeny. The contact with humans is important because humans interact with captive apes in different ways than their conspecifics, for instance by attempting to direct their attention towards self or third objects or events. When humans display these behaviours towards captive apes, captive apes acquire a different set of social skills than their wild conspecifics, specifically suited for contact with humans. For instance, Tomasello and Call (2004) have shown that captive apes that varied in the degree of enculturation also varied in their degree of understanding of accidental actions versus intentional goals. Itakura and Tanaka (1998) also found that captive chimpanzees with the most exposure to contact with humans performed best when using experimenter given cues to solve an object-choice experimental paradigm concerning communicative outcomes.

Language-trained apes are of particular relevance to this debate; they not only routinely interact with humans during every day activities but are specifically trained to produce and comprehend linguistic and nonverbal conventions (Call and Tomasello, 1996). Linguistic interaction is of paramount importance in the current context because it plays a causal role not only in understanding that others have goals and visual attention but more importantly it is fundamental in the development of understanding that others have intentions and beliefs (Garfield et al., 2001). For instance, Call and Tomasello (1994) reported that Chantek, an orangutan who underwent a ape sign language training programme, was able to comprehend the function of human pointing significantly better than the chimpanzee reared in more standard captive conditions.

While these theoretical considerations of social cognitive enhancement appear plausible in light of data from captivity, some authors interpret these findings with caution and instead suggest the need for further systematic studies of cognitive skills underlying social behaviour in wild apes. For instance, Suddendorf and Whiten (2001) argue that apes develop their most sophisticated cognitive skills in the wild and that the apparent effects of enculturation on cognition and behaviour in captive apes are due to differences in degree of impoverishment of the social environment rather than its enhancement (see also Boesch, 2007, Boesch, 2008). Bering (2004) suggests that great ape cognition in captivity does not change in any fundamental way when interacting with humans, but rather that interactions with humans lead to a change in behaviour in that these apes acquire different problem solving skills on novel objects. For instance, humans may influence the subjects' cognitive and affective states by modifying the subjects' behavioural strategies whenever apes fail to achieve their desired outcomes, and in turn, subjects learn that observing and reproducing human actions is the most effective way of accomplishing their desired goals.

However, it is currently difficult to fully assess whether the cognitive skills underlying intentional communication as displayed by captive and language-trained chimpanzees are acquired via contact with humans or are a synapomorphic trait with our common ancestor. Moreover, it is difficult to assess whether human contact and linguistic instruction only transform pre-existing cognitive skills in captive great apes, or whether these experiences during ontogeny create a novel set of cognitive abilities (Tomasello and Call, 2004). Answering these questions is important because they have wider implications for the questions about the evolution of the cognitive skills underlying language evolution. For instance, it is still unclear whether the last common ancestor of humans and chimpanzees possessed certain components of our human social cognition and evolution modified those pre-existing cognitive skills into more complex abilities, or whether the cognitive processing underlying the capacity for intentionality is a uniquely human development, arising rapidly since our split from other apes with no previous pre-existing skills of social cognition in the common ancestor of humans and chimpanzees (Bering, 2004). These questions cannot be addressed systematically, because the cognitive skills underlying communicative behaviour in wild great ape populations have to date not received sufficient research attention.

There is a paucity of data on the cognitive skills underlying communicative behaviour in wild apes and moreover, our knowledge is mainly based on largely anecdotal or qualitative accounts. For instance, Matusmoto-Oda and Tomonaga (2005) reported three episodes where individuals intentionally controlled the sound of leaf clipping, which suggests that chimpanzees may understand that other chimpanzees comprehend the causal relationship between the sound production and subsequent events. Until recently, field studies of cognitive skills underlying communication have been largely anecdotal because of an assumption that field studies have no role in understanding the cognitive basis of behaviour (Byrne, 2007). For instance, in most instances it is not possible to subject wild apes to controlled experimentation in the field and to compare the performance of wild apes on cognitive tasks directly with that of laboratory animals (Bering, 2004). However, it is important to investigate social cognition in wild apes using observational methods because free-ranging apes may differ from captive populations, in terms of the selective pressures involved in learning and the acquisition of behaviour. Thus, the comparative study of the cognitive skills underlying gestural communication in free-ranging chimpanzees, and language trained chimpanzees, is a necessary and important addition to the existing data on captive chimpanzees, in order to explore the potential influence of human rearing and instruction on the cognition underlying use of communicative gestures.

AIMS OF THE STUDY

This study of cognition underlying gestural communication in wild and language trained chimpanzees aims to contribute to the debate of the evolution of language, specifically in relation to the debate on the evolutionary transition from pre-linguistic to linguistic communication in humans. It will examine which underlying cognitive abilities underlying human language evolution are most likely to have been present in our last common ancestor with chimpanzees and which are unique to humans. Further, it aims to clarify how the gestural repertoire of wild and language trained chimpanzees might resemble hominid communication, in terms of what wild and language trained chimpanzees might understand about their own gestural communication. For instance, do signallers realise that they can influence comprehension states of their recipients to achieve their goals by communicative means? Do signallers know that they can use different means to achieve the same end? Do recipients understand that signallers have specific goals and intentions? Do recipients cooperate with individual gestures even if overall the signaller's intentions are not immediately beneficial to them? I will examine these research questions in the first systematic study into the repertoire and intentionality underlying manual gestures in the wild chimpanzee community at Budongo Forest, Uganda and a group of language trained chimpanzees at the Language Research Centre, at Georgia State University (Atlanta, USA). By combining an observational and an experimental approach with video analysis I aim to complement previous work in several important ways.

In chapter two I aim to establish an inventory of the gestural repertoire in wild chimpanzees. In contrast to previous qualitative approaches I aim to avoid biases posed by qualitative determination of gesture types and over inclusion of contexts and meanings within gesture types. In order to determine whether quantitative statistical methods can reliably differentiate between gesture types, clustering techniques are used to group morphological components of gestural events, and these groupings are then validated using discriminate function analysis to determine gesture types quantitatively and statistically. Additionally, I aim to examine the distinctiveness of morphology of gesture types and establish quantitative profiles for each gesture type, in terms of each of its morphological components. Finally, I aim to compare the repertoire of manual gestures obtained quantitatively with the repertoire of manual gestures determined qualitatively by previous studies in order to assess the efficacy of the quantitative methodology.

In chapter three, I evaluate the evidence that wild chimpanzee communication is goal directed by examining evidence of persistence and elaboration in the face of communicative misunderstandings. These data will be used to explore whether chimpanzees have a priori knowledge that these goals can be achieved by use of gestures. Specifically I examine whether these communicative repairs are just stereotypic and frustrated reflexes in response to a recipient's lack of responsiveness, or whether chimpanzees do in fact repair their communicative failures in more flexible, creative and cognitively demanding ways. Finally, I aim to address whether chimpanzees are able to evaluate their own level of communicative success and manoeuvre recipients towards achieving the desired goal, as evidenced by a display of specific repair tactics to aid recipients' comprehension.

In chapter four, I build upon the findings of the chapter three and explore wild chimpanzee understanding of signaller's goals and intentions. I examine the characteristics of chimpanzee gesture comprehension by using a novel approach; looking more closely at the congruence of responses with the predicted meaning of a gesture, and importantly in relation to relative rank of the recipients to determine semantic meanings of gestures. I aim to determine the goals of the signaller quantitatively by looking at types of behaviours which occurred at the end of each communicative episode. Based on this determination of a signal meaning and signaller's goals, I am able to examine whether recipients understand the signaller's goals and intentions, and whether recipients accept or reject gesture requests differently in relation to the type of goal intended by the signaller, namely whether it is a cooperative or competitive goal.

Finally, in chapter five I attempt to further explore role of understanding intentions in shaping communicative strategies in chimpanzees exposed to language-training procedures using an experimental approach. Although the task is based on previous studies with captive apes, I examine a more complex task that requires cooperative communication between a knowledgeable chimpanzee and a naïve trainer in order to locate a hidden food item. Thus, I aim to examine whether language-trained chimpanzees persist and elaborate in their gestural communication in response to failure of comprehension by the experimenter. Moreover, with this approach I attempt to gain insight into whether language-trained chimpanzees comprehend function of the pointing gesture and adjust their signalling behaviour accordingly.

We address these research questions in chimpanzees (*Pan troglodytes*) in the wild and in captivity. Chimpanzees are a good model species to investigate homologous traits in cognition and communication with human system of communication and cognition because they are genetically our closest living relatives together with bonobos (who are equidistant ;Olson and Varki, 2003) and they display several important cognitive skills in both physical and social domains of cognition. Chimpanzees have been shown to display social awareness as evidenced by sensitivity to other's visual attention, gaze following and acts of tactical deception (Tomasello and Carpenter, 2007). Further, chimpanzees utilise these complex skills of social awareness in managing demands of life in the wild in the complex fission-fusion social system. For instance, wild chimpanzees remember and are able to track other's social relationships, despite frequent lack of physical proximity form coalitions to achieve their social gains (Newton-Fisher, 2006). It is therefore important to examine how these complex skills of social cognition would shape the communicative system of manual gestures in chimpanzees. In this thesis, I present a systematic study of cognition and gestural communication in wild and language trained chimpanzees.

Chapter 2: Formulating a dictionary of wild chimpanzee manual gestures - statistical analyses of a graded repertoire system

BACKGROUND

A key component in understanding the origin of traits of human language is to understand the breadth of traits of communicative system in our closest living relatives (Zuberbühler, 2005). Analysis of the repertoire of communicative signals is an important first step in addressing questions about the phylogeny of communication and provides basis for comparative investigations of function, ontogeny and adaptive significance of communicative signals (Altmann, 1967). The repertoire of communicative signals can be defined as a collection of actions or cues within a species which are used to initiate change in behaviour of a recipient (Bradbury and Vehrencamp, 1998). In particular, the gestural repertoire, such as movements of hands without the use of objects is important; manual gestures are among a few ancestral traits within the communicative repertoire that humans share with their primate relatives and may be an evolutionary precursor to a spoken language (de Waal, 2003).

Whilst preliminary first steps towards compiling the repertoire of gestural communication have already been made for some primate species (see e.g. Pollick and de Waal, 2007), these accounts have only been descriptive and contain biases posed by descriptive methodology, such as a difficulty in establishing and maintaining the same level of categorisation. On the other hand, more systematic quantitative assessment based on statistical determination of the units of gestures has not been carried out and a unified framework for the quantitative analysis of gestural communication in primates is lacking. East African chimpanzees (*Pan troglodytes schweinfurthii*) are our closest living relatives (Reynolds, 2005) and display features of social life and ecology characteristic of the early humans populations such as fission-fusion society on the forest/savannah interface (Goodall, 1986). The study of the gestural communication in wild chimpanzees is therefore an important first step towards our better understanding of the probable features of gestural communication in our common ancestor and the adaptive pressures which led early humans into the development of the language.

Many authors in search of phylogenetic origins of human language have focused their research efforts on compiling the repertoire of chimpanzee facial expressions and vocalizations (see e.g. van Hooff, 1971, van Hooff, 1967, Parr et al., 2007, Parr et al., 2002, Marler and Tenaza, 1977, Marler and Hobbett, 1975, Marler, 1969, Mitani et al., 1999, Mitani et al., 1996, Mitani, 1996). Repertoire of manual gestural communication in chimpanzees to date received limited research attention and has been studied within broader framework of the whole gesture repertoire focusing on all communicative bodily movements.

Additionally, repertoires of manual gestures have primarily been described for captive populations. These catalogues of gestural behaviour from captivity were compiled in greatest detail by van Hooff (1971), Tomasello (Tomasello and Zuberbühler, 2002, Tomasello et al., 1985, Tomasello and Frost, 1989, Tomasello and Camaioni, 1997, Tomasello et al., 1997, Tomasello et al., 1984), Liebal (Liebal et al., 2004a) and Pollick (Pollick and de Waal, 2007). Moreover, some research effort has been made to compile repertoires of gestural communication in wild populations of chimpanzees. The Kasakela group of East African chimpanzees in Gombe (Tanzania) is among the most extensively studied chimpanzee groups in Africa (see e.g. van Lawick-Goodall, 1968, van Lawick-Goodall, 1967, Goodall, 1986, Plooij, 1978, Plooij, 1979 see also, Sugiyama, 1969, Nishida, 1970, Nishida et al., 1999, 2010, Reynolds, 1963 for gesture reports from other chimpanzee populations).

Whilst gesture repertoire studies in captivity have been reasonably systematic, gesture research in the wild has been mainly opportunistic and is frequently based on gesture categorisations by usage rather than morphology. Gestural repertoires have not been studied systematically in the wild because until recently it was believed that the behaviour of captive apes is representative of wild populations (Byrne, 2007). However to obtain the repertoire representative of typical chimpanzee communication it is necessary to also examine gestures in wild populations. This is because of the influence of different adaptive pressures on cognition underlying gestures in captive apes as opposed to that of wild conspecifics such as frequent contact with humans during ontogeny (Tomasello and Call, 2004). Contact with humans is important because humans interact with captive apes in different ways than their conspecifics, for instance, by attempting to direct their attention towards self or third object or events. When humans display these behaviours towards captive apes, captive apes acquire a different set of communicative skills specifically shaped for interactions with humans compared to their wild conspecifics. For instance, captive apes frequently point to distal objects, a behaviour which is currently thought to be absent in the wild conspecifics (Leavens et al., 1996, De Waal, 2001, Leavens et al., 2009).

Studies of gestural communication in the wild present a good solution to these problems of enculturation because they allow collection of data of natural chimpanzee behaviours, with little influence of humans on the subjects during ontogeny. Studies of wild chimpanzee gestural behaviour are thus the most representative of the typical chimpanzee gestural repertoire and present the best starting point for comparisons of communicative patterns between apes and humans to illuminate likely features of communicative patterns in the common ancestor.

Furthermore, the studies of gestural repertoire have typically been descriptive and consist of a list in which detailed morphology of behaviour patterns is given as descriptively as possible. Whilst detailed descriptions of behaviour patterns form the basis for many behavioural studies, the validity of this qualitative approach may be lower than quantitative, statistical determination of gesture units. For instance, in two descriptive gesture repertoire studies of the same group of chimpanzees, across similar number of observation hours and at the same facility one author reported five manual gesture types (see Liebal et al., 2004a) while others reported sixteen manual gestures (see Pollick and de Waal, 2007). These inconsistent results are found because of the difficulty in objectively deciding what forms of behavioural pattern should be lumped together and what forms should be split up. Additionally, it is difficult to systematically maintain the same level of splitting and lumping when faced with a variety of behavioural characteristics. In chimpanzees, for instance, it is possible to observe a number of different ways in which a signaller extends the hand towards another with its hand movement differing in intensity and hand and arm shape differing in form. The arm extend movement may vary from smooth, sweeping movements to forceful, stretched in a line arm extends. Forceful arm extend may furthermore be divided into movements with fingers stretched or fingers flexed in a fist, arm moving from downwards to above, from upwards to below or straight to the side.

Systematic categorisation of gestures is important because use of too broadly or too narrowly defined elements of behaviour may reduce the validity of results of studies of the homology of gesture repertoires both within and across species. For instance, repertoires which are categorised too broadly are difficult to compare with repertoires of other species; it is difficult to assess whether any behaviours not listed in one species’ repertoire are truly absent or have been lumped with other categories of behaviour. Quantitative analysis presents a good solution to these problems of categorisation because it allows a more objective subdivision of movements without any prior necessity to identify behaviour elements or a priori assumptions as to context or likely function of gestures. It can classify gestures into groups based on a large number of different morphological components and identify statistically the way in which cases should be clustered into groups (Bortz, 1993).

Subsequently, quantitative analysis provides the most rigorous and systematic way to analyse the repertoire of gestural communication. Taking into consideration that quantitative categorisation of gestural behaviour has not yet been done, it is reasonable to argue that current descriptive studies have to progress before gestural repertoires can be reliably described for our nearest living relatives.

The statistical analysis of gesture structure and coding schemes for analysis of a gesture is still in its infancy. As a result, the quantitative profile for each gesture type, in terms of each of its morphological characteristics, is not known; this means we cannot describe which features of a gesture discriminate it from other types and which gestures share similar characteristics. It is important, however, to know the characteristic features of gestural signals because it helps us in understanding the structure of repertoires, such as which repertoires consist of signals with no intermediates between signal types (discrete repertoires), which repertoires have signals which change and grade from one prototypical form to another (graded repertoires) and which repertoires are a mix of the two types (Marler, 1976, Green and Marler, 1979). The structure of a communicative repertoire can in turn aid us with information about social and ecological environments which accompanied ritualisation and evolution of communicative signals. For instance, graded repertoires could be favoured in conditions where individuals live in relatively open habitat and interact at close range with conspecifics. In contrast, discrete repertoires may have evolved to improve signals propagation capacities when signals must operate in unfavourable conditions for visual and contextual transmission (see e.g. Marler, 1976 for more information about evolution of graded and discrete repertoires).

To date, there are no studies which have empirically shown the extent to which gestural repertoires are discrete or graded; it is reasonable to conclude that investigations into repertoires of gestural communication need to develop further before studies of socio-ecological factors underpinning evolution of human language can also be advanced.

Additionally, the structure of a communicative repertoire can inform us about the cognitive and ontogenetic processes underlying gesture production. For instance, patterns of gradation in gesture forms may be replicated across all individuals in the group, indicating a genetically descended gesture structure (Tomasello et al., 1993, Genty et al., 2009, Fischer et al., 2000). Differences in gradation between individuals along the gradient of relatedness and association patterns may on the other hand indicate ontogenetic acquisition of gesture forms (Whiten et al., 1999, Hauser, 1992). Considering that so far there are no studies which have empirically explored variation in gesture structure it is reasonable to suggest that research methodology into the repertoire of gestural communication needs to be advanced further before ontogenetic and cognitive processes accompanying evolution of language can be reliably explored.

The study of gestural repertoire in wild chimpanzees helps us to provide answers for key questions about phylogenetic origin of human communication, such as which communicative behaviours were present in the common ancestor of human and chimpanzees and which gestural behaviours are unique to humans. It aids us in understanding of phylogeny of language as well as ontogenetic and adaptive significance of gesture structure. Thus, in order to advance knowledge in these areas, we provide the first systematic insight into the repertoire of manual gestures in wild East African chimpanzees of Budongo Forest Reserve, Uganda using quantitative analysis. First, we establish an inventory of the gestural repertoire in chimpanzees using commonly used clustering techniques and validating these clusters using a discriminate function analysis. Second, these gestural groupings are compared to previously reported captive and wild repertoires to enable the exploration of the differences in gestural repertoires. Finally, variability in gestural communication is quantitatively catalogued and examined in relation to other modalities of communication to explore possible ontogenetic, social and ecological factors acting upon structure of gestural communication.

METHODS

Study site and subjects

Manual gestures of one community of habituated East African chimpanzees were examined over an 8 month period divided into three study phases (September 2006, April - July 2007 and March - May 2008) at Budongo Conservation Field Station, Budongo Forest Reserve in Uganda (see Appendix 1 for map of Uganda with indication of a study site and Appendix 2 for map of the study site). The study area is situated in western Uganda on the edge of the western Rift Valley (1˚37'- 2˚00'N; 31˚22'- 31˚46'E) at the mean altitude of 1100 m. (Eggeling, 1947). The reserve area covers 793 km^2 and is composed of grassland; forest and semi-deciduous tropical forest with predominantly continuous forest cover of 428 km2 (see e.g. Eggeling, 1947, Reynolds, 2005 for detailed descriptions of floral composition of the study area).

The chimpanzee community under study varied from 76 to 79 individuals (see Appendix 3 for details of all chimpanzees in the community under study), habituated to humans and tolerating human observers at a close distance of approximately 5 m (see table in Appendix 4 for additional details on the observed chimpanzee subjects). In this study the gestural behaviour of 12 adult individuals was examined. Study individuals were selected using the criteria that they did not have limb injuries and that they could be distinguished according to two rank categories (i.e. 3 high-ranking and 3 low-ranking males and females, determined from the Budongo project long-term records). A limited number of individuals without injuries precluded inclusion of larger number of focal subjects. Additionally, we aimed that both sexes were equally represented. A limited number of adult males during the period of study further restricted the number of focal subjects which could be included. All females selected as focal subjects were parous. Additionally, *ad libitum* data on subadult subjects were collected in non-play contexts to expand the data set of gestures in food and locomotion contexts. The data set on subadult subjects contributed a small number of observations, i.e. 15 out of 218 gesture events in total (see Table 2.1).

Table 2.1: Frequency of use of gesture types across focal and ad libitum observations

HCA gesture type	Nick	Bwoba	Musa	Squibs	Kato	Hawa	Nambi	Zimba	Ruhara	Melissa	Kwera	Kutu	Adult male	Adult female	Subadult	Juenile	Infant
Arm beckon (Ab)	1						1					1					
Arm drop (Ad)								1						1			
Arm extend, flexed wrist (Fw)					1												
Arm extend, limp hand (Lh)	2	9	1	4	2	1				2	2	2					
Arm extend, palm stretched (Pp)				1		3											1
Arm extend, palm upwards, hand cupped (Ap)							1			1	1					1	5
Arm extend, palm vertical towards body (Pv)	4					2	4	8	9	13	4	4			1	1	1
Arm flap (Af)	2	2	2		2	2	7		2	4	1	1					
Arm raise (Ar)	2	3	2	1								1				1	
Backward hand extend (Be)											1	1					
Backward hand sweep (Bs)							5	4	1	1	1						
Elbow raise (Er)							1	3	2			2					
Fingers rounded sweep (Rs)							1				1						
Fingers sweep (Fs)				1					1		3						

Fist flail (Ff)											1						
Forceful arm extend (Fe)	1	1					1						2				
Hand bend (Hb)			3	3	6	2	2		1				1	1	1		
Hand clap (Hc)													1				
Hand swing (Hs)			3						2		1						
Reach arm extend (Pe)							1										1
Reach finger swing (Ps)											1						
Reach finger swing/stroke (Pf)							1										
Reach hand swing (Ph)											4						
Reach stroke (Pt)							1									2	
Stiff arm extend (Se)	2		1		1												
Stiff arm extend, palms upwards, closed fists (Sc)			1														
Stiff arm raise, palm downwards, closed fists (Sd)						1											
Stiff swing, bilateral (Sb)	1																
Stiff swing, unilateral (Su)	3	1			1												
Stiff swing, stretched palm (Ss)					1	1											
Total gesture types	9	5	7	5	7	7	12	4	7	5	12	7					
Total gesture events	18	16	13	10	14	12	26	16	18	21	21	14	4	1	2	5	8

Data collection

Quantitative focal continuous follows and opportunistic, qualitative *ad libitum* samples were used to establish an inventory of gestures for each of the focal subjects. The focal individual was followed for a standardised period of 20 minutes, sampling each individual in the group equally at different times of the day and across the study periods.

Gestures and behavioural context (i.e. eliciting context and response by a recipient) were recorded continuously using a digital video camera recorder (SONY DCR – HC18E and SONY DCR – HC32E), with the camera focusing on the focal subject but also taking a wider view to include interactants (see chapter 3 for detailed description of data collection for context). Such a sampling protocol enabled 250 hours of focal footage to be collected, of which a mean (SD) of 17.21 (1.29) hours of good visibility, independent focal data per each focal individual could be used for analyses.

Video analysis

As the first step in analyses, an inventory of gesture types was derived from video recordings. Two hundred and eighteen manual gestures were extracted from video recordings where quality of footage allowed accurate coding of morphological details. For each gesture event, the sender and recipient of a gesture were identified as well as a response by a recipient and the context which elicited production of a gesture (see chapter 3 for detailed information about coding of response and eliciting context). The signaller was identified as an individual performing a gesture. The recipient of a gesture was coded as the individual at whom the gesture was most clearly directed, i.e. an individual at whom the signaller is looking during or immediately after performing the gesture. When more than one individual could be considered as a recipient, the behaviour of most visible subject was coded for analyses.

Behaviour was scored as a manual gesture if it was an expressive movement of the limbs which was visual and mechanically ineffective (did not touch recipient or any object and did not affect behaviour change in the recipient by mechanical means), communicative (i.e. overall consistently induced change in the behaviour of recipient) and intentional (Pollick and de Waal, 2007). Behaviour was considered to be intentionally produced if consistently accompanied by goal directedness (i.e. the signaller looking at recipient during or after gesture production) or persistence and elaboration in gesture use in the event of lack of response from a recipient (Bates et al., 1979).

An ethogram with multi-state categorical elements was used to code morphological characteristics of each gesture event. Morphology of a manual behaviour was examined during the period of time between successive rests of the hands, from the moment the limb began to move to the moment when it returned to the resting position. The gesture phrase was divided into two broad phases. The first phase - preparation phase - was coded from the moment when the limb moved from the resting position to a position in gesture space where the stroke began or movement was ceased without performing a stroke and held at the point of greatest remove from the resting position. The stroke phase was coded at the peak of movement in the gesture which was followed by retraction of the limb to resting position. Resting position was assumed when the hand was returned to a position of relaxation (see Kendon, 2004 for other categorisations of phases within gesture phrase).

Twenty nine features of gestures were coded for each gesture phrase (see Table 2.2 for detailed description of the coding scheme for structure of manual gestures and Appendices 5, 6 and 7 for illustration of body parts and planes discussed in the coding scheme). Broadly, morphology can be executed in two different ways, i.e. depending on the location of stimulus such as recipient or object relative to the signaller or independently of such a position. For instance, while the orientation of an arm in a given gesture such as stiff swing unilateral is usually independent of the recipient’s location (i.e. signaller does not orient arm in the direction of recipient), arm orientation in other gestures such as arm extend depends fully on where the recipient is relative to signaller. For instance, if a recipient is in front, then signaller will extend its hand horizontally towards the recipient. If on the other hand the recipient is above the signaller on a branch, then the recipient will extend the hand upwards. Such a distinction is applicable to many features of gestures, such as how much the arm, wrist or fingers are extended (i.e. if the recipient is close or far away from the signaller). It may also be important that a recipient is faced with certain part of the arm, for example, in arm extend, palm vertical towards body, where a recipient is always presented with the inner part of the arm and hand. In such cases the way the arm is positioned as well as wrist flexion will be adjusted to present the inner part of arm and hand to the recipient. Additionally, manual gestures do not use objects for communicative purposes, however in some instances gestures with objects were included if the object was not integral to gesturing. For example, in some cases of elbow raise, a subject held fruit in the hand while the elbow was engaged in a communicative action. Since food in the hand did not play a role (gesture was invitation for approach to breast feed) we included these gestures in the repertoire.

Table 2.2: Coding scheme for manual gestures

Broad category	**Morphological feature code**	**Morphological feature description**
Preparation phase of gesture		
Number of arms	1A	gesture performed with one hand
	1B	gesture performed with both hands
Transfer of motion	2A	no transfer of motion between hands (scored when only one hand is used)
	2B	synchronous actions: both arms perform same movement at the same time
Arm orientation	3A	arm orientation depends on where the recipient is relative to the signaller
	3B	dorso-palmar axis of arm is directed vertically towards the signaller's body, parallel to the sagittal plane
	3C	dorso-palmar axis of the arm is directed downwards, parallel to the transverse plane of the signaller's body
	3D	dorso-palmar axis or arm is directed upwards, parallel to the transverse plane of the signaller's body
Upper arm position	4A	upper arm position depends on where the recipient is relative to the signaller
	4B	upper arm position depends on where the referent is relative to the signaller
	4C	upper arm is stretched vertically downwards
	4D	upper arm is stretched vertically upwards
	4E	upper arm is stretched horizontally
Forearm position	5A	forearm position depends on where the recipient is relative to the signaller
	5B	forearm bent fully downwards
	5C	forearm position depends on where the referent is relative to the signaller
	5D	forearm lacks flexion
	5E	forearm half bent downwards
	5F	forearm half bent upwards
Stiffness of arms	6A	arms are flexible and relaxed

Broad category	**Morphological feature code**	**Morphological feature description**
	6B	arms rigid and not flexible
Hand orientation	7A	hand orientation depends on where the recipient is relative to the signaller
	7B	dorso-palmar axis of the hand is directed vertically towards the signaller's body, parallel to the sagittal plane
	7C	dorso-palmar axis of the hand is directed downwards, parallel to the transverse plane of the signaller's body
	7D	dorso-palmar axis of the hand is directed upwards, parallel to the transverse plane of the signaller's body
Arm bending	8A	arm flexion depends on where the recipient is relative to the signaller
	8B	angle between the arm and forearm is decreased from a stretched position
	8C	arm flexion depends on where the referent is relative to the signaller
	8D	angle between the arm and forearm widens and straightens and the arm is extended from a flexed position
Wrist bending	9A	angle between the forearm and hand is decreased from a stretched position
	9B	wrist flexion depends on where the recipient is relative to the signaller
	9C	hand holding an object, non communicative
	9D	wrist flexion depends on where the referent is relative to the signaller
	9E	angle between the forearm and hand widens and straightens and is extended from a flexed position
Wrist bending strength	10A	hand is fully flexed towards the forearm
	10B	degree of wrist flexion depends on where the recipient is relative to the signaller
	10C	hand holding an object, non communicative
	10D	degree of wrist flexion depends on where the referent is relative to the signaller
	10E	hand is stretched

Broad category	**Morphological feature code**	**Morphological feature description**
	10F	hand is flexed mid way towards the forearm
Fingers bending	11A	fingers are stretched
	11B	fingers flexion depends on where the recipient is relative to the signaller
	11C	hand holding an object, non communicative
	11D	fingers are flexed at both the distal and proximal interphalangeal joints
	11E	fingers are flexed at the proximal interphalangeal joint
	11F	index finger is stretched while all other fingers are flexed
	11G	fingers are flexed at the distal interphalangeal joint
Fingers bending strength	12A	fingers are stretched
	12B	degree of fingers flexion depends on where the recipient is relative to the signaller
	12C	hand holding an object, non communicative
	12D	fingers are flexed mid way towards the palm
	12E	fingers are fully flexed towards the palm
Stroke phase of gesture		
Whether arm held at preparatory apex	13A	stroke phase is executed - arm makes movement
	13B	stroke not executed - arm held in the position and shape assumed at the peak of the preparatory phase
Trajectory of arm movement	14A	trajectory of arm movement is elliptical – a curved flattened circular shape
	14B	stroke not executed arm held in the position and shape assumed at the peak of the preparatory phase
	14C	trajectory of arm movement is linear
	14D	trajectory of arm movement depends on where the referent is relative to the signaller
Plane of arm movement	15A	plane of arm movement is vertical, from up to down
	15B	stroke not executed and arm held in the position and shape

Broad category	**Morphological feature code**	**Morphological feature description**
		assumed at the peak of the preparatory phase
	15C	plane of arm movement is from the mid-sagittal plane and towards to away from signaller
	15D	plane of arm movement is vertical, from down to up
	15E	plane of arm movement depends on where the recipient is relative to the signaller
	15F	plane of arm movement is executed in the horizontal plane, from towards the signaller's body to away
	15G	plane of arm movement depends on where the referent is relative to the signaller
	15H	plane of arm movement is from away to towards the mid-sagittal plane
Location of arm movement	16A	location of arm movement is in front of the signaller's body
	16B	stroke not executed and arm held in the position and shape assumed at the peak of the preparatory phase
	16C	location of arm movement is behind the signaller's body
	16D	location of arm movement depends on where the referent is relative to the signaller
Tempo of arm movement	17A	arm movement dischronically transitions from one speed of movement to another
	17B	stroke not executed and arm held in the position and shape assumed at the peak of the preparatory phase
	17C	arm movement transitions from one movement to another smoothly
Joint of arm movement	18A	joint of arm movement depends on where the recipient is relative to the signaller
	18B	stroke not executed and arm held in the position and shape assumed at the peak of the preparatory phase
	18C	joint of arm movement depends on where the referent is relative to the signaller
	18D	movement of arm is executed from the elbow joint
	18E	movement of arm is executed from the shoulder joint

Broad category	Morphological feature code	Morphological feature description
Arm movement repetition	19A	movement of arm is executed once
	19B	stroke not executed and arm held in the position and shape assumed at the peak of the preparatory phase
	19C	movement of arm is executed repetitively
Whether hand held at preparatory apex	20A	stroke executed - hand makes movement
	20B	stroke not executed and hand held in the position and shape assumed at the peak of the preparatory phase
	20C	execution of hand stroke depends on where the recipient is relative to the signaller
Trajectory of hand movement	21A	hand movement is elliptical – a curved, flattened circle shape
	21B	stroke not executed and hand held in the position and shape assumed at the peak of the preparatory phase
	21C	hand movement is linear
	21D	hand movement is circular
	21E	trajectory of hand movement depends on where the recipient is relative to the signaller
	21F	trajectory of hand movement depends on where the referent is relative to the signaller
Plane of hand movement	22A	hand movement is executed in vertical plane, from up to down
	22B	stroke not executed and hand held in the position and shape assumed at the peak of the preparatory phase
	22C	hand movement is executed away from the mid-sagittal plane
	22D	hand movement is executed in vertical plane, from down to up
	22E	plane of hand movement depends on where the referent is relative to the signaller
	22F	hand movement is executed towards the mid-sagittal plane
	22G	hand movement is executed in the horizontal plane, from towards the signaller's body to away
	22H	plane of hand movement depends on where the recipient is

Broad category	**Morphological feature code**	**Morphological feature description**
		relative to the signaller
Location of hand movement	23A	location of hand movement depends on where the recipient is relative to the signaller
	23B	stroke not executed and hand held in the position and shape assumed at the peak of the preparatory phase
	23C	location of hand movement depends on where the referent is relative to the signaller
	23D	hand movement is executed in front of the signaller's body
	23E	hand movement is executed behind the signaller's body
Tempo of hand movement	24A	hand movement dischronically transitions from one speed of movement to another
	24B	stroke not executed and hand held in the position and shape assumed at the peak of the preparatory phase
	24C	hand movement smoothly transitions from one movement to another
	24D	tempo of hand movement depends on where the recipient is relative to the signaller
Joint of hand movement	25A	hand movement is executed from the wrist joint
	25B	stroke not executed and hand held in the position and shape assumed at the peak of the preparatory phase
	25C	joint of hand movement depends on where the referent is relative to the signaller
	25D	hand movement is executed from knuckles at the base of the hand
	25E	joint of hand movement depends on where the recipient is relative to the signaller
Hand movement repetition	26A	movement of hand is executed once
	26B	stroke not executed and hand held in the position and shape assumed at the peak of the preparatory phase
	26C	movement of hand is executed repetitively
	26D	repetition of hand movement depends on where the recipient is relative to the signaller

Broad category	**Morphological feature code**	**Morphological feature description**
Arm and hand direction of movement during stroke phase	27A	movement executed towards the signaller and away from the recipient
	27B	stroke not executed and hand held in the position and shape assumed at the peak of the preparatory phase
	27C	movement executed away from the signaller and towards the recipient
	27D	movement executed neither towards nor away from the signaller or the recipient
	27E	direction of movement depends on where the referent is relative to the signaller
Other		
Gesture aim	28A	gesture is made towards the recipient
	28B	gesture is made towards a specific place on the recipient's body
	28C	gesture is made towards an external referent
	28D	gesture is made towards the signaller himself
Part of hand and arm facing recipient	29A	recipient facing exterior part of arm or hand
	29B	recipient facing interior part of arm or hand
	29C	part of hand facing the recipient depends on where the recipient is relative to the signaller
	29D	part of hand facing recipient depends on where referent is relative to recipient
	29E	recipient facing both interior and exterior parts of arm and hand

Note: Appendices 5, 6 and 7 contain diagrams illustrating body parts and planes referred to in this coding scheme

Statistical analysis

Due to the small sample size, observations from all individuals were pooled together for analyses to examine morphology. Such procedure has been used in other studies of gestural communication (see e.g. Pollick and de Waal, 2007, Genty et al., 2009). In order to avoid pseudoreplication only one manual gesture type was included per gesture sequence in the discriminate function analysis. This data selection procedure reduced the amount of data from 218 to 205 cases, but was necessary as it increased reliability of the repertoire analyses by reducing pseudoreplication. The data presented in this chapter were categorical, meaning that normal distribution could not be assumed. For this reason in this chapter we used non-parametric statistical tests where parametric assumptions did not apply, such as normally distributed, continuous data and homogeneity of variance.

For cluster analysis all 218 observations were examined because it was the aim of cluster analysis to determine gesture types, prior to cluster analysis assumption about gesture types has not been made. In order to determine the statistically significant grouping of gestures into distinct clusters, standard hierarchical agglomerative clustering analysis (HCA) was first performed on an entire morphology data set. The multistate categorical variables from the ethogram (see Table 2.2) formed the input for analyses employing an average between-group linkage algorithm and assuming squared Euclidean distance as the metric of distance between elements of each cluster (see e.g. Lattin et al., 2003 for detailed review of cluster algorithms). Hierarchical cluster analyses measures the inter-point distances between morphological features of all gestures to determine the similarity between gesture cases, in terms of each of their specific characteristics, such that the gestures grouped in the same cluster are similar to each other in morphological terms and different from gestures located in another cluster group (Sokal and Michener, 1958).

Next, the multistate categorical variables were converted into binary variables representing the presence or absence of each state using a computer program designed by Dr Quentin Atkinson (University of Oxford). The binary variables were then submitted to simultaneous discriminate function analysis to validate gesture types identified by the hierarchical clustering techniques and to test morphological variables influenced by gesture type, such as which morphological components had most diversifying effect on gesture types (see Table 2.2 for list of categorical variables tested in this study). The discriminate function analysis identifies a linear combination of quantitative predictor variables (i.e. morphological features of gestures) that characterize the differences between gesture types. Predictor variables (i.e. morphological features of gestures) are combined into n - 1 discriminant functions (where n is the number of gesture types in the analysis), which are plotted onto a two dimensional graph to demonstrate the grouping patterns of gestures. The grouping patterns are informative in that gestures can either be assigned to an appropriate group (i.e. the group assigned by cluster analysis) or to a different group, which produces the percentage of correct assignment into categories (Bortz, 1993). The results obtained from discriminant function analyses were then validated by using the “leave one out” classification procedure, for which discriminant functions are computed from cases where group membership has been determined a priori by cluster analysis and applied to variables where group membership has not been previously known.

Finally, Fisher’s exact test was performed on the uncorrelated morphological features of gestures with the highest correlation to both the first and second discriminant functions to examine how these morphological features differentiated between gesture types. Since the value of correlations was relatively low overall, the value of 0.1 was taken (on the scale of 0, the lowest correlation to 1, the highest correlation) as the smallest value of correlation acceptable. All data analyses were performed using statistical package SPSS 17.0.

Inter-observer reliability test

To assess inter-observer reliability, a random sample of 34 gestures were assigned to the gesture types defined by the cluster analyses based on morphological features (see Table 2.3). A second coder (Sarah-Jane Vick) correctly assigned 27/34 (79.41%) gestural events to the same 12 original gesture types coded. Cohen's Kappa [calculated as Probability observed – Probability expected/ 1 – Probability expected = (0.79 – 0.11)/(1 - 0.11)] was good-excellent at 0.76 (Bakeman and Gottman, 1997). Agreement on context was excellent with 23/24 (95.83%) cases correctly assigned to the same broad context (5 of 6 broad contexts correctly identified: copulation, nursing, grooming, submission and travel; food access was not correctly identified).

Table 2.3: Agreement matrix

	C2														
C1	Ab	Lh	Pp	Ap	Pv	Af	Ar	Bs	Er	Fe	Hc	Hs	Se	Sd	Total
Ab	1														1
Lh		1													1
Pp			3		1										4
Ap				1											1
pv		2	1		6										9
Af						3									3
Ar							3								3
Bs								3							3
Er						1			1						2
Fe										1					1
Hc											1				1
Hs												2		1	3
Se													1		1
Sd							1							0	1
Total	1	3	4	1	7	4	4	3	1	1	1	2	1	1	34

Note: frequencies on the diagonal indicate correctly assigned gestures (coder 1 categories in left column, coder 2 given on top row).

For two of the five incorrectly assigned gesture types, the confusion corresponded with the single confusion identified by the cross validation procedure. Specifically, one out of the two incorrectly assigned arm extend, palm vertical towards body gestures, was assigned to arm extended palm stretched gesture category; the same error occurred for 2% of this gesture type during cross validation. Also in agreement with the cross validation analyses was the incorrect assignment of the single case of stiff arm raise, palm downwards, closed fist, into the arm raise gesture category.

RESULTS

Determining manual gesture types in wild chimpanzees

Hierarchical cluster analysis produced a tree representing thirty gesture types. Figures 2.1 and 2.2 show dendrograms of gesture clusters and frequency distributions of all cases categorised within each cluster of gesture type respectively. Overall the morphological differences between gesture clusters were small. Twenty two gesture types (73%) were separated by distances smaller than 5 (on the scale of 0 to 25), whereas 3 gesture types (10%) were separated by distances larger than 15.

Figure 2.1: Dendrogram of manual gesture types using average linkage between groups

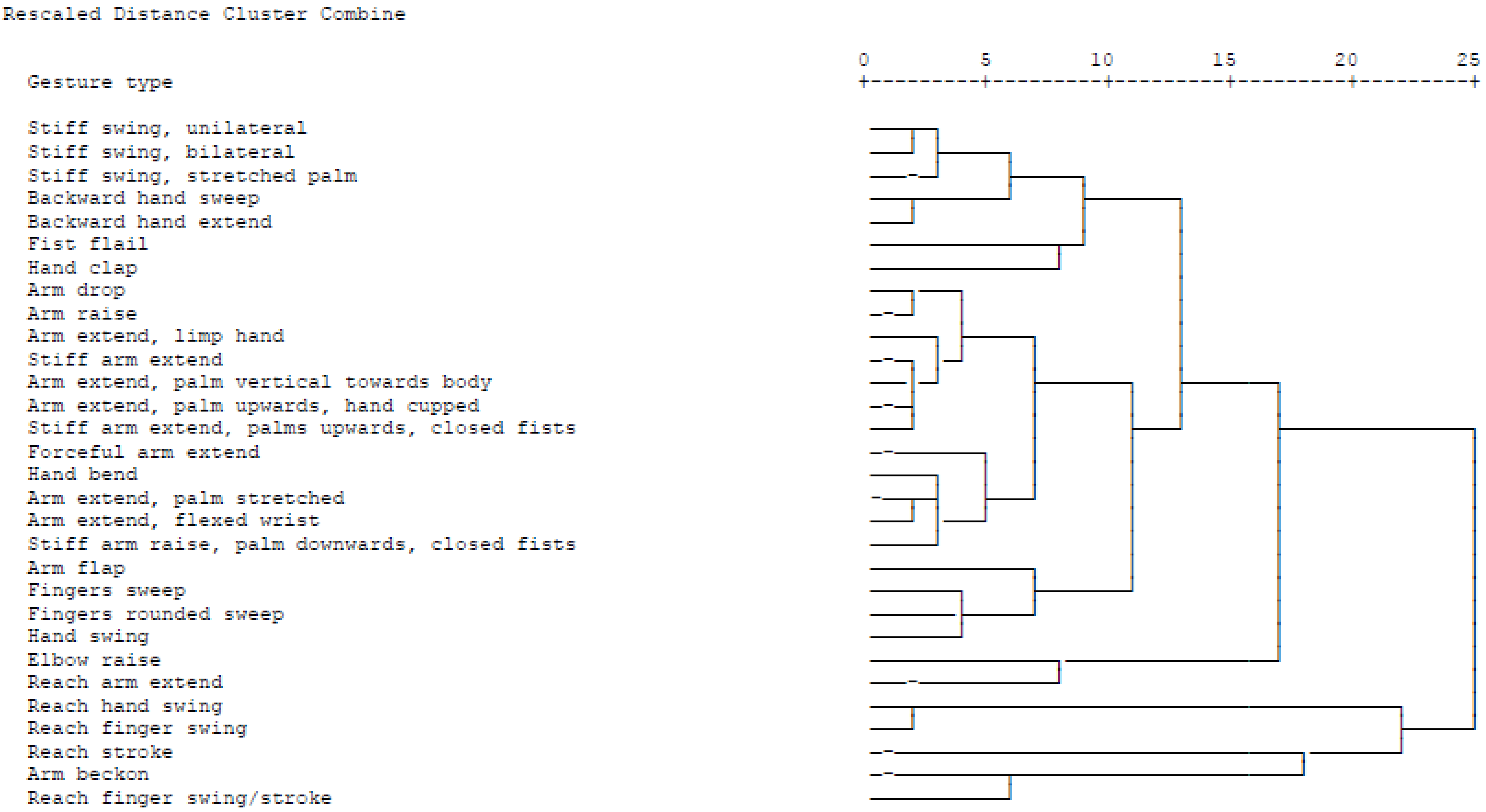
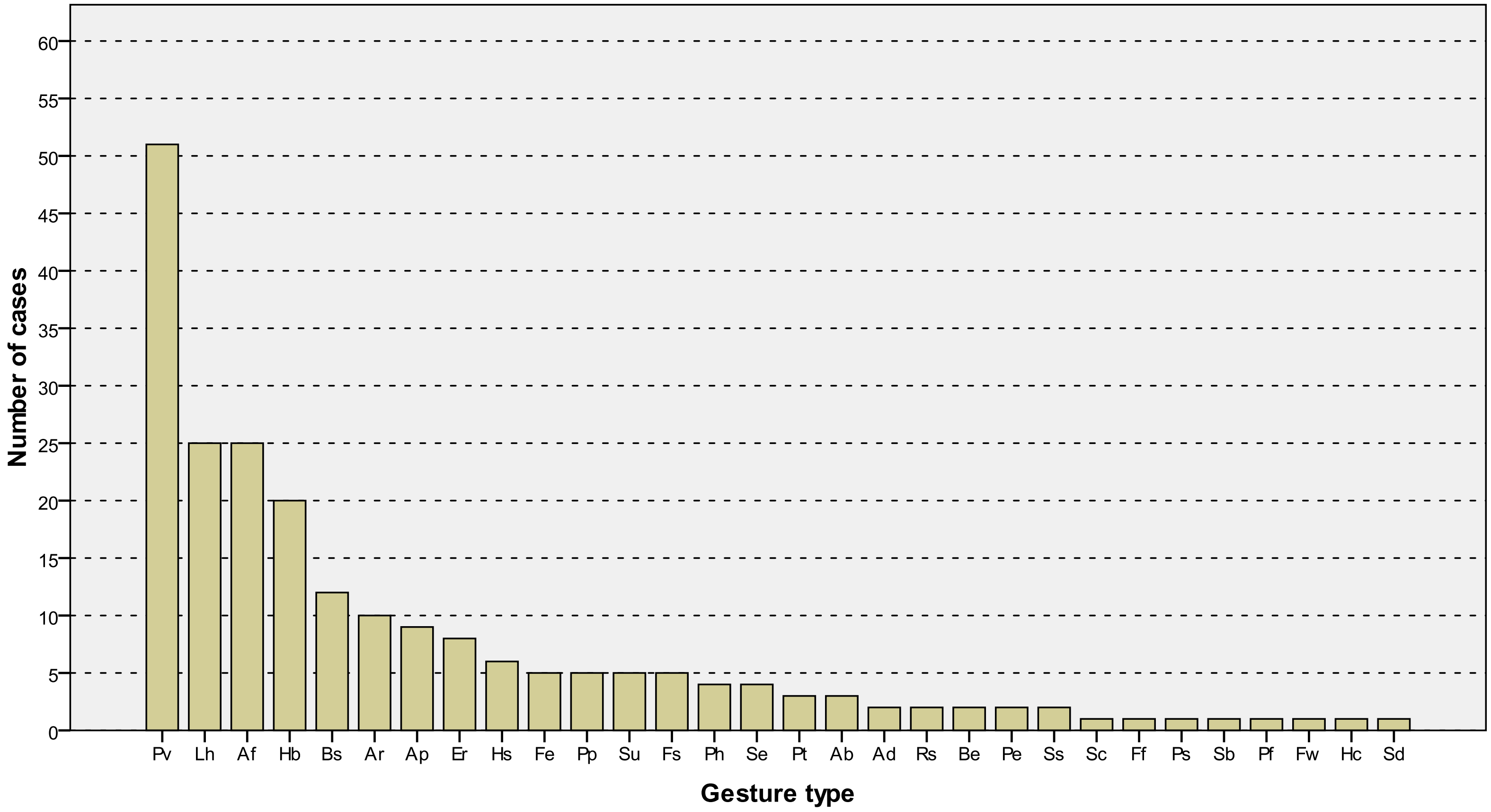


Figure 2.2: Number of gesture cases within manual gesture type clusters identified by hierarchical cluster analysis



Gesture abbreviations: Arm extend, palm vertical towards body (Pv); Arm extend, limp hand (Lh); Arm flap (Af); Hand bend (Hb); Backward hand sweep (Bs); Arm raise (Ar); Arm extend, palm upwards, hand cupped (Ap); Elbow raise (Er); Hand swing (Hs); Forceful arm extend (Fe); Arm extend, palm stretched (Pp); Stiff swing, unilateral (Su); Fingers sweep (Fs); Reach hand swing (Ph); Stiff arm extend (Se); Reach stroke (Pt); Arm beckon (Ab); Arm drop (Ad); Fingers rounded sweep (Rs); Backward hand extend (Be); Reach arm extend (Pe); Stiff swing, stretched palm (Ss); Stiff arm extend, palms upwards, closed fists (Sc); Fist flail (Ff); Reach finger swing (Ps); Stiff swing, bilateral (Sb); Reach finger swing/stroke (Pf); Arm extend, flexed wrist (Fw); Hand clap (Hc); Stiff arm raise, palm downwards, closed fists (Sd)

A discriminant function analysis was conducted with gesture type as the grouping variable to test the hypothesis that the hierarchical cluster analysis tree is an accurate representation of the gesture types and hence that manual gesture types identified by hierarchical cluster analysis are morphologically different. Wilks's lambda revealed significant differences across the means of discriminant functions, $\Lambda=0.000$, $\chi^2(696) = 7575.81$, $p < 0.001$, indicating that the discriminate model was appropriate and gesture types identified by cluster analysis were morphologically different.

Additionally, it is important to compare how the membership of each gesture case defined by cluster analysis would compare with the membership into gesture type assigned by discriminate function analysis. Tables 2.4 and 2.5 present original and cross-validated predicted categorisations for each gesture type identified by the cluster analysis. The average correct assignment into gesture type was 97.6%, with a cross-validated assignment of 90.7%. Thirty gesture types were classified above chance level by discriminate function analysis with the original classification whereas 20 gesture types were classified above chance level with cross-validated classification. Thus, discriminate function analysis confirmed that 20 gesture types were morphologically distinct from each other as well as those gesture types which received validated predicted classifications at chance level (see Figure 2.3).

Furthermore, it is interesting to consider classification results per individual gesture type. Overall, 50% (15 gesture types) received 100% correct assignment, 5 gesture types were classified above chance level between 50% and 98%, and 10 gesture types were classified below chance level at 0%. This suggests that while statistically it was possible to distinguish 20 gesture types from their morphological features, not all gestures were completely discrete and some gestures contained morphological features intermediate between prototypical forms.

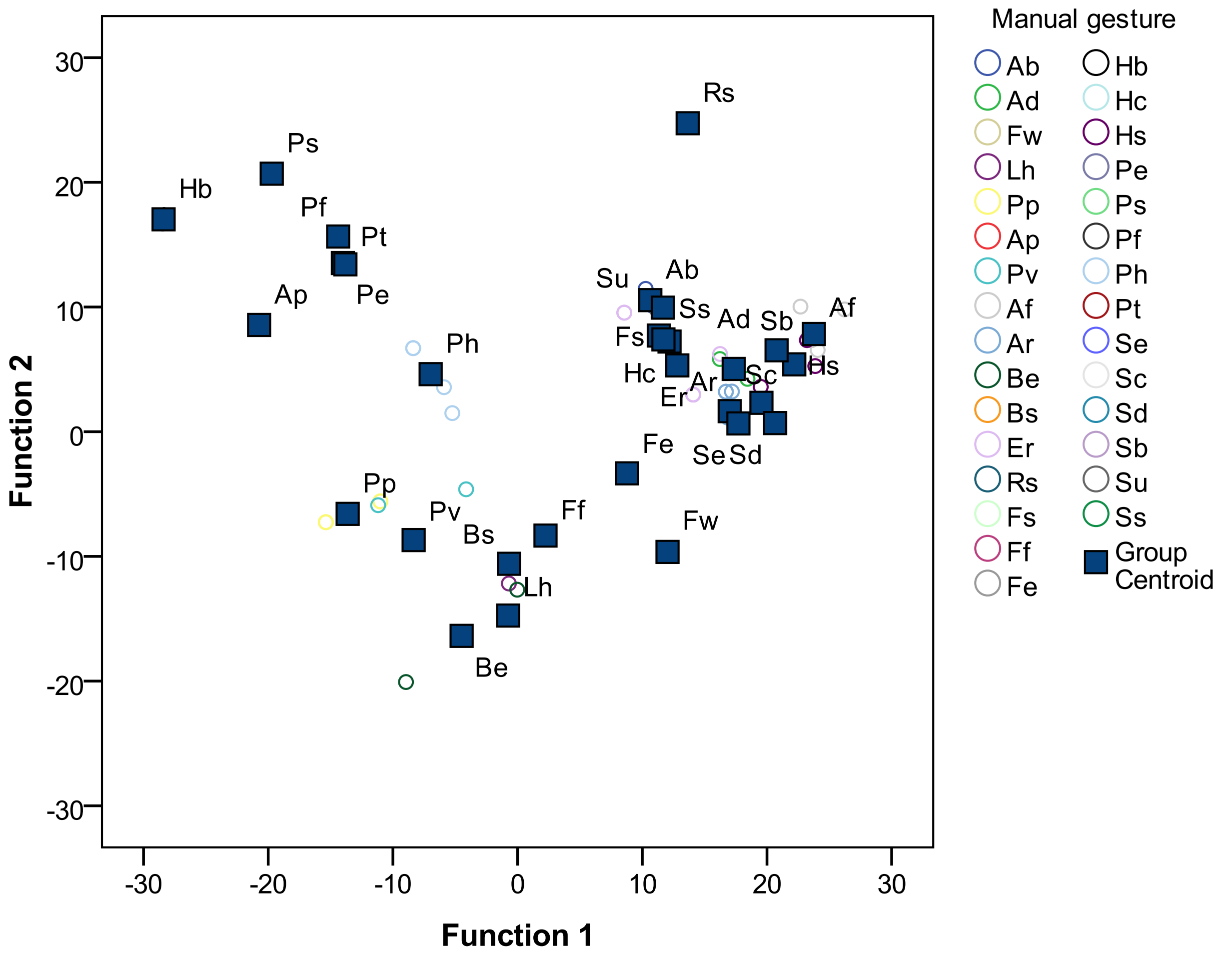


Figure 2.3: The distribution of discriminant scores along two standardized canonical discriminant functions for all gesture types established by cluster analysis. Gesture abbreviations are: Arm extend, palm vertical towards body (Pv); Arm extend, limp hand (Lh); Arm flap (Af); Hand bend (Hb); Backward hand sweep (Bs); Arm raise (Ar); Arm extend, palm upwards, hand cupped (Ap); Elbow raise (Er); Hand swing (Hs); Forceful arm extend (Fe); Arm extend, palm stretched (Pp); Stiff swing, unilateral (Su); Fingers sweep (Fs); Reach hand swing (Ph); Stiff arm extend (Se); Reach stroke (Pt); Arm beckon (Ab); Arm drop (Ad); Fingers rounded sweep (Rs); Backward hand extend (Be); Reach arm extend (Pe); Stiff swing, stretched palm (Ss); Stiff arm extend, palms upwards, closed fists (Sc); Fist flail (Ff); Reach finger swing (Ps); Stiff swing, bilateral (Sb); Reach finger swing/stroke (Pf); Arm extend, flexed wrist (Fw); Hand clap (Hc); Stiff arm raise, palm downwards, closed fists (Sd)

Table 2.4: Percentage of agreement between original predicted classifications and manual gesture types identified by cluster analysis.

Manual gesture types identified by cluster analysis																														
	Ab	**Ad**	**Fw**	**Lh**	**Pp**	**Ap**	**Pv**	**Af**	**Ar**	**Be**	**Bs**	**Er**	**Rs**	**Fs**	**Ff**	**Fe**	**Hb**	**Hc**	**Hs**	**Pe**	**Ps**	**Pf**	**Ph**	**Pt**	**Se**	**Sc**	**Sd**	**Sb**	**Su**	**Ss**
Ab	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ad	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fw	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lh	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pp	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ap	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pv	0	0	0	0	2	0	**98**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Af	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ar	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Be	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bs	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Er	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rs	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fs	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ff	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0

Manual gesture types identified by cluster analysis																														
	Ab	**Ad**	**Fw**	**Lh**	**Pp**	**Ap**	**Pv**	**Af**	**Ar**	**Be**	**Bs**	**Er**	**Rs**	**Fs**	**Ff**	**Fe**	**Hb**	**Hc**	**Hs**	**Pe**	**Ps**	**Pf**	**Ph**	**Pt**	**Se**	**Sc**	**Sd**	**Sb**	**Su**	**Ss**
Hc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0
Hs	0	0	0	0	0	0	0	33	0	0	0	0	0	0	0	0	0	0	**67**	0	0	0	0	0	0	0	0	0	0	0
Pe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**50**	0	0	0	50	0	0	0	0	0	0
Ps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0
Pf	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0
Ph	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0
Pt	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0
Se	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0
Sc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0
Sd	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0
Sb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0
Su	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**80**	20
Ss	0	0	0	0	0	0	0	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**50**

Percentage of agreement between gesture types identified by cluster analysis and the predicted group membership are represented by diagonal row from top left and in bold type. These numbers represent percentage of cases within each gesture type which achieved correct predicted classifications (i.e. were assigned to its appropriate group as identified by cluster analysis), other numbers (not in bold type) refer to percentage of cases which were misclassified (i.e. were assigned to other group than the one identified by cluster analysis). Gesture abbreviations are explained section 2.

Table 2.5: Percentage of agreement between cross-validated classifications and manual gesture types identified by cluster analysis.

Manual gesture types identified by cluster analysis																														
	Ab	**Ad**	**Fw**	**Lh**	**Pp**	**Ap**	**Pv**	**Af**	**Ar**	**Be**	**Bs**	**Er**	**Rs**	**Fs**	**Ff**	**Fe**	**Hb**	**Hc**	**Hs**	**Pe**	**Ps**	**Pf**	**Ph**	**Pt**	**Se**	**Sc**	**Sd**	**Sb**	**Su**	**Ss**
Ab	**67**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	0	0	0	0	0	0	0
Ad	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fw	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lh	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pp	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ap	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pv	0	0	0	0	2	0	**98**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Af	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ar	0	10	0	0	0	0	0	0	**70**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0	0	0	0
Be	0	0	0	0	0	0	0	50	0	**0**	0	0	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	0	0	0
Bs	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Er	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rs	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fs	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ff	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0	0	0	0	0	0	0

Manual gesture types identified by cluster analysis																														
	Ab	**Ad**	**Fw**	**Lh**	**Pp**	**Ap**	**Pv**	**Af**	**Ar**	**Be**	**Bs**	**Er**	**Rs**	**Fs**	**Ff**	**Fe**	**Hb**	**Hc**	**Hs**	**Pe**	**Ps**	**Pf**	**Ph**	**Pt**	**Se**	**Sc**	**Sd**	**Sb**	**Su**	**Ss**
Hc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0	0	0	0	0	0	0	0	0	100
Hs	0	0	0	0	0	0	0	33	0	0	0	0	0	0	0	0	0	0	**67**	0	0	0	0	0	0	0	0	0	0	0
Pe	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**50**	0	50	0	0	0	0	0	0	0	0
Ps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	**0**	0	0	0	0	0	0	0	0	0
Pf	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	100	0	0	0	0	0	0
Ph	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0	0
Pt	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0	0
Se	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0	0	0	0	0
Sc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	100	0
Sd	0	0	0	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0
Sb	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	100	0
Su	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**100**	0
Ss	0	0	0	0	0	0	0	0	0	0	0	0	0	50	0	0	0	50	0	0	0	0	0	0	0	0	0	0	0	**0**

Cross-validated percentage of agreement between gesture types identified by cluster analysis and the predicted group membership are represented by bold type. These numbers represent percentage of cases within each gesture type which achieved correct predicted classifications (i.e. were assigned to its appropriate group as identified by cluster analysis), other numbers (not in bold type) refer to percentage of cases which were misclassified (i.e. were assigned to other group than the one identified by cluster analysis). Gesture abbreviations are explained section 2.

Determining variability in gestures

As a next aim of the study, we tested the variability underlying differences between gesture types. Discriminant function analysis identified 24 standardized canonical functions where first 21 functions differentiated between gesture types significantly (see Table 2.6 for significance tests of all functions). Thus, differences between gesture types could be explained in terms of 21 underlying dimensions, which indicates that gestures had complex morphology and possessed many morphological attributes. Additionally, of the 24 functions, the first two functions accounted for over 67% of total variance with canonical effect size $R^2=1$ and $R^2=0.99$ respectively, whilst the remaining 22 functions combined accounted for 33% of variance (see Table 2.7 for importance of each discriminant function in explaining the variance). Thus, of 21 underlying dimensions, the two first functions had greatest discriminating effect and the remaining functions had small or moderate effect on differences between gesture types.

Table 2.6: Significance tests of the discriminant functions

Test of Functions	Wilks' Lambda	Chi-square	df	Significance
1 through 24	0.000	7575.81	696	< 0.001
2 through 24	0.000	6573.94	644	< 0.001
3 through 24	0.000	5708.61	594	< 0.001
4 through 24	0.000	4989.65	546	< 0.001
5 through 24	0.000	4312.26	500	< 0.001
6 through 24	0.000	3726.92	456	< 0.001
7 through 24	0.000	3158.57	414	< 0.001
8 through 24	0.000	2665.56	374	< 0.001
9 through 24	0.000	2234.25	336	< 0.001
10 through 24	0.000	1896.92	300	< 0.001
11 through 24	0.000	1579.21	266	< 0.001
12 through 24	0.001	1293.54	234	< 0.001
13 through 24	0.003	1031.61	204	< 0.001
14 through 24	0.010	813.645	176	< 0.001
15 through 24	0.029	624.059	150	< 0.001
16 through 24	0.074	461.182	126	< 0.001
17 through 24	0.148	338.679	104	< 0.001
18 through 24	0.276	227.995	84	< 0.001
19 through 24	0.417	154.662	66	< 0.001
20 through 24	0.563	101.572	50	< 0.001
21 through 24	0.729	55.931	36	0.018
22 through 24	0.844	30.119	24	0.181
23 through 24	0.931	12.641	14	0.555
24	0.991	1.624	6	0.951

Table 2.7: The relative importance of the discriminant functions in explaining the variance

Function	Eigenvalue	% of Variance	Cumulative %	Canonical Correlation	Effect size (R^2)
1	286.234	45.9	45.9	0.998	1
2	131.808	21.2	67.1	0.996	0.99
3	57.083	9.2	76.2	0.991	0.98
4	44.927	7.2	83.5	0.989	0.98
5	26.304	4.2	87.7	0.982	0.96
6	23.804	3.8	91.5	0.980	0.96
7	15.206	2.4	93.9	0.969	0.94
8	10.436	1.7	95.6	0.955	0.91
9	5.725	0.9	96.5	0.923	0.85
10	5.019	0.8	97.3	0.913	0.83
11	4.023	0.6	98.0	0.895	0.8
12	3.392	0.5	98.5	0.879	0.77
13	2.426	0.4	98.9	0.842	0.71
14	1.919	0.3	99.2	0.811	0.66
15	1.510	0.2	99.5	0.776	0.6
16	0.998	0.2	99.6	0.707	0.5
17	0.869	0.1	99.8	0.682	0.46
18	0.513	0.1	99.8	0.582	0.34
19	0.350	0.1	99.9	0.509	0.26
20	0.294	0.0	99.9	0.477	0.23
21	0.157	0.0	100.0	0.368	0.14
22	0.104	0.0	100.0	0.307	0.09
23	0.064	0.0	100.0	0.246	0.06
24	0.009	0.0	100.0	0.096	0.01

Determining groupings of gestures

As a further aim of the study, a scatter plot of the discriminant function scores for each gesture case grouped according to the type to which that gesture belonged was examined to determine which gesture types validated by discriminant function analysis were similar to each other and which gesture types were more distinct (see Figure 2.3). Gestures denoted at either end of the plot show the greatest differences in morphology, whereas those in closer proximity show least difference. In general, discriminate scores for gesture types were generally clumped rather than being at a large distance from each other. This suggests that the gestures possessed a few distinguishing features and therefore were more similar to each other than they were markedly different. Additionally, gestures had overlapping discriminate scores for number of gesture types. This indicates that repertoire contained both discrete signals and signals with intermediates between gesture classes with continuous morphological variation both within and between gesture types. The gestures most different from each other are those which were discriminated by functions accounting for most of the variance. The first discriminant function discriminated between the following gestures: hand bend; reach stroke; reach arm extend; reach hand swing; arm extend, palm stretched; arm extend, palm vertical towards body; arm extend, palm upwards, hand cupped; arm extend, limp hand and backward hand sweep from forceful arm extend; fingers rounded sweep; arm beckon; fingers sweep; elbow raise; arm drop; arm raise; stiff arm extend; stiff swing, unilateral; hand swing and arm flap. The second function discriminated hand bend; reach stroke; reach arm extend; arm extend, palm upwards, hand cupped; reach hand swing; fingers rounded sweep; arm beckon; stiff swing, unilateral; fingers sweep; elbow raise; arm drop; arm raise; stiff arm extend; hand swing; arm flap from arm extend, limp hand; arm extend, palm stretched; arm extend, palm vertical towards body; backward hand sweep; forceful arm extend.

Determining distinguishing features of gestures

Next, the discriminate function correlation coefficients for all uncorrelated morphological features were studied to determine which morphological features discriminated most between gesture types and which features had least importance to the differentiation of gesture types validated by discriminant function analysis (see Table 2.8). The values of correlation coefficients indicate the magnitude of contribution of each morphological feature to group separation. Morphological features with high values of discriminate function correlation coefficients contribute most to separation between gesture types whereas those with low values exert the least influence on gesture type differences. In general no single feature loaded strongly on functions which accounted for most of the variance. The highest values of correlation coefficients were 0.32 and 0.37 for function 1 and 2 respectively. Similarly, the largest absolute correlations between each variable and any discriminant function were weak. Additionally, the highest values of absolute correlation coefficients were observed for functions with weak influence on separation between gesture types. The highest absolute values were 0.76 for function 13 and 0.60 for function 6. The lowest values were 0.37 for function 21 and 0.37 for function 7. This indicates that gestures were indistinct and no single feature had a strong discriminating effect between gesture types. The features which were most distinctive, i.e. had highest correlation to either first or second discriminant function (r > 0.10) were wrist flexion dependent on recipient location (r = -0.32), fingers flexed at proximal interphalangeal joint (r = -0.16), single movement of hand (r = 0.13), wrist flexion at maximum (r = 0.12), arm flexed at wrist joint (r = 0.11), recipient facing exterior part of arm or hand (r = 0.10), hand directed vertically towards signallers body (r = -0.10) and fingers stretched (r=0.10).

Morphological features with the highest correlation with the second discriminate function were: fingers flexion depends on where recipient is relative to signaller (r = -0.37), fingers are flexed at proximal interphalangeal joint (r = 0.24), wrist flexion depends on where recipient is relative to signaller (r = -0.31), recipient facing exterior part of arm or hand (r = 0.15) and recipient facing interior part of arm or hand (r = -0.13).

Moreover, the discriminate function correlation coefficients can give information as to how morphological features influence the differences between gesture types. Morphological features with same sign of coefficients, e.g. two positive or two negative coefficients, contribute to group separation in the same way; morphological features with opposite values of correlation coefficients, e.g. one positive and one negative coefficient contribute to group separation in opposite ways (see Table 2.8). Overall, functions which accounted for most of the variance discriminated between gesture types in similar way. Five out of eight morphological features had the same sign of correlation coefficients thus indicating that gestures displayed a lot of similarity in their morphological components. Thus, in terms of function one, gestures which had wrist flexion dependent on recipient location were also likely to have fingers flexed at proximal interphalangeal joint and hand directed vertically towards signaller's body but unlikely to have single movement of hand, wrist flexion at maximum, arm flexed at wrist joint, recipient facing exterior part of arm or hand and fingers stretched. Similarly, when considering differences between gesture types discriminated by function two, gestures which had fingers flexion dependent on where recipient is relative to signaller were also likely to have wrist flexion dependent on where recipient is relative to signaller and recipient facing interior part of arm or hand, whereas they were unlikely to have fingers are flexed at proximal interphalangeal joint and recipient facing exterior part of arm or hand.

Table 2.8: Pooled within-groups correlations between uncorrelated, discriminating morphological features and significant standardized canonical discriminant functions

Significant discriminant function																					
Morphological feature	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
recipient facing exterior part of arm or hand	**.100**	**.149**	**.205**	**.337**	**-.491**	.026	**.211**	-.069	**.259**	-.087	.003	**.205**	**-.106**	.045	.061	**-.252**	.091	**.109**	**-.329**	**-.205**	**.147**
fingers distal, proximal interphalangeal joint flexion	.039	.015	-.080	-.072	.077	**-.604**	**.341**	**-.174**	**.117**	**.400**	**-.155**	-.049	.099	**.200**	-.050	.073	.019	.078	**.104**	**.286**	**.182**
gesture is made towards external referent	-.035	.084	**-.227**	**-.316**	**-.137**	**.325**	**.378**	-.059	**-.183**	.078	-.087	**.239**	.073	**.260**	**-.111**	.040	**-.267**	**.102**	-.042	**-.136**	**.373**
fingers flexion relative to recipient	-.075	**-.376**	.062	-.010	-.014	**.136**	-.025	**.440**	**.411**	**.295**	**.154**	**-.288**	-.060	-.044	**-.176**	**.208**	.021	**.126**	**-.305**	.066	**.214**
hand directed vertically towards signaller's body	**-.105**	.047	**-.127**	**.132**	**.243**	.097	**.245**	**.441**	**.467**	.085	**-.316**	-.080	**-.256**	.014	**-.337**	.059	-.098	**-.114**	**.148**	**-.166**	**-.175**
movement of hand is executed once	**.132**	.057	**.371**	**-.299**	**.154**	**.336**	-.006	**-.168**	**.175**	**.385**	**-.364**	**-.184**	.003	**-.102**	-.013	**-.118**	.001	.005	**.171**	**-.344**	-.061
hand is stretched	.041	.025	-.087	**.116**	.044	**-.110**	**.171**	**-.239**	**.134**	**.333**	**.410**	**.163**	.075	**-.198**	-.057	.010	**.300**	**-.340**	-.010	**-.261**	-.084
hand is fully flexed towards the forearm	**.123**	.091	**.110**	-.045	.036	-.042	.008	**.295**	**-.192**	**-.141**	**-.401**	**.284**	**-.116**	.036	**.390**	**-.289**	**-.288**	**.236**	**.165**	**.235**	**-.102**
arm directed vertically towards signaller's body	-.096	-.046	-.083	**.168**	**-.100**	.082	**.259**	**.377**	**.371**	**.134**	**-.390**	**-.146**	**-.196**	-.064	**-.325**	**.154**	**-.132**	**-.154**	**.260**	**-.102**	**-.266**
fingers are stretched	**.106**	.068	.071	**.106**	.099	**.156**	.013	-.078	**-.261**	**-.230**	**-.186**	**.465**	**.218**	-.031	**.101**	**-.222**	-.061	-.039	**.459**	**.335**	-.085
index finger stretched all other fingers flexed	-.013	.028	-.058	-.065	-.036	.068	**.123**	.088	-.049	-.032	.068	**-.171**	**.768**	-.083	**.475**	.075	**.173**	**.135**	**-.150**	-.099	-.001
fingers flexed at joint proximal interphalangeal	**-.166**	**.241**	.060	-.059	**-.168**	-.050	**-.111**	-.052	**-.235**	.081	**.358**	.060	**-.595**	-.072	**-.134**	-.046	-.069	-.043	-.055	**.501**	.075

Significant discriminant function																					
Morphological feature	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
gesture performed with one hand	-.012	.005	.035	-.049	-.049	.018	-.054	.070	-.004	**-.116**	**-.310**	**-.144**	**-.168**	**.476**	**.393**	.015	**.403**	**-.279**	-.018	**.127**	.034
arm downwards, parallel to body	.031	-.022	-.045	-.052	.046	.053	-.094	**-.402**	**.218**	**-.192**	**.404**	**.108**	.036	.029	**.432**	-.099	**.139**	**.405**	**-.207**	**.263**	**.221**
fingers are mid way flexed towards the palm	-.042	.087	-.038	-.030	-.041	-.021	.078	**-.141**	**-.150**	**.200**	**.152**	.022	**-.268**	**.279**	.003	**.447**	**.325**	**.134**	**-.217**	**-.349**	**-.271**
recipient facing interior part of arm or hand	-.069	**-.131**	-.057	-.053	**.409**	.051	**-.414**	.028	-.070	**.221**	.019	**-.307**	**.166**	.007	**-.160**	**.434**	-.085	.062	**.162**	**.189**	**.114**
movement towards signaller/away recipient	.045	.004	**.148**	**-.131**	.043	.055	**-.109**	.016	**.170**	.045	**.264**	.019	**.133**	**.279**	.093	-.061	**-.150**	**-.431**	**.291**	.008	**-.121**
movement of arm is executed once	.029	.057	**.243**	**-.186**	**.114**	-.027	.072	**-.181**	**.142**	**-.190**	**-.325**	**.240**	**.103**	**-.274**	-.087	**.256**	-.026	**-.357**	**-.489**	**.265**	-.028
wrist flexion relative to recipient	**-.322**	**-.311**	**.280**	**.148**	-.012	.029	**-.327**	.098	**.119**	**.237**	.097	**-.200**	**.150**	.080	**-.284**	**.286**	.019	**.117**	**-.234**	-.064	**.373**
hand movement from up to down vertically	.020	.012	.034	-.018	.012	.001	.016	-.003	-.057	.023	-.064	-.045	.021	-.061	-.092	**-.315**	**.347**	-.070	**.113**	-.072	-.078
arm movement from up to down vertically	.021	.008	.031	-.033	.018	-.031	.042	.034	-.058	-.041	-.058	-.022	-.077	**-.201**	.024	**-.144**	**.358**	**-.115**	**.226**	**-.157**	**.116**
arm move away from mid-sagittal plane	.020	.007	.023	-.051	.018	**-.133**	.066	.006	-.051	-.061	-.085	.025	.042	-.041	**-.114**	.044	**-.142**	**.501**	**-.278**	.017	**-.473**
arm flexed at wrist joint	**.118**	.074	**.126**	-.014	.082	-.007	**.162**	**.158**	**-.274**	**-.291**	**-.366**	-.034	**-.206**	**.116**	**.355**	**-.210**	**-.360**	**.227**	.074	**.182**	**-.126**
arm movement from down to up vertically	.024	.016	.045	-.008	.012	.028	.021	.012	-.083	-.064	-.026	**-.109**	.029	.027	**-.212**	-.027	**.228**	.048	.046	**.161**	**.363**

Shaded cells represent largest absolute correlation between each variable and any discriminant function. Morphological feature loadings onto discriminant functions ≥ 0.1 are represented in bold type.

Finally, Fisher’s exact test was performed on uncorrelated morphological features with the highest correlation to the first and second discriminant functions to determine the nature of the influence of morphological features on the gesture type differences. Whilst correlation coefficients indicate how morphological features influence differences between gesture types in relation to each other, they do not inform us directly about the differences in the frequency of association between each gesture type and each morphological component. See Tables 2.9 and 2.10 for percentages of occurrence of all morphological features with the highest loadings onto the first and second discriminant functions across gesture types validated by discriminate function analysis. See Table 2.11 for significance tests of the strength of these associations. On average each most distinguishing feature was significantly associated with 52% of all gesture types (range 33 to 63%). Thus, gestures shared many distinguishing features and were therefore not very morphologically distinctive. The gestures which shared similar distinguishing features and thus were most similar to each other were associated with functions one and two. For instance when examining the first function which distinguishes the following gestures: arm extend, limp hand; arm extend, palm stretched; arm extend, palm upwards, hand cupped; arm extend, palm vertical towards body; backward hand sweep; hand bend; reach hand swing; a reach stroke was associated with presence of arm flexed at wrist joint, hand fully flexed towards the forearm, fingers stretched, movement of hand is executed once and recipient is facing the exterior part of arm or hand. In contrast, hand directed vertically towards signaller's body, wrist flexion relative to recipient and fingers flexed at joint proximal interphalangeal, were less often present in those gestures.

On the contrary, the following: arm beckon; arm flap; arm raise; elbow raise; fingers rounded sweep; fingers sweep; forceful arm extend; hand swing; stiff arm extend; stiff swing, unilateral, were associated with the absence of arm flexed at wrist joint, hand fully flexed towards the forearm, fingers stretched, movement of hand executed once and recipient facing exterior part of arm or hand. Hand directed vertically towards signaller's body, wrist flexion relative to recipient and fingers flexed at joint proximal interphalangeal were more often present in those gestures.

When looking at second function: arm extend, limp hand; arm extend, palm stretched; arm extend, palm vertical towards body; backward hand sweep and forceful arm extend, were associated with the presence of fingers flexed at joint proximal interphalangeal and recipient facing exterior part of arm or hand. They were associated with the absence of wrist flexion relative to recipient, fingers flexion relative to recipient and recipient facing interior part of arm or hand. On the other hand: arm extend, palm upwards, hand cupped, hand bend, reach hand swing, reach stroke; arm beckon; arm flap; arm raise; elbow raise; fingers rounded sweep; fingers sweep; hand swing; stiff arm extend and stiff swing, unilateral were all associated with presence of wrist flexion relative to recipient, fingers flexion relative to recipient and recipient facing interior part of arm or hand, but with absence of fingers flexed at joint proximal interphalangeal and recipient facing exterior part of arm or hand.

Table 2.9: Distinguishing features of gestures as determined by function 1.

Sign		-										+									
Sign	Morphological features	Manual gesture																			
		arm extend, limp hand	arm extend, palm stretched	arm extend, palm vertical towards body	backward hand sweep	arm extend, palm upwards, hand cupped	hand bend	reach hand swing	reach stroke	forceful arm extend	arm beckon	arm drop	arm flap	arm raise	elbow raise	fingers rounded sweep	fingers sweep	hand swing	reach arm extend	stiff arm extend	stiff swing, unilateral
-	wrist flexion relative to recipient	100	100	98	100	100	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	hand directed vertically towards signaller's body	0	0	98	0	0	100	50	100	0	100	0	0	0	29	0	100	0	50	0	100
	fingers flexed at joint proximal interphalangeal	0	0	0	0	100	100	50	100	0	0	0	0	0	0	100	0	0	50	0	0
+	recipient facing exterior part of arm or hand	100	0	0	0	0	100	0	0	0	100	50	96	100	14	100	100	100	0	100	100
	arm flexed at wrist joint	0	0	2	0	0	0	0	0	100	100	0	100	50	0	0	100	100	0	0	0
	hand is fully flexed towards the forearm	0	0	2	0	0	0	0	0	100	100	100	100	40	0	100	100	100	0	0	0
	fingers are stretched	0	100	4	0	0	0	0	0	0	100	100	96	70	0	0	100	100	0	100	0
	movement of hand is executed once	0	0	0	100	0	0	25	0	0	100	0	100	0	0	0	0	33	0	0	0

Grey cells as opposed to white cells denote contrast in percentage of occurrence of morphological features across gesture types as determined by discriminate function analysis

Table 2.10: Distinguishing features of gestures as determined by function 2.

sign	Sign	-					+														
	Morphological features	Manual gesture																			
		forceful arm extend	arm extend, limp hand	arm extend, palm stretched	arm extend, palm vertical towards body	backward hand sweep	arm extend, palm upwards, hand cupped	hand bend	reach hand swing	reach stroke	arm beckon	arm drop	arm flap	arm raise	elbow raise	fingers rounded sweep	fingers sweep	hand swing	reach arm extend	stiff arm extend	stiff swing, unilateral
-	fingers flexion relative to recipient	0	100	0	96	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	recipient facing interior part of arm or hand	0	0	100	98	100	100	0	0	0	0	50	4	0	86	0	0	0	0	0	0
	wrist flexion relative to recipient	0	100	100	98	100	100	100	0	0	0	0	0	0	0	0	0	0	0	0	0
+	fingers flexed at joint proximal interphalangeal	0	0	0	0	0	100	100	50	100	0	0	0	0	0	100	0	0	50	0	0
	recipient facing exterior part of arm or hand	0	100	0	0	0	0	100	0	0	100	50	96	100	14	100	100	100	0	100	100

Grey cells as opposed to white cells denote contrast in percentage of occurrence of morphological features across gesture types as determined by discriminate function analysis

Table 2.11: Associations between gesture types validated by discriminant function analysis and morphological features most strongly associated with first and second discriminant functions

Morphological feature	Manual gesture																	
	arm beckon	arm extend, limp hand	arm extend, palm stretched	arm extend, palm upwards, hand cupped	arm extend, palm vertical towards body	arm flap	arm raise	backward hand sweep	elbow raise	fingers rounded sweep	fingers sweep	forceful arm extend	hand bend	hand swing	reach hand swing	reach stroke	stiff arm extend	stiff swing, unilateral
hand directed vertically towards signaller's body	-	0.001	-	0.005	**0.001**	0.001	0.005	0.001	-	-	**0.017**	-	**0.001**	-	-	-	-	**0.017**
arm flexed at wrist joint	**0.013**	0.001	-	-	0.001	**0.001**	-	-	-	-	**0.001**	**0.001**	0.008	**0.013**	-	-	-	-
wrist flexion relative to recipient	-	**0.001**	-	**0.014**	**0.001**	0.001	0.001	**0.004**	0.002	-	0.011	0.011	**0.001**	-	0.027	-	0.027	0.011
hand is fully flexed towards the forearm	**0.016**	0.001	-	-	0.001	**0.001**	-	0.039	-	-	**0.001**	**0.001**	0.004	**0.016**	-	-	-	-
fingers are stretched	**0.022**	0.001	**0.002**	-	0.001	**0.001**	**0.007**	0.022	-	-	**0.002**	-	0.002	**0.022**	-	-	**0.006**	-
fingers flexion relative to recipient	-	**0.001**	-	0.011	**0.001**	0.001	0.006	**0.001**	0.043	-	-	-	0.001	-	-	-	-	-
fingers flexed at joint proximal interphalangeal	-	0.009	-	**0.001**	0.001	0.009	-	-	-	**0.033**	-	-	**0.001**	-	-	**0.033**	-	-
movement of hand is	**0.009**	0.003	-	-	0.001	**0.001**	-	**0.001**	-	-	-	-	0.015	-	-	-	-	-

Morphological feature	Manual gesture																	
	arm beckon	arm extend, limp hand	arm extend, palm stretched	arm extend, palm upwards, hand cupped	arm extend, palm vertical towards body	arm flap	arm raise	backward hand sweep	elbow raise	fingers rounded sweep	fingers sweep	forceful arm extend	hand bend	hand swing	reach hand swing	reach stroke	stiff arm extend	stiff swing, unilateral
executed once																		
recipient facing exterior part of arm or hand	-	**0.001**	0.025	0.001	0.001	0.001	**0.002**	0.001	-	-	-	0.025	**0.001**	-	-	-	-	-
recipient facing interior part of arm or hand	-	0.001	**0.012**	**0.001**	**0.001**	0.001	0.006	**0.001**	**0.043**	-	-	-	0.014	-	-	-	-	-

Two-tailed Fisher exact test was used to examine association between each morphological feature and gesture type. All values denote significance levels (p), bold font indicates positive association, standard font indicates negative association, - hyphen indicates non significant test result. Note that gestures Ad and Pe were removed from the table as all associations were non-significant

Describing repertoire of manual gestures

Gestures cross-validated above chance level

Table 2.12 displays inventories of gesture types identified in other studies and comparison with current analysis. The gesture types validated by discriminant function analysis above chance level displayed the following characteristics (see Tables 2.9, 2.10 and 2.11 for percentages of occurrence and significance tests of core distinguishing features within each gesture type):

Arm beckon (Ab)

Gestures within the arm beckon cluster are made with one hand. The arm and hand are directed vertically towards the signaller's body; the arms are flexible with arm and wrist bent, and with the hand flexed fully towards the forearm with fingers stretched. Upper and forearm position and trajectory, and the plane, location and joint of both arm and hand movements depend on where the recipient is relative to the signaller. The arm and hand movement is executed once, accompanied by a smooth transition from preparatory phase. This gesture is made in response to proximity to a receptive female and elicits a neutral approach by the female (see Figure 2.4).

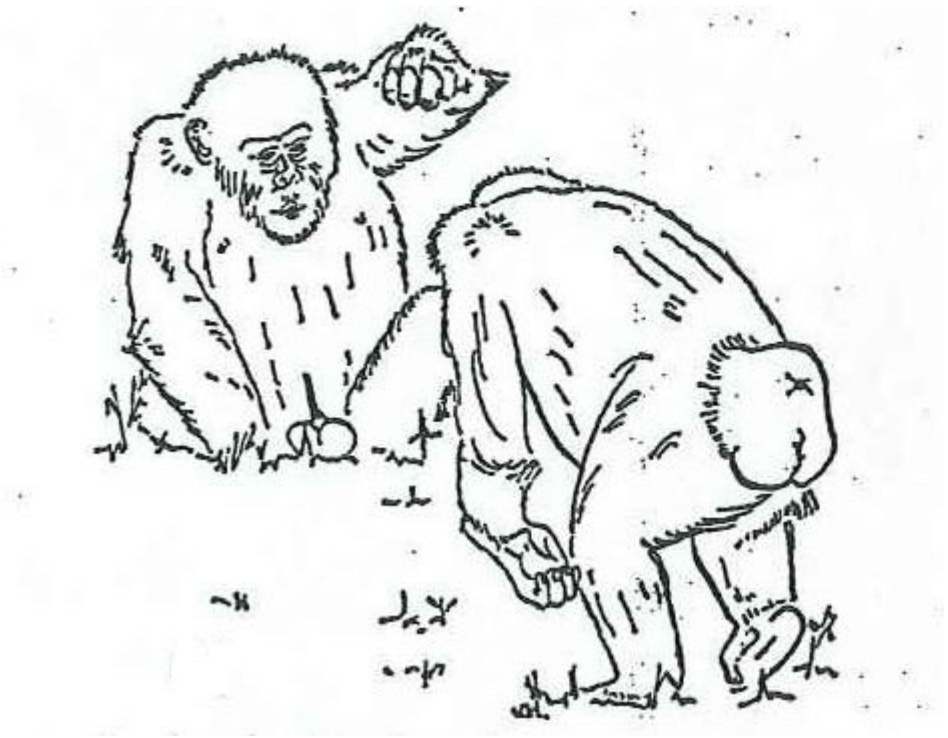


Figure 2.4: Arm beckon; from van Hooff (1971)

Arm drop (Ad)

Arm drop gestures are made with one hand, and the upper arm is stretched vertically downwards, with the forearm flexed upwards at approximately 90 degrees. The arm and hand are directed downwards or upwards, with the hand stretched at the wrist joint and fingers outstretched. The arm and hand are flexible and remain in the position assumed at the peak of the preparatory phase, with either interior or exterior of the arm facing the recipient. This gesture is made when a recipient is stationary and close to the signaller, or is riding on signaller's back and it elicits climbing onto the back of a signaller, or a neutral leave by a recipient.

Arm extend, limp hand (Lh)

Arm extend, limp hand gestures are performed with one hand. The arm is oriented vertically towards signaller's body or downwards with the hand usually directed downwards. Position of the upper arm and forearm and flexion of arm: wrist and fingers depend on where recipient is relative to signaller. A stroke is not executed and the arm is held in position assumed at the peak of preparatory phase, oriented towards a specific place on recipient’s body, with the exterior part of hand facing the recipient. This gesture is made primarily in affiliative and submission contexts: in response to neutral or offensive approach, scratch in grooming context or genital inspection. Responses include the recipient presenting specific areas on the body for grooming, accepting a grooming bout from a signaller or by a defensive leave by a recipient.

Arm extend, palm stretched (Pp)

Arm extend palm stretched gestures are performed with one hand. The arm and hand are orientated downwards or upwards. The position of upper arm and forearm, and flexion of the arm and wrist depend on where recipient is relative to signaller. Fingers are stretched and arms flexible. Movement is made towards the recipient, once, abruptly, in a straight line and in front of the signaller’s body. The plane and joint of arm movement depend on where the recipient is relative to signaller. This gesture is made primarily in agonistic contexts in response to receiving offensive approach or observing aggressive behaviour on third party. Responses include a cessation of antagonistic behaviour by a recipient (see Figure 2.5).

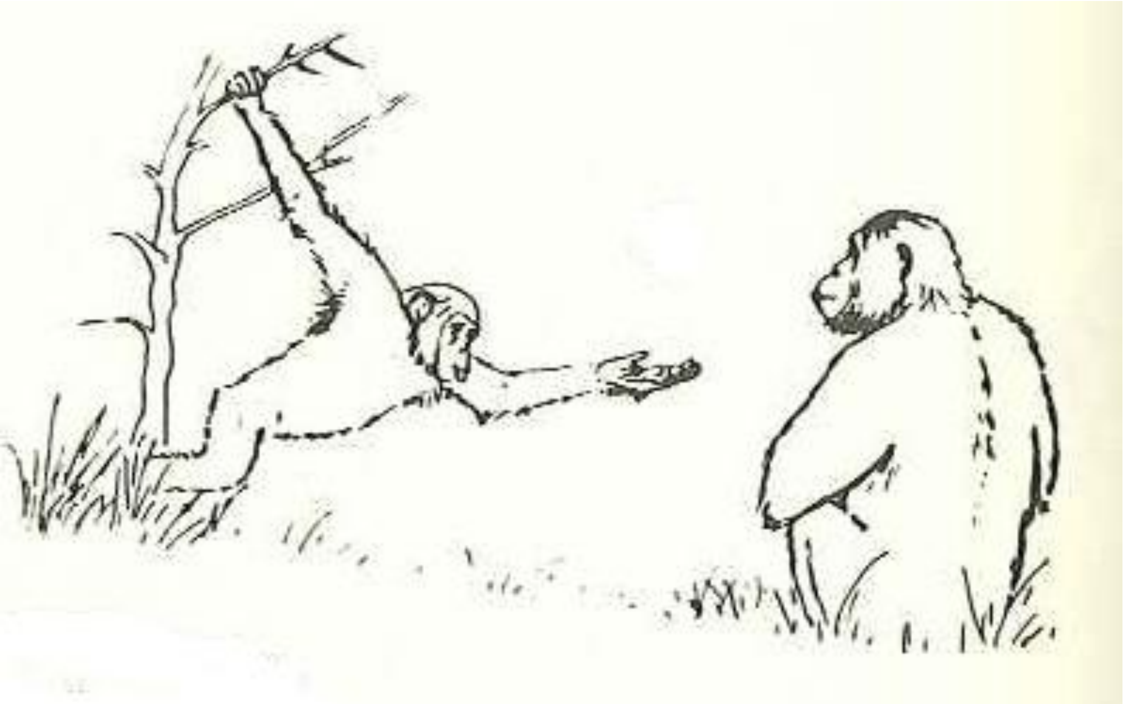


Figure 2.5: Arm extend, palm stretched; from Plooij (1984)

Arm extend, palm upwards, hand cupped (Ap)

Arm extend, palm upwards, hand cupped gestures are performed with one hand. Both arm and hand are directed upwards. Both upper arm and forearm position, and arm and wrist flexion depend on where recipient is relative to signaller, fingers are flexed mid way at the proximal interphalangeal joint. The arm and hand are flexible and after assuming preparatory shape and position they remain held at the peak of the preparatory phase, facing recipient with the interior part of arm. This gesture is most frequently made in response to observing the recipient making reaching gestures towards an object or when observing a recipient in the possession of a highly desirable food item. Responses to this gesture include sharing of the desirable item by a recipient or defensive or offensive rejection of the sharing initiation by a recipient (see Figure 2.6).

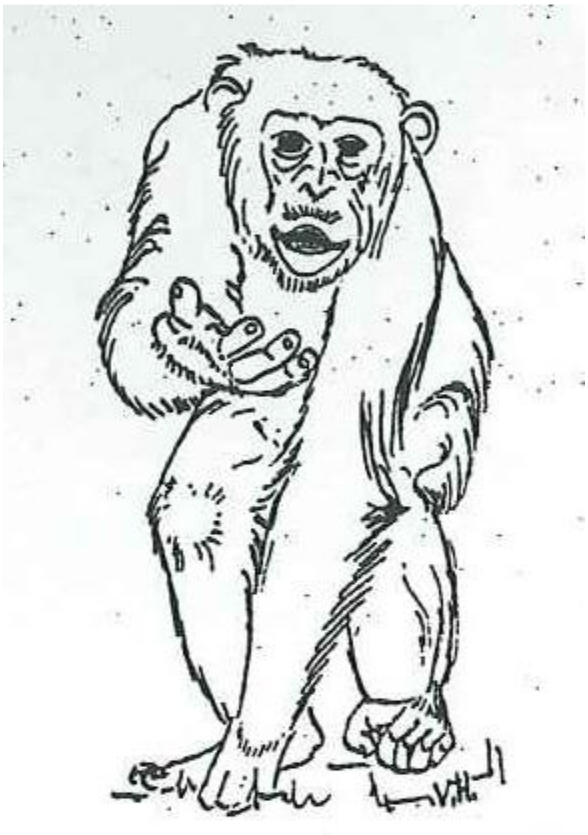


Figure 2.6: Arm extend, palm upwards, hand cupped; from van Hooff (1971)

Arm extend, palm vertical towards body (Pv)

Arm extend, palm vertical towards body gestures are performed with one or both hands. When both hands are used they perform the same movement at the same time. The arm(s) and hand(s) are oriented vertically towards signaller's body. Position of upper arm and forearm and arm, and wrist and fingers flexion depend on where recipient is relative to the signaller. Arm and hand are flexible, and after assuming shape and position these remain held at the peak of the preparatory phase, facing the recipient with the interior part of arm. This gesture is made in response to: neutral and affiliative behaviour such as neutral or affiliative approach or neutral sitting in close proximity; defensive approach by a recipient signalled by pant-grunting and whimpering calls; neutral or defensive leave; solitary play; or when receiving grooming from a recipient. Responses include predominantly a neutral or defensive approach, breast-feeding or cessation of potentially antagonistic behaviour, such as an aroused approach.

Arm flap (Af)

Gestures within the arm flap cluster are performed with one hand. The position of upper arm and forearm, arm and hand orientation and arm flexion depend on where the recipient is relative to the signaller. The hand is fully flexed at the wrist joint, with fingers stretched or flexed mid way at the distal interphalangeal joint. Arms and hands are flexible and perform an abrupt, single movement in shape of an ellipse. The plane of arm and hand movement is vertical, up to down, or down to up, or horizontal from towards to away from the signaller's body, or from away to towards the signaller's body. The location of arm and hand movement depends on where the recipient is relative to the signaller. Movement of hand is executed from wrist joint, while joint of movement of the arm depends on where the recipient is relative to the signaller. This gesture is made most often in agonistic contexts to defer contact with the recipient such as in response to offensive, defensive or neutral approach, or stopping an undesirable activity, such as requesting sharing of an item by a recipient or copulation by a recipient with a desirable female. Responses to this gesture include defensive leave by a recipient including pant-grunting and cowering behaviour, stopping of approach, defensive approach or offensive approach in retaliation (see Figures 2.7 and 2.8).

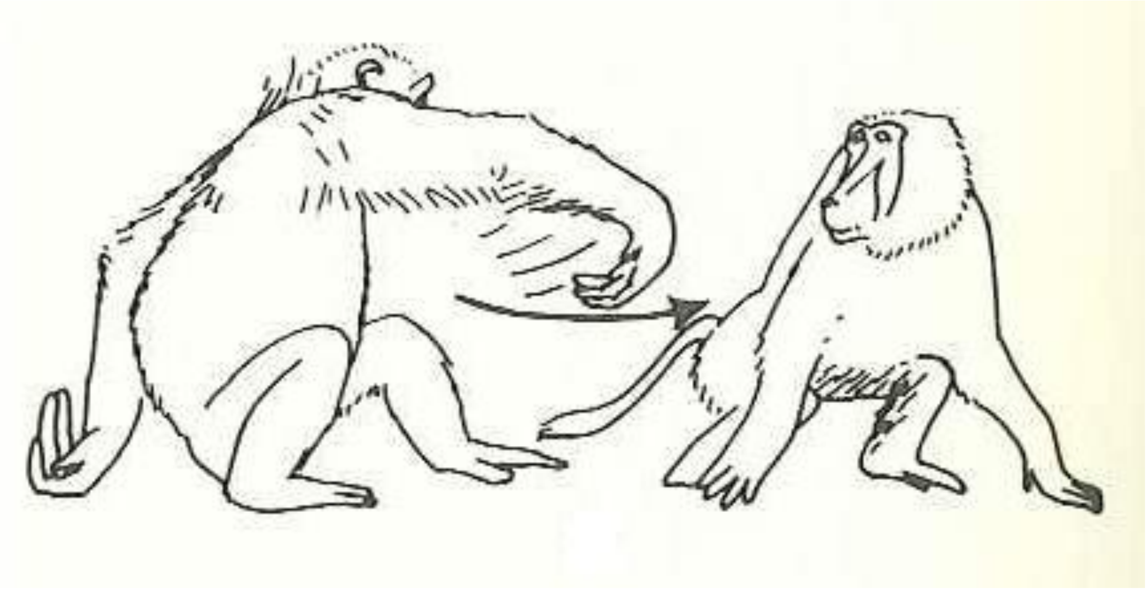


Figure 2.7: Arm flap (from downwards to above); from Plooij (1984)

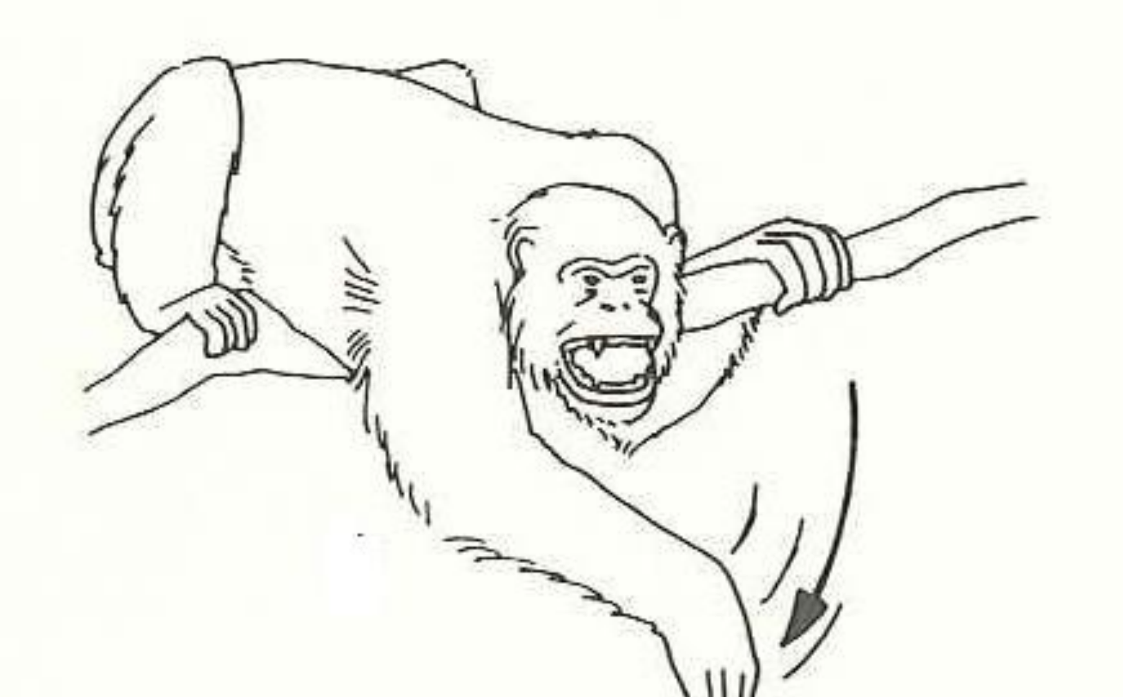


Figure 2.8: Arm flap (from upwards to down); from Plooij (1984)

Arm raise (Ar)

Arm raise gestures are performed with one hand; arm and hand are directed downwards, with the upper arm stretched vertically upwards and the forearm half bent downwards. The arm is flexed at the elbow joint, with wrist joint stretched or flexed mid way or fully towards the forearm. Fingers are stretched or flexed mid way towards the palm at the distal interphalangeal joint. Arm and hand are flexible and after assuming preparatory shape and position they remain held at the peak of the preparatory phase, facing the recipient with the exterior part of arm. An arm raise gesture is primarily performed in affiliative context in response to: observing scratching by a recipient in a grooming context; receiving or giving grooming by a recipient; affiliative approach or neutral behaviour. Responses include the recipient accepting grooming from the signaller, grooming of the signaller by a recipient, or neutral leave by a recipient (see Figure 2.9).

Figure 2.9: Arm raise; from Plooij (1984)

Backward hand sweep (Bs)

The backward hand sweep gesture is performed with one hand. Both arm and hand are directed downwards with both upper and lower arms stretched vertically downwards. Arm, wrist and fingers flexion depend on where the recipient is relative to the signaller. Arms are flexible and make single, abrupt movement forming a horizontal line, executed from towards to behind signaller's body. The hand makes a simultaneous single and abrupt movement which has shape of an ellipse and is executed from down to up in the vertical plane behind the signaller's body. Hand movement is executed from the wrist joint towards the recipient, facing the recipient with interior part of the arm or hand. This gesture is made in response to neutral and affiliative behaviour: affiliative approach; body contact with the recipient; in response to the recipient unsuccessfully attempting to climb onto the back of a signaller. Responses include the successful climbing of signaller's back and riding on the signaller (see Figure 2.10).

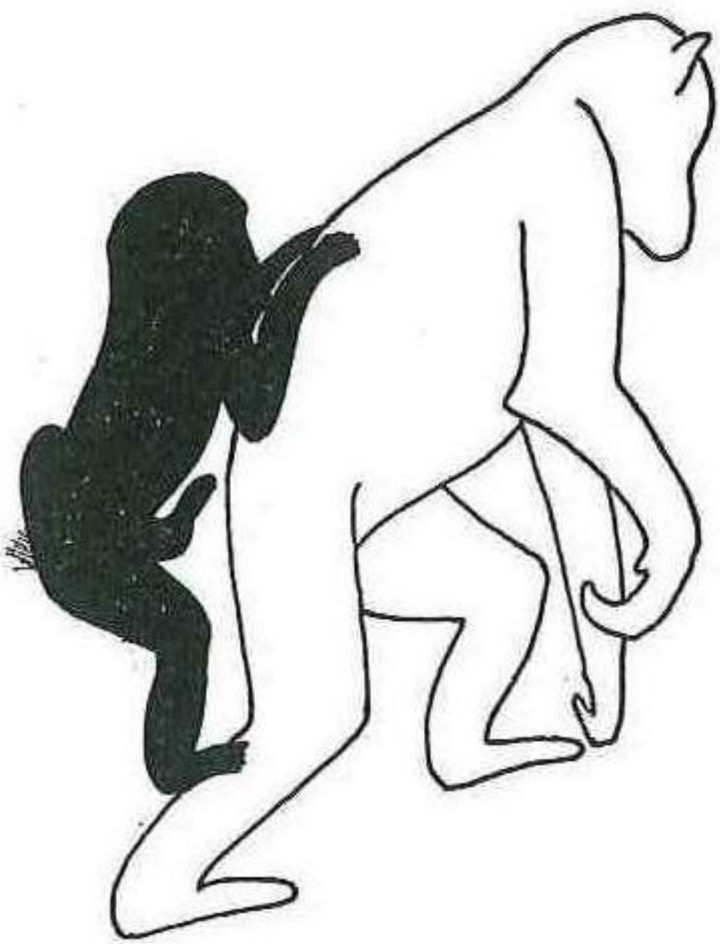


Figure 2.10: Backward hand sweep; from van Lawick-Goodall (1967)

Elbow raise (Er)

An elbow raise gesture is performed with one hand. The arm and hand are directed vertically towards signaller's body or downwards. Upper arm position depends on where the recipient is relative to the signaller, while the forearm remains fully flexed downwards, the hand may be holding object but use of object in this gesture is not communicative. Arms and hands are flexible and after assuming their preparatory shape and position remain held at the peak of the preparatory phase, facing the recipient with the exterior or interior part of the arm. This gesture is made in response to neutral behaviour by a recipient, such as sitting in proximity to the signaller, as well as following affiliative behaviour such as pouting facial expressions or whimpering calls. Response predominantly involves neutral approach of signaller by the recipient.

Fingers rounded sweep (Rs)

The fingers rounded, sweep gesture is performed with one hand and with both arm and hand directed upwards. The position of the upper arm and forearm and arm flexion depend on where the recipient is relative to the signaller. The wrist is stretched or fully flexed towards the forearm. Fingers are fully flexed at the proximal interphalangeal joint. Arms are flexible and remain held in the shape assumed at the peak of the preparatory phase of the gesture. The hand makes repetitive, smooth movements that form circles from towards signaller’s body to away in the horizontal plane. Movement is executed from the knuckles at the base of the hand in front of signaller’s body with the recipient facing exterior part of arm or hand. This gesture is made in response to recipient’s neutral or affiliative behaviour such as sitting in close proximity to the recipient or solitary play. The observed response to this gesture was by initiation of play with the signaller.

Fingers sweep (Fs)

A fingers sweep gesture is performed with one hand and with both arm and hand directed vertically towards the signaller's body. The position of the upper arm and forearm and arm flexion depend on where the recipient is relative to the signaller. The arm is relaxed and fully flexed at the wrist with fingers stretched. While the arm is held in a position assumed during the preparatory phase, the hand performs repetitive, an abrupt circular movement. The signaller moves their hand in front of the body, executing movement from the knuckles at the base of hand. This gesture is made in response to offensive behaviour by a recipient while approaching or stationary. Responses include either offensive leave or approach, cessation of antagonistic behaviour, or appeasement behaviour such as grooming of the signaller by a recipient (see Figure 2.11).

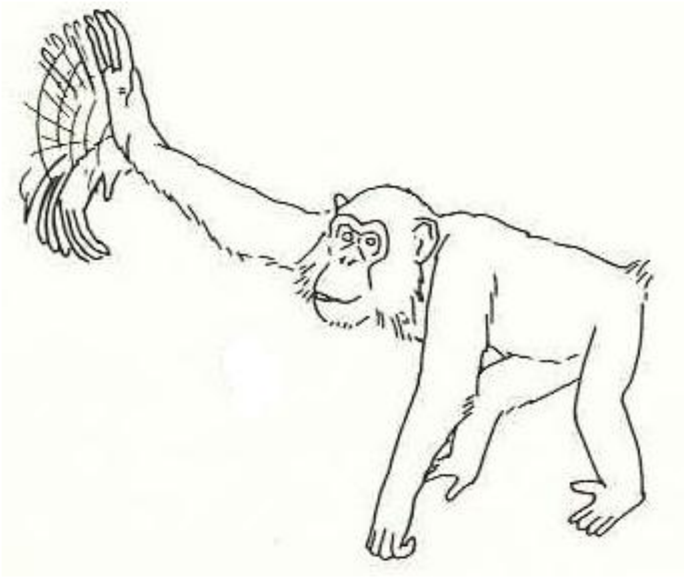


Figure 2.11: Fingers sweep; from Plooij (1984)

Forceful arm extend (Fe)

Gestures within forceful arm extend cluster are performed with one hand. Arm and hand orientation, arm flexion and position of both upper and lower arm depend on where the recipient is relative to the signaller. The arm is fully flexed at the wrist joint and fingers are stretched or flexed at both the distal and proximal interphalangeal joints. Arms are flexible and execute a single, abrupt linear movement either from up to down vertically or horizontally from towards to away from the mid-sagittal plane. In contrast, the hand is held in the position assumed at the peak of the preparatory phase. This gesture is made in response to offensive or defensive approaches, or requesting of an item by a recipient. Responses predominantly involve defensive behaviours, such as defensive leave or approach accompanied by pant-grunts or cowering behaviour (see Figure 2.12).

Figure 2.12: Forceful arm extend; from Plooij (1984)

Hand bend (Hb)

Hand bend gestures are performed with one arm and hand directed vertically towards the signaller's body. The position of upper arm and forearm, and arm and wrist flexion depend on where the recipient is relative to the signaller. Fingers are midway or fully flexed at the proximal interphalangeal joint. Arms are flexible and perform single or repetitive abrupt linear movement. Both the plane and joint of arm movement depend on where the recipient is relative to the signaller. The hand is held in a position assumed at the peak of the preparatory phase towards the recipient, with exterior part of arm or hand presented. This gesture is made predominantly in greeting and submissive contexts such as in response to neutral or offensive approach by a dominant recipient. Responses include a cessation of an aroused state by a recipient or cessation of approach, greeting behaviour such recipient genitally inspecting signaller, or grooming of a signaller by a recipient (see Figures 2.13 and 2.14).

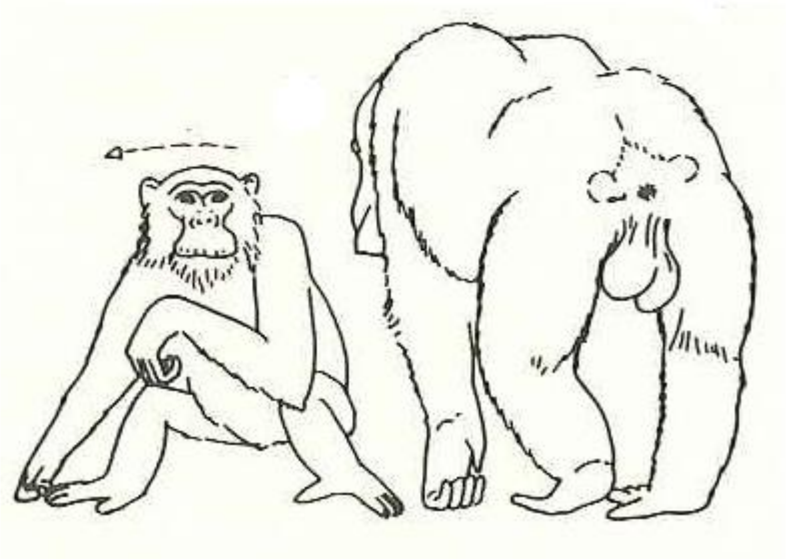


Figure 2.13: Form of hand bend; from Plooij (1984)

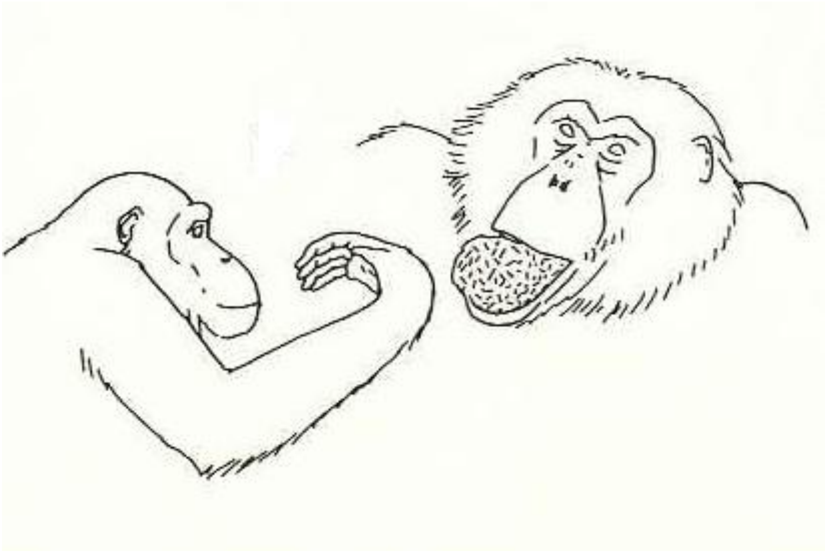


Figure 2.14. Form of hand bend; from Plooij (1984)

Hand swing (Hs)

Hand swing gestures are performed with one hand. Arms and hands are directed downwards or upwards. The position of both upper and forearms and arm flexion depend on where the recipient is relative to the signaller. The hand is fully flexed at the wrist, towards the arm with fingers stretched. Arms are flexible and relaxed. The arm is held in the shape assumed at the preparatory phase, while the hand performs smooth, single or repetitive movements in an elliptical shape. The gesture is executed from the knuckles at base of hand towards signaller's body to away in the horizontal plane. Hand swing gestures are performed in response to neutral approach, solitary play by a recipient or social play by a recipient with a third party. The response is initiation of play between signaller and a recipient (see Figure 2.15).

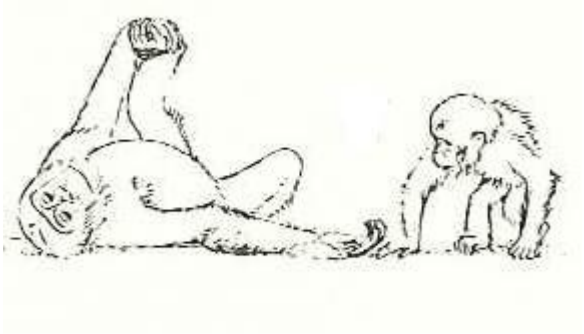


Figure 2.15. Hand swing; from Plooij (1984)

Reach arm extend (Pe)

Reach arm extend gesture is performed with one hand. The arm and hand are orientated vertically towards the signaller's body or downwards. The position of the upper and forearm, as well as arm and wrist flexion depend upon where the object is relative to signaller. Fingers are flexed midway at the proximal interphalangeal joint or the index finger is stretched while all other fingers are flexed. Arms and hands are flexible and are held in a position assumed at the preparatory phase. This gesture is made in response to a recipient feeding on a desirable food item or reaching towards a desirable food item. It may elicit sharing of food item with the signaller.

Reach hand swing (Ph)

Reach hand swing gesture is performed with one hand. The arm and hand are directed vertically towards the signaller’s body or downwards. Both the position of upper and forearm, and the flexion of the arm and wrist depend upon where an object is relative to the signaller. The fingers are flexed midway towards the palm at either the proximal or distal interphalangeal joints. The arm is flexible and held in position assumed at preparatory phase. In contrast, the hand performs a single or repetitive, smooth linear movement. The plane, location and joint of the hand movement depend upon where object is relative to the signaller. This gesture is made in response to the recipient or the signaller reaching the desirable food item or feeding on desirable food. The responses include a recipient redirecting their attention towards the desirable food or reaching towards it.

Reach stroke (Pt)

Reach stroke gesture is performed with one hand. Both the arm and hand are directed vertically towards the signaller's body. Both the position of the upper and forearm, and arm and wrist flexion depend upon where the object is relative to the signaller. Fingers are flexed midway at the proximal interphalangeal joint. The arm is flexible and performs an abrupt, single or repetitive movement. The trajectory, plane, location and joint of movement depend on where the object is relative to the signaller. The hand is held in the position assumed at the preparatory phase. This gesture is made in response to reaching an item by a recipient or in response to a recipient leaving the object. It elicits responses such as a recipient approaching or reaching a desirable item.

Stiff arm extend (Se)

A stiff arm extend gesture is always performed with both hands assuming the same position and performing same movement in synchrony. The arms, hands and fingers are rigid and stretched vertically downwards. Both the arms and hands are held in a position assumed at the peak of the preparatory phase, with the exterior of the arms and hands facing the recipient. This gesture is made in response to an offensive approach or a defensive leave. The recipient responds with antagonistic behaviour such as pant hoots or a defensive behaviour such as defensive leave (see Figures 2.16 and 2.17).

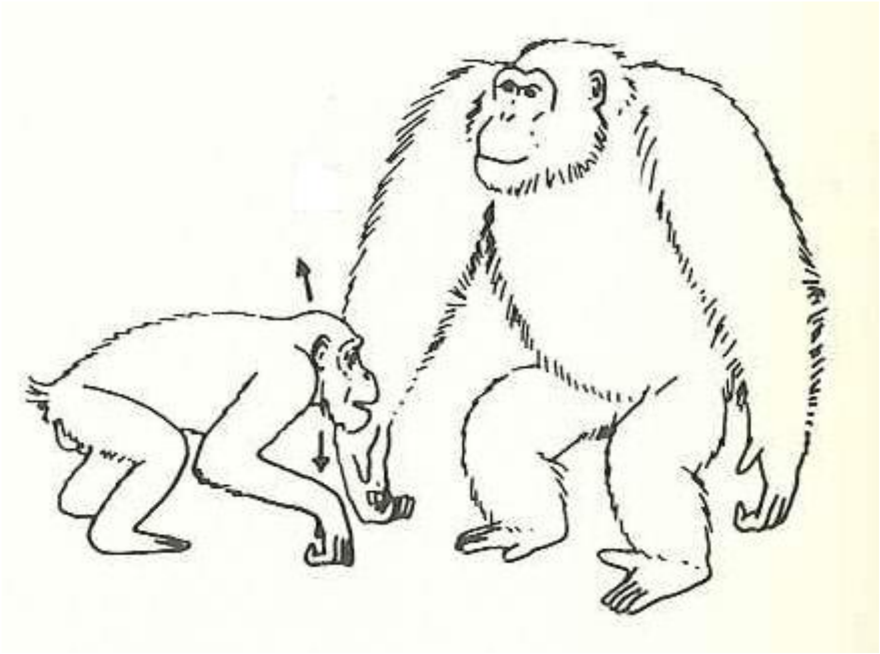


Figure 2.16: Stiff arm extend whilst standing; from Plooij (1984)

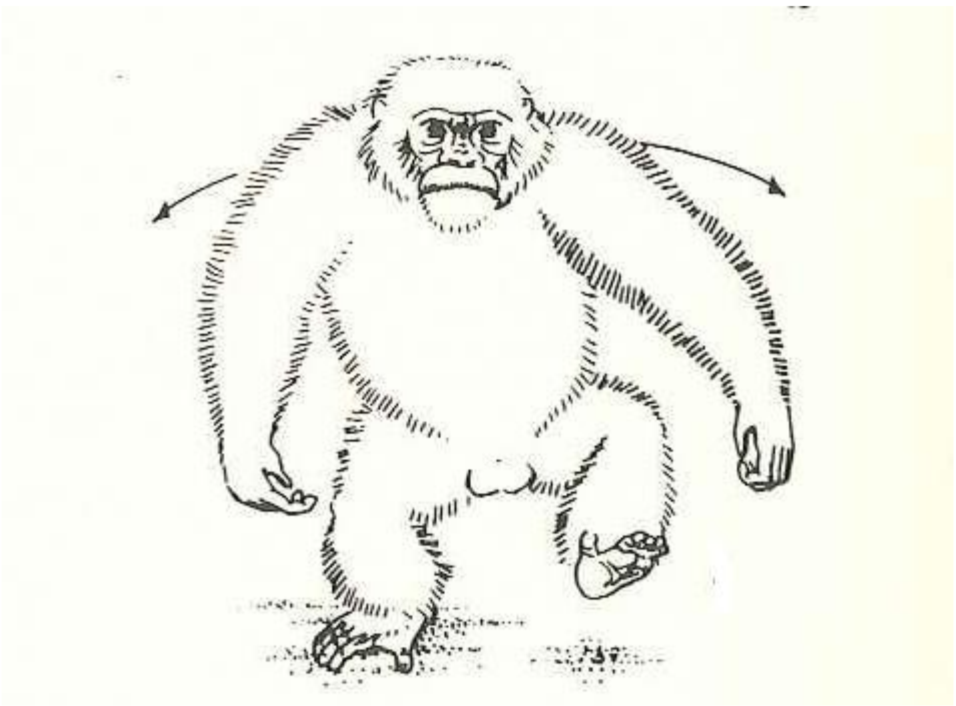


Figure 2.17: Stiff arm extend whilst walking; from Plooij (1984)

Stiff swing, unilateral (Su)

Stiff swing, unilateral gesture is performed with one hand. One arm and hand is directed vertically towards signaller's body. Arm and hand is rigid and directed vertically downwards. The fingers are flexed midway at the distal interphalangeal joint, or at both the distal and proximal interphalangeal joints. The arm makes abrupt, repetitive linear movements in front of the body, directed from towards the signaller’s body to away in the horizontal plane. This arm movement is executed from the shoulder joint. The hand is held in the position assumed at the peak of the preparatory phase, with the exterior part of arm and hand facing the recipient. This gesture is made in response to an approach or to stationary offensive or defensive behaviour, or in response to proximity of signaller to a desirable female. It elicits responses such as a neutral approach by the female.

Gestures cross-validated at chance level

The gesture types validated by discriminate function analysis below chance level, displayed the following morphology (see Table 2.12 to compare with gesture types identified in other studies):

Arm extend, flexed wrist (Fw)

An arm extend, flexed wrist action is performed with one hand, with both the arm and hand directed vertically towards the signaller's body. Both the position of upper and forearm, and the flexion of the arm and fingers depend upon where the recipient is relative to the signaller. The hand is fully flexed at the wrist joint, towards the signaller's body, with the exterior part of the outstretched fingers facing the recipient. The arm makes a sharp, linear movement from up to down in the vertical plane in front of the signaller's body. The joint of the arm movement depends upon where the recipient is relative to the signaller and the arm movement is executed once with a flexible arm. This gesture is made in response to being in proximity to a receptive female and elicits an approach by the female.

Backward hand extend (Be)

Backward hand extend gestures are performed with one hand. The arm and hand are directed downwards or upwards, with both upper and lower arm stretched vertically downwards. Arm, wrist and finger flexion depend upon where the recipient is relative to the signaller. The arm is flexible and performs a single, abrupt linear movement, executed from towards to behind the signaller's body in the horizontal plane. The hand remains held in the position and shape assumed at the peak of the preparatory phase. This gesture is made in response to a neutral approach by a recipient, or a recipient unsuccessfully attempting to climb the back of a female. It elicits response such as successfully positioning on the back in order to ride on the signaller.

Fist flail (Ff)

A fist flail gesture is performed with one hand with both the arm and hand directed downwards. Both the upper arm and lower arm are stretched vertically upwards, flexed at the elbow, stretched at the wrist, with fingers fully flexed at both the distal and proximal interphalangeal joints. Both arm and hand are flexible and perform abrupt, repetitive linear action vertically from up to down. This gesture is elicited by an offensive approach by a recipient and the response includes a defensive leave by a recipient.

Hand clap (Hc)

The hand clap gesture is performed with both hands, performing the same action simultaneously. Both arms and hands are directed vertically towards the signaller's body, with the upper arm stretched downwards and forearm flexed upwards. Arms are relaxed and wrists and fingers are stretched. Both arms and hands are performing abrupt, repetitive linear movement, bringing hands together in contact. Movement of the arms and hands is horizontal from away to towards the mid-sagittal plane in front of signaller’s body. This gesture is made in response to hearing pant-hoots or an offensive approach by a recipient.

Reach finger swing (Ps)

Reach finger swing gesture is performed with one hand. The arm and hand are directed vertically towards the signaller’s body. Both the position of upper and forearm, and flexion of the arm and wrist depend on where the object is relative to the signaller. The index finger is stretched while all other fingers are fully flexed towards the palm. The arm is flexible and remains held at the position reached at the peak of the preparatory phase. The hand is performs a smooth, repetitive linear movement, with the plane, location and joint of movement dependent on where the object is relative to the signaller. This gesture is made in response to a signaller seeing desirable food and it redirects the recipient’s attention towards the desirable food.

Reach finger swing/stroke (Pf)

Reach finger swing/stroke gesture is performed with one hand. Both the arm and hand are directed vertically towards the signaller's body. Both upper and forearm position, and arm and wrist flexion depend upon where an object is relative to the signaller. Fingers are flexed midway at the proximal interphalangeal joint. The arm is flexible and performs single, abrupt movement; the trajectory, plane, location and joint of arm movement all depend upon where the object is relative to the signaller. The hand also performs a single, abrupt linear action; the plane, location and joint of movement depend upon where the object is relative to the signaller. This gesture is made in response to a recipient reaching towards a desirable food item.

Stiff arm extend, palms upwards, closed fists (Sc)

A stiff arm extend, palms upwards, closed fist gesture is performed with both hands, acting in synchrony. The arms and hands are directed upwards with the arms rigid and fully stretched vertically downwards. The fingers are fully flexed at both the distal and proximal interphalangeal joints. The arms and hands are held in a static position, assumed at peak of preparatory phase with interior part of arms facing the recipient. This is antagonistic gesture made in response to a recipient approaching neutrally. In response to this gesture, the recipient continues their approach but in a defensive manner.

Stiff arm raise, palm downwards, closed fist (Sd)

Stiff arm raise, palm downwards, closed fist gesture is performed with one hand. Both arms and hands are directed downwards, the arms are rigid and stretched horizontally. The arms are bent midway at the wrist joint and the fingers are stretched. The arms make an abrupt and repetitive linear action that moves from down to up, vertically in front of the signaller’s body. The hand does not execute a stroke, remaining held in the position assumed at the peak of the preparatory phase. This gesture is made in response to the signaller observing a receptive female in proximity and initiated copulation with the female.

Stiff swing, bilateral (Sb)

Stiff swing, bilateral gesture is performed with both hands, acting in synchrony. The arms and hands are directed downwards. The arms and hands are rigid and stretched vertically downwards. The fingers are flexed midway at both the distal and proximal interphalangeal joints. The arms move in a linear action, from towards to away from the mid-sagittal plane in front of the signaller’s body. The movement is single and abrupt, and is executed from shoulder joint. The hands are held in the position assumed at the peak of the preparatory phase of the gesture, with the exterior of the arm and hands facing the recipient (see Figure 2.18).

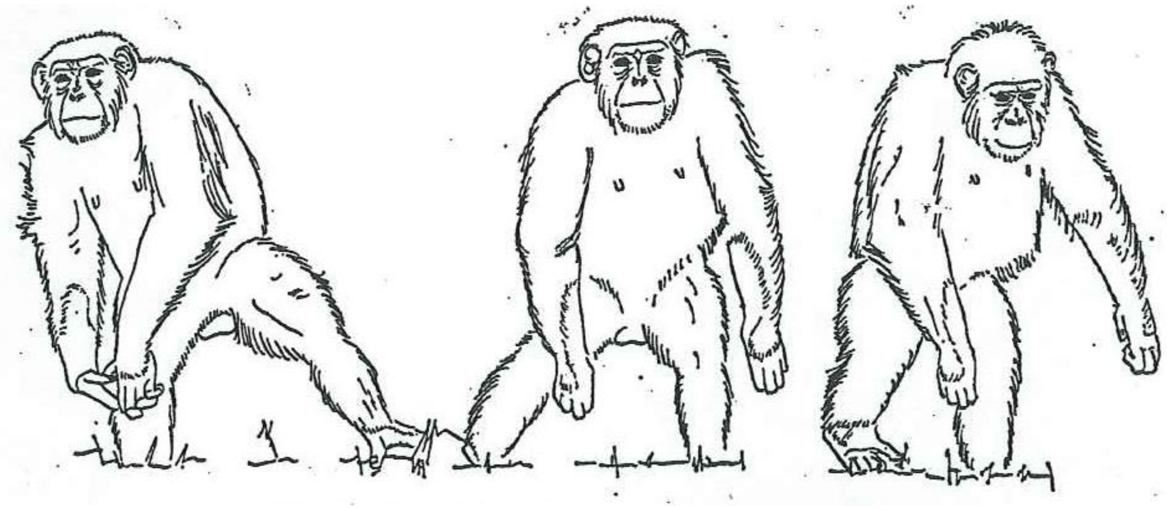


Figure 2.18: Stiff swing bilateral; from van Hooff (1971)

Stiff swing, stretched palm (Ss)

A stiff swing, stretched palm gesture is performed with one hand. The arm and hand are directed vertically towards the signaller's body. The arm is rigid and is stretched vertically downwards. The arm is stretched or fully flexed at the wrist with stretched fingers. The arm performs a linear movement, executed from towards signaller’s body to away in horizontal plane. This movement is abrupt and repetitive and made from the shoulder joint, in front of the signaller’s body. The hand maintains the shape assumed at the peak of the preparatory phase, with the exterior of the arm and hand facing the recipient.

Table 2.12: Inventory of manual gestures in chimpanzees across wild (W) and captive (C) studies

Sonso community at Budongo Forest Reserve, Uganda (W)		**Kasakela community at Gombe National Park, Tanzania (W)**		**M community at Mahali Mountains National Park, Tanzania (W)**	**Chimpanzee community at the Arnhem Zoo, the Netherlands (C)**	**Chimpanzee community at the Yerkes National Primate Research Center, USA (C)**	
This study	**Yukimaru Sugiyama (1969)**	**Frans Plooij (1982)**	**Jane van Lawick – Goodall (1968)**	**Toshisada Nishida et al (2010)**	**J.A.R.A.M. van Hooff (1971)**	**Katja Liebal (2004)**	**Amy Pollick (2007)**
Validated by DFA above chance level							
arm beckon	-	beckoning	beckon	-	beckon (form 1)	-	beckon
arm drop	-	lowering back	-	extend arm as ladder	-	-	-
arm extend, limp hand	-	-	-	present (no name given)	-	-	-
arm extend, palm stretched	-	extending hand, palm downwards/ extending hand, palm upwards	reaching towards	extend hand, palm downward	-	-	reach out down/reach out up
arm extend, palm upwards, hand cupped	Hold out hand?	begging with hand	begging	extend hand, palm upward	hold out hand (form 1)	-	beg with hand

Sonso community at Budongo Forest Reserve, Uganda (W)		**Kasakela community at Gombe National Park, Tanzania (W)**		**M community at Mahali Mountains National Park, Tanzania (W)**	**Chimpanzee community at the Arnhem Zoo, the Netherlands (C)**	**Chimpanzee community at the Yerkes National Primate Research Center, USA (C)**	
This study	**Yukimaru Sugiyama (1969)**	**Frans Plooij (1982)**	**Jane van Lawick – Goodall (1968)**	**Toshisada Nishida et al (2010)**	**J.A.R.A.M. van Hooff (1971)**	**Katja Liebal (2004)**	**Amy Pollick (2007)**
arm extend, palm vertical towards body	-	reaching for?	reach hand toward	present (no name given)	stretch over	reach?	reach out side
arm flap	-	flapping	flapping	raise arm quickly/ flail	upsway	arm raise	flap
arm raise	-	arm high	raising one arm high	raise arm with elbow bent	-	-	arm raise
backward hand sweep	-	-	climb aboard	-	beckon (form 2)	-	-
elbow raise	-	-	raise arm	-	-	-	-
fingers rounded sweep	-	-	-	present (no name given)	beckon (form 3)	-	finger flex
fingers sweep	-	wristshaking	-	shake hand side to side quickly	-	-	-
forceful arm extend	-	arm raise	arm raising/hitting away	present (no name given)	-	-	throw hold

Sonso community at Budongo Forest Reserve, Uganda (W)		**Kasakela community at Gombe National Park, Tanzania (W)**		**K and M communities at Mahali Mountains National Park, Tanzania (W)**	**Chimpanzee community at the Arnhem Zoo, the Netherlands (C)**	**Chimpanzee community at the Yerkes National Primate Research Center, USA (C)**	
This study	**Yukimaru Sugiyama (1969)**	**Frans Plooij (1982)**	**Jane van Lawick – Goodall (1968)**	**Toshisada Nishida et al (2010)**	**J.A.R.A.M. van Hooff (1971)**	**Katja Liebal (2004)**	**Amy Pollick (2007)**
hand bend	-	bending away/ wristbending	wrist bending/bending away	offer arm/reach wrist toward/extend hand, palm sideways	hold out hand (form 2)/parry	wrist offer	bent wrist
hand swing	-	lies down on back	-	present (no name given)	-	-	-
reach arm extend	-	-	reaching with hand?	-	-	-	point?
reach hand swing	-	-	-	-	-	-	-
reach stroke	-	-	-	-	-	-	-
stiff arm extend	-	bipedal swagger/ rearing/ hunching	-	present (no name given)	-	-	-
stiff swing, unilateral	-	bipedal arm waving and running?	arm waving?	swinging one arm sideways, up or down	arm sway?	-	swing? /arm wave?

Sonso community at Budongo Forest Reserve, Uganda (W)		**Kasakela community at Gombe National Park, Tanzania (W)**		**M community at Mahali Mountains National Park, Tanzania (W)**	**Chimpanzee community at the Arnhem Zoo, the Netherlands (C)**	**Chimpanzee community at the Yerkes National Primate Research Center, USA (C)**	
This study	**Yukimaru Sugiyama (1969)**	**Frans Plooij (1982)**	**Jane van Lawick – Goodall (1968)**	**Toshisada Nishida et al (2010)**	**J.A.R.A.M. van Hooff (1971)**	**Katja Liebal (2004)**	**Amy Pollick (2007)**
Validated by DFA at chance level							
fist flail	-	-	-	present (no name given)	-	arm shake	flail/shake wrist
hand clap	-	-	-	-	-	hand clap	clap hands or feet
arm extend, flexed wrist	-	-	-	-	-	-	-
backward hand extend	-	-	-	present (no name given)	-	-	-
reach finger swing	-	-	-	-	-	-	-
reach finger swing/stroke	-	-	-	-	-	-	-
stiff arm extend, palms upwards, closed fists	-	-	-	-	-	-	-

Sonso community at Budongo Forest Reserve, Uganda (W)		**Kasakela community at Gombe National Park, Tanzania (W)**		**M community at Mahali Mountains National Park, Tanzania (W)**	**Chimpanzee community at the Arnhem Zoo, the Netherlands (C)**	**Chimpanzee community at the Yerkes National Primate Research Center, USA (C)**	
This study	**Yukimaru Sugiyama (1969)**	**Frans Plooij (1982)**	**Jane van Lawick – Goodall (1968)**	**Toshisada Nishida et al (2010)**	**J.A.R.A.M. van Hooff (1971)**	**Katja Liebal (2004)**	**Amy Pollick (2007)**
stiff arm raise, palm downwards, closed fists	-	-	-	present (no name given)	-	-	-
stiff swing, bilateral	-	-	-	-	-	-	-
stiff swing, stretched palm	-	-	-	-	-	-	-

Note: Gestures were allocated to their category based on that they best fitted description of a gesture. The fitting was made using information on morphology and behavioural context. Gestures were included in only one category (best fit) even if they could fit more than one category. If a gesture fitted more than one category that was indicated by a question mark next to a gesture. If more than one gesture type fitted the category found in this study they were all quoted for the gesture type.

Studies have reported following manual gestures (unless otherwise indicated the text is direct copy of the original description of a gesture):

1) Jane van Lawick Goodall, 1968

Hitting away – a hitting movement with the back of the hand directed towards the threatened animal or toward the object.

Arm raising – either the forearm or the entire arm is raised with a rapid movement. The palm of the hand is normally orientated towards the threatened individual and the fingers are slightly flexed.

Flapping - a downward slapping movement of the hand in the direction of the threatened individual.

Arm waving – individual raised one or both arms rapidly in the air while standing upright facing the threatened individual.

Reaching towards - holding the hand towards a higher-ranking individual – the wrist and fingers are extended and the hand may be held palm upward or occasionally downward.

Wrist bending – the wrist is flexed and the back of the hand or wrist may then be held towards the lips of a dominant chimpanzee.

Bending away – subordinate individual flexes its elbow and wrist at the same time drawing its arm close to its body and leaning slightly away from the higher ranking animal.

Beckon – the male raised one arm level with or higher than his head and then makes a swift sweeping towards himself movement, his hand making an arc through the air.

Raise arm – recipient whimpered and signaller raised arm to give access to nipples.

Reaching with hand – form of begging, reaching with hand to touch the food or toward desired food.

Reach hand toward - subject reaches hand toward the recipient who is moving away, in response recipient returns to the signaller.

Raising one arm high - male is raising one arm high in the air (holding an overhead branch if available) giving a series of vigorous scratches from elbow to belly. This served as a signal to the other to approach and join him for a grooming session.

Climb aboard - mother reaches back with a characteristic climb aboard gesture (like beckoning).

- Toshisada Nishida, 1968; Toshida Nishida et al., 2010

Reach out one hand towards – gesture made in greeting context, when chimpanzees meet one another after a period of separation or in appeasement situation

Beg – subject reaches out his hand palm uppermost, gesture made in food sharing context

Swinging one arm sideways, up or down – gesture made in an agonistic context

- Yukimaru Sugiyama, 1969

Hold out hand – used in a food sharing context

2) J.A.R.A.M. van Hooff, 1971

Arm sway – the animal may also swing its arms rhythmically in a parallel fashion in front of its body in a lateral plane or wave them about more or less irregularly above its head.

Upsway – the arm, which in its normal supporting, resting or manipulatory position is directed more or less downwards, is moved upwards and forwards in a short jerky movement, usually in a pronated position (i.e. hand palm downwards). While swinging forwards the hand hangs down rather limp, its back turned forwards. When the arm stops moving at a more or less horizontal position the hand may swing out and upwards. The fingers are in the normal semi-flexed position.

Hold out hand – a variety of forms were observed. Actor extends its arm roughly horizontally towards a fellow. The arm is in position about midway between pronation and supination. The hand may be bent at the wrist so that its back is turned to the partner with the fingers bent or fully stretched.

Parry – one or sometimes both arms are raised. The forearm is kept in a roughly horizontal position over or in front of the head, thus shielding it from possible beats from a fellow.

Beckon – individual is stretching his arm and then making sweeping movements towards himself, the hand making an arc through the air. Also form of beckon was observed in sexual context by female, when female made similar beckoning movements, looking back while stretching out one arm backwards, parallel to the body axis, during mount-presenting. Another form of beckon was observed when adolescent male, keeping its arms in the supinated position, beckoned by bending and stretching the wrist and simultaneously bending and stretching its four fingers rapidly.

Stretch over – adult males are seen to stretch one or sometimes both hands forwards and slightly upwards, hand palm down, over the back of a presenting female.

3) Frans Plooij, 1982

Arm high – raising one arm high in the air combined with scratching, with long strokes, from elbow to side across the armpit or vice versa. If the side is directed towards another individual, this usually elicits a grooming response.

Arm raise – raising the arm, which initially hangs more or less down, forwards with usually a rather quick, jerky movement. The fingers are flexed slightly and the palm of the hand may be oriented tow2ards the other individual and upwards or away from the other individual and downwards. The arm stops rising at a more or less horizontal position. The hand may swing further upwards. The other individual is never seen to be struck.

Bipedal arm waving and running – rising to a bipedal position, while facing another individual (often a baboon as well), and raising one or both arms rapidly into the air. This is followed by running bipedally towards the other individual, waving arms in the air.

Beckoning – raising one or both arms forwards and upwards rather sweepingly and stiffly with the elbows more extended than in the arm raise. The hands are hanging down rather limp. This movement is held at the end of the upward swing while the individual stress fixedly at the other individual and may rock.

Bending away – flexing elbow and wrist and at the same time drawing both arms close to its body and leaning slightly away from the stimulus, usually another chimpanzee

Bipedal swagger – adopting an upright or semi-upright posture and shifting the body weight, often rhythmically, from one foot to the other. During this swaying movement the chimpanzee may or may not be locomoting and the feet may or may not be lifted from the ground the bipedal swagger is often combined with hunched shoulders and the arms are held out from the body.

Begging with hand – placing one or both hands around or under the lips, or chin and lips of another individual that has food in his mouth or touching the hand of the other individual containing the food, or touching the food itself.

Extending hand, palm downwards – holding a hand towards another individual by extending the arm, wrist, and hand in a more or less horizontal position, and stretching the fingers while the hand palm is directed downwards. The other individual is not being touched

Extending hand, palm upwards – the same as extending hand palm downwards except that the palm of the hand is directed upwards

Flapping – raising one arm and hand and making a downward slapping movement of the hand in the direction of another individual

Reaching for – holding the hand(s) or foot (feet) towards another individual. The hands are in the normal semi-flexed position and the arm is in a position somewhere in between pronation and suppination.

Rearing – changing abruptly from a quadrupedal to a bipedal position by raising the torso towards a more vertical position. The upper arms are directed downwards, the lower arms upward and the wrists are bent, stretching the hands forwards

Wristbending – flexing the wrist (often the fingers as well) while holding the back of the hand out towards another individual

Wristshaking – shaking the own hand vigorously with flexible wrist, while extending the arm fully or partly towards another individual

Lies down on back – lying down on the back while keeping the head lifted from the ground and extending the arm and hand towards another individual while looking at that individual

Hunching – rounding the back, pulling the shoulders up and forwards, drawing the head down, holding the upper arms slightly outwards and forwards and the forearms slightly upwards. The chimpanzee may sit, or stand bipedaly or quadrupedally.

Lowering back – a mother lowering her hindquarters in front of her infant in such a way that she is nearly sitting, leaning forward on her hands.

- Katja Liebal, 2004

Arm raise – subject raises its arm (as if to hit)

Arm shake – subject shakes its one hand or both repeatedly with rapid movements

Reach – subject extends its arm to the other

Wrist offer – subject extends the back of its flexed wrist to the other

Hand clap – subject slaps its own wrist or hand

- Amy Pollick, 2007

Arm raise – one or both arms raised with usually a quick, jerky movement, fingers are flexed slightly and palm of hand may be orientated toward the other individual and upwards, or away from the other individual and downwards, no contact.

Arm wave – rising to a bipedal position while facing another individual and either swinging arms in front of torso or raising one or both arms rapidly into the air

Beckon – one or both arms raised forward and upward sweepingly and stiffly with the elbows more extended than in the arm raise; hands are hanging down limply with finger flexes usually; movement is held at end of upward swing while individual stares at recipient

Beg with hand – placing one or both hands around or under other's lips and /or chin or touching the hand by the mouth of chewing individual

Bent wrist – flexing the wrist while holding the back or side of hand out toward another individual, contact possible

Clap hands/feet – flat palms of hands are brought into contact with each other either in vertical or horizontal position, can be repetitive

Flail – arms and hands are completely raised above head and are shaken in rapid succession. Repetitive

Flap – one arm and hand raised and makes a downward slapping movement of the hand in direction of another individual – no forceful contact with substrate

Finger flex – palm can be up or down, and wrist is not bent; fingers move rapidly back and forth

Point – either whole hand or one or more digits directed to recipient, another individual or object in environment

Reach out down – holding out a hand toward another individual by extending the arm, wrist and hand in more or less horizontal position, and stretching the fingers while palm is facing downwards, other individual is not touched

Reach out side – same as reach out down except the palm of the hand is directed sideways

Reach out up – same as reach out down except that the open palm of the hand is directed upward

Shake wrist – shaking the hand vigorously with flexible wrist towards another individual. Repetitive

Swing – arm is swung in an underhanded arch – can involve contact

Throw hold – arm is raised above head, as if in a throw, but movement not carried out for at least 2 s if at all

DISCUSSION

This study provides the first systematic analysis of the repertoire of manual gestures in wild adult chimpanzees. The results show that chimpanzees have a multifaceted and complex signal repertoire of manual gestures. These gestures may be described as prototypes, within which there is variation, and between which the boundaries are not always clear-cut but there is gradation apparent along several morphological components. While previous research has focused on examining the morphological complexity of vocal behaviour and facial expressions, our research is the first empirical demonstration of such complexity in gestural behaviour. The quantitative analysis of the repertoire of gestural communication in wild chimpanzees illustrates these intricacies.

First, this study demonstrates statistically that chimpanzees display at least 20 gesture types in their repertoire. These gestures occurred across a variety of affiliative, agonistic, mother-infant contexts, and were primarily concerned with the regulation of immediate responses towards the signaller or objects in environment. Amongst the repertoire of manual gestures, previously unreported gesture types were arm extend, limp hand, reach hand swing and reach stroke. The repertoire of manual gestures could be characterised as rich and diverse but clearly based on some key components such as arm extend, arm swing, reach and flail. For instance, among the gestures within the group of "reach" we could find: gestures where the arm and hand were positioned towards an object and held at the point of greatest remove in the direction of desired object; a reach with a sharp rounded movement of the whole arm in the vertical plane and directed at the desired object; and finally reach gestures where the arm was held towards the object at the point of greatest remove, but the hand was also performing a sharp rounded movement in the direction of desired object.

In addition, in our analysis we defined gesture type as those gesture units which were validated above chance level by a cross-validation procedure of the discriminate function analysis. However, it is possible that the current number of 20 gesture types may be expanded by future studies to 30 gesture types, as initially indicated by cluster analysis. Gesture types cross-validated by the discriminate function analysis at chance level may be of importance in future studies of repertoire of manual gestures in wild chimpanzees because solution of discriminant function analysis could be unstable where there is a small sample size. This is evident when examining the scatter-plot of the discriminant scores which indicates that group differences between validated below and above chance level gestures types may be large. This could further be supported by the fact that few of these validated at chance gesture types have been documented in great ape repertoires in other studies, for example hand clap or fist flail. Whilst we were unable to include those gesture types validated at chance in our analyses, future studies may show these to be distinct gesture types in wild chimpanzees.

Our findings on repertoire size are similar to the work by Plooij, Goodall and Pollick. For instance Plooij (1984, 1978, 1979) distinguished 17 gesture types, Goodall (1968, 1967, 1986) distinguished 14 gestures, Pollick (Pollick and de Waal, 2007) found 16 gesture types. However, our results are in contrast with other research which reported fewer manual gesture types. For instance, amongst the studies in the wild, Nishida (1970) reported only 3 gestures and Sugiyama (1969) only reported one gesture type. Amongst studies from captivity van Hooff (1971) found 9 gestures and Liebal (Liebal et al., 2004a) found 5 gesture types. These inconsistent results may be due to the difficulty in objectively establishing the level of categorisation of gesture units, as evidenced in variability in splitting and lumping of morphological features across gesture repertoire studies. For instance, a hand bend gesture categorised as a unitary gesture type in current study was split into two gesture types by Plooij (1984, 1978, 1979), Goodall (1968, 1967, 1986) and van Hooff (1971). Reaching gestures which were categorised as one gesture type by Liebal (Liebal et al., 2004a) was split into 9 gesture types by current analysis. Additionally the difficulty of repertoire analysis is to maintain the same level of categorisation across all gestures to avoid variability in splitting and lumping within gesture studies. Pollick (Pollick and de Waal, 2007) for instance described and categorised some gesture types using relatively broad categories (i.e. 'point' which was classified as three different types of reach in our analysis) whilst the categorisation used for other gestures was more fine grained (i.e. reach out down and reach out up, which was lumped as one gesture type by current analysis). While gesture types determined quantitatively here do broadly corresponded with the categories of gestures defined qualitatively in previous approaches, the variance in repertoire size of 5 to 17 from other studies suggests that in previous research categorisation of gesture types at same level was not maintained consistently. This in turn bears on validity of previous repertoire studies and whether the more subjective qualitative assessment is reliable method of examining units of gestural repertoire. Research in the future should aim at developing a 'gold standard' tool to allow objective determination of gesture units if gestures are to be compared across populations and sites.

In addition, the gestural repertoire size identified here is similar to the repertoire size reported for both vocal and facial modes of communication in chimpanzees, across other research in captive and wild populations. For instance, Parr (2002) reviewed evidence on the communicative repertoire in chimpanzees and found that there are 20 to 30 different chimpanzee facial expressions and vocalisations types (see also van Hooff, 1971, van Hooff, 1967, Parr et al., 2007, Marler and Tenaza, 1977, Marler and Hobbett, 1975, Marler, 1969, Mitani et al., 1999, Mitani et al., 1996, Mitani, 1996). The similarity of the repertoire size of gestures, facial expressions and calls indicates that manual gestures are at least as complex a communicative system as other modality types. Manual gestures have the potential to convey diverse information types to recipients. Additionally, the resemblance in the repertoire size of gestures to the repertoire size of facial expressions and calls is reflective of complexity in cognition and social organisation displayed by the chimpanzees. For instance McComb (McComb and Semple, 2005) demonstrated that a large vocal repertoire size is correlated with both the complexity of the social system and the complexity of cognitive skills in primates (see also Aiello and Dunbar, 1993, Dunbar, 1998, Dunbar, 1993, Dunbar, 1996). Future studies could similarly address the relationship between gestural repertoire size, complexity of social organisation and cognition in primates, to illuminate the role of manual gestures in maintaining social complexity.

Second, this study reveals statistically the variation in the morphological features that chimpanzees display in their gestural repertoire. Overall, gestures in the chimpanzee repertoire varied along a number of combinations of morphological components but only two combination types had strong influence on differentiation between gesture types. Additionally, no single feature had a strong differentiating effect between gesture types and most distinguishing features were associated with over half of gesture types. These results suggest that while chimpanzees in our study had gestures which possessed many morphological attributes, they were nevertheless relatively indistinctive and displayed a lot of similarity in their morphological components. This is in contrast to findings from vocal behaviour studies which show that acoustic features of calls are highly unique. For instance, in a study of chacma baboons (see Fischer et al., 2001) the values of correlation coefficients for morphological features were significantly higher (i.e. majority fell between 0.2 and 0.6 range) than those reported here for gestural behaviour, which indicates greater distinctiveness of calls compared to gestures. This difference in distinctiveness between gestures and calls may suggest differences in adaptation to the transmission habitat. These gestural signals appear more graded than discrete, with less salient unique features and a lower degree of distinctiveness, suggesting that gestures may be adapted to transmission across short distances and open habitat, where other visual cues may be used in interpreting the signal by a recipient. More distinctive morphology in calls on the other hand may allow efficient decoding of information across larger distances and across a more obscured visual channel (see also Marler, 1976, Green and Marler, 1979 for comparison of characteristics of short distance and long distance calls in relation to features of habitat). Future detailed analyses of gestural communication across open and closed habitats in primates may elucidate whether the differences in distinctiveness of gestures and calls reflect differences in adaptation to the habitat.

Third, this study shows statistically the degree of morphological specificity in the gestural repertoire. Overall, the morphology of the gesture types was more clumped and overlapping than distanced greatly from each other. For instance, there were gesture types whose morphologies could be categorised across more than one gesture type in the discriminate function analysis classification procedure and therefore producing a morphological specificity result below 100%. This organisation of signals within the repertoire system suggests that chimpanzees have a graded and mixed repertoire; gestures are not completely discrete but contain morphological types that are intermediate between prototypical forms. This lower specificity in gestural signal production is in agreement with the characteristics of other forms of communication in chimpanzees, that is, vocalisations and facial expressions. The similarity in signal gradation between gestures and other modalities of communication may be because form of gestures is also stereotypical and determined by the affective state of a signaller. The evidence for stereotypic gesture production would be that small variability in affective states would underlie the gradation of gesture seen; the automatic expression of highly specific gesture subtypes would be seen in response to highly specific stimuli. For instance, gradation in the structure of calls was reflected in small differences in context and affective state in Barbary macaques and baboons (see e.g. Fischer et al., 2000, Fischer, 1998). Gradation in facial expressions was related to motivational conflict in the signaller in situations of high risk of attack and physical injury (see e.g. Parr et al., 2005). Alternatively, flexibility in the production of gestures would be evident in the absence of an association between production of gesture subtypes and specific affective states, and instead suggest difficulty in reproducing gestures in the same form each time. Future studies of gesture production and gesture usage should clarify whether gesture forms vary with differences in affective states of the signaller.

Additionally, the similarity in signal gradation between gestures and other modalities of communication may be because the precise form of gestures, as for signals in other modalities, is genetically determined. For instance, the pattern of gradation in vocalisations was replicated across all individuals within two groups of Old World primates (Fischer et al., 2001). Differences in gradation between individuals along the gradient of relatedness and association patterns may on the other hand indicate ontogenetic acquisition of gesture forms. Studies of variability in gesture form within and between individuals across related and unrelated individuals will provide clues to the ontogenetic processes underlying production of gesture structure. Those studies on ontogeny of gesture structure, however, can only be meaningfully executed using a clear, well defined gestural ethogram and statistical analysis of the gesture structure.

In conclusion, this study has identified the repertoire of manual gestures observed in a wild chimpanzee population of Budongo forest, Uganda. This study has shown that gestures have a relatively large repertoire, which is comparable to the repertoire size of both facial expressions and calls. Gestures appear relatively indistinct compared to vocalisations, but they are graded like other modalities of communication. These characteristics suggest that gestures are a complex component of chimpanzees' communicative system, playing an important role in maintaining social complexity. Gestures may also be learned, produced non-stereotypically and they may be adapted to short distance transmission in open habitat. Future studies of contextual usage, intra and inter-individual variability and socio-ecological factors will clarify these aspects of gestural communication. Such studies will allow further comparisons of gesture characteristics with features of human gestural communication to identify features of gestural communication in our common ancestor.

The results of this chapter have been submitted for publication:

Roberts, A.I. Vick, S-J.; Roberts, S.G.B.; Buchanan-Smith, H.M. & Zuberbühler, K. Structure-based repertoire of manual gestures in wild chimpanzees: Statistical analyses of a graded communication system

Chapter 3: Communicative intentions in wild chimpanzees

INTRODUCTION

An important element in understanding the cognitive abilities underlying human language evolution is to understand the cognitive skills that underlie communication in our closest living relatives (Tomasello and Zuberbühler, 2002). Intentionality is amongst the most cognitively demanding features of human language and the onset of intentional communication marks the onset of symbolic capacities in humans. Intentional communication can be defined as use of communicative behaviour in which the sender has a goal, and repeats or elaborates his behaviour until the goal is obtained or failure is clearly indicated (Bates et al., 1979). One key mode of intentional communication is that of gestural signalling, defined as voluntary movements of arms or legs or body postures used with the aim to initiate a desired action (Liebal et al., 2004a, Pollick and de Waal, 2007). Gestural communication is important because the onset of intentional gestures precedes the transition to verbal symbolic expression in human infants and may be an evolutionary precursor to human language (Corballis, 2003). While intentionality in gestural communication has been thoroughly examined in human infants (see e.g. Golinkoff, 1993, Golinkoff, 1986, Bretherton and Beeghly, 1982, Shwe and Markman, 1997), we currently have limited understanding of similar processes underlying gestural communication in our nearest living relatives, the chimpanzees. However, understanding these processes in great apes is important because it provides vital insights into which cognitive abilities underlying language use were present in the common ancestor of humans and chimpanzees and which abilities evolved uniquely in humans (Suddendorf and Whiten, 2001).

East African chimpanzees *(Pan troglodytes schweinfurthii)* are our closest living relatives (Reynolds, 2005) and they exhibit remarkable cognitive skills in various aspects of their social behaviour in captivity, such as the ability to understand that others are intentional beings with perspective states which can be altered by a signaller's behaviour (see e.g. Kaminski et al., 2008, Hare et al., 2000, Hare et al., 2001). However, it is not currently clear to what extent these cognitive abilities seen in captive apes are acquired via contact with humans and which features are typical of chimpanzees in general (Bering, 2004, Boesch, 2008, Boesch, 2007, Call and Tomasello, 1996, Tomasello and Call, 2008, Tomasello and Call, 2004). Therefore it is important to investigate cognitive capacities in wild populations because wild apes may exhibit a divergent cognitive make-up more characteristic of the social and ecological environment of the common ancestor when compared with captive populations. To what extent intentionality in social behaviour seen in chimpanzee behaviour in captivity will be observed in gestural communication in wild East African chimpanzees is thus a particularly exciting question.

Several behavioural criteria for defining intentionality in humans have been investigated in the studies of gestural communication with captive apes. One part of the supporting evidence for intentional communication is based on the influence of an audience on the propensity to produce gestures by the chimpanzees. For instance, Leavens et al. (2004) observed that the rate of gesture production decreased significantly when an experimenter was absent compared to when experimenter was present in full view of the chimpanzees. Furthermore, chimpanzees take into account visual attention of recipient and this influences the propensity to gesture. For example, Liebal et al. (2004a) found that within a captive group of chimpanzees the rate of gesture production increased when the recipient was looking at the signaller. Genty et al. (2009) have reported that the visual gestures of wild and captive gorillas were produced more often than tactile or auditory gestures when the recipient was looking at a signaller. Krause and Fouts (1997a) found that chimpanzees used attention getting behaviours such as vocalisations and auditory gestures to attract the experimenter's attention before employing pointing or other visual gestures.

While these studies have shown flexible use of gestures in response to presence and visual attention of audience, a more compelling set of supporting evidence for complex cognitive skills underlying gestural communication comes from studies of communicative persistence. Persistence can be defined as the repetition of signals in the face of communicative failure and shows that the signaller has a definite goal, while elaboration is substitution of original signals which failed to communicate the goal, and indicates flexibility in achievement of the desired goal (Bates et al., 1979). The cognitive abilities underlying repetition and elaboration are important because they demonstrate a capacity for secondary representation such as means-ends reasoning, i.e. that individuals recognise their desired goal state and understand which necessary steps need to be taken to achieve their goals (Suddendorf and Whiten, 2001). Moreover, the processing underlying repetition and elaboration in communication is cognitively demanding because individuals may be attributing mental states to their recipients when attempting to achieve their desired goal (Tomasello & Call, 1997).

Despite the importance to understanding of cognitive skills underlying language evolution in humans, only a few studies have addressed great apes' ability to persist in communicative attempts in interactions between conspecifics. For instance, Liebal et al. (2004a) examined gesture sequences in captive chimpanzees to illuminate the causal phenomena behind the emergence of gesture sequences. They hypothesized that gesture sequences may arise due to: the manipulation of the attentional state of conspecifics before using visually based gestures; persistence in communicating to elicit a response by a recipient; or pre-planned constructs to increase gesture efficiency. They found that individuals did not construct gesture sequences based on the attentional state of the recipient prior to gesture production. Moreover, there was no difference in sequence position of gestures based on whether the gesture was classified as more or less effective in eliciting a response from a recipient, showing that intention to increase effectiveness of a gesture does not motivate production of sequences. However, there was an influence of a presence or absence of a response on the production of gesture sequences. Thus, in the absence of an appropriate response to the first gesture, Liebal et al. (2004a) observed that sequences of two more effective gestures were more likely to occur than expected by chance. Moreover, Liebal et al. (2004a) found that the frequency of response to the first gesture in a sequence was significantly lower than to single gestures. The authors concluded that chimpanzees did not combine their gestures in a premeditated fashion to increase responsiveness to less effective gestures. Instead, gesture sequences may have emerged in the absence of an appropriate response from a recipient to the first gesture.

Similarly, Genty and Byrne (2009) explored the causal processes behind the emergence of gesture sequences in captive and wild western lowland gorillas. Firstly, they examined whether gesture sequences were made to increase the efficiency of single gestures, i.e. whether sequences were made to increase overall frequency of response from recipients. Alternatively, they examined whether sequences were made to produce new meanings from combinations of single gestures, i.e. whether evidence for syntax could be found in gesture sequences. They found that sequences were not typically made in response to a failure in communication and the efficiency of gestures was not an underlying factor in sequence formation. For instance, the probability of failing to get a response did not vary with the length of repetition sequences in gorillas. Additionally, gesture sequences did not have higher effectiveness than single gestures. When examining the second hypothesis, Genty and Byrne (2009) found that sequences of gestures were not constructed to alter the meaning of single gestures and there were no syntactic effects of sequential combination. For instance, the overall meaning of sequences did not vary significantly from that shown by a single gesture. They thus concluded that gorillas form gesture sequences to regulate the tempo and nature of the ongoing interaction rather than producing semantic structures or sequences in response to lack of responsiveness by a recipient.

Thus, there is currently a lack of agreement in captive studies examining communication between conspecifics about the causal factors behind sequence formation and also whether great apes persist and elaborate in their communication when faced with communicative failure. One reason for this disagreement is that studies have not focused specifically on communicative persistence but instead focused on illuminating syntactic structures in gestural signalling. Thus, the methodologies employed have not been adequate to answer questions posed in our research. For instance, Genty and Byrne (2009) did not examine whether a response to a gesture in a sequence had occurred at any stage during the production of a sequence; they instead examined what type of the response was present overall following sequence production. However, it is crucial to take behaviour of the recipient during the sequence into account because these interactions are dynamic and any responses made by recipient during sequence production may have influenced the propensity of a signaller to repeat or substitute the signals, i.e. to repair the misunderstanding or prompt further execution of a response.

Moreover, previous studies did not make any assumptions that the gestures were directed towards achieving a particular goal. However, without assumptions that gestures were made towards achieving specific goals and what these goals would be, inferences about the success or failure of communication cannot be made (Golinkoff, 1986). This is because the mere presence of a change in behaviour of a recipient is not informative enough with respect to whether the signaller achieved their desired goal. For instance, if a signaller signalled a desire to be approached but the recipient responded by moving away, then the change in the behaviour of the recipient is not consistent with what the signaller wanted, even though it could be interpreted as a response. Thus, methodological shortcomings of previous observational studies do not currently allow direct examination of whether great apes persist in their communicative attempts with conspecifics. Further studies are needed to illuminate whether gesture sequences are made in response to communicative failure and to guide their recipients towards the desired response, or instead are formed to regulate the nature of the ongoing interaction.

More conclusive findings about communicative persistence have come from experiments that examine communicative persistence between nonhuman primates and a human experimenter. For instance, Leavens et al. (2005b) and Cartmill and Byrne (2007b) presented captive chimpanzees and orang-utans respectively with a problem where subjects had to request an out of reach food item from a human experimenter. They experimentally manipulated whether chimpanzees were understood or misunderstood. In both studies, the experimenters first simultaneously displayed undesirable (primate chow) and highly desirable (a banana) food items to the subjects. After a period of 30 seconds during which subjects displayed communicative behaviours about the desired food, the experimenters manipulated the success of the communicative attempts of the subjects by delivery of the desirable food item (successful communication), half of the desirable food item (partially successful communication) or the undesirable food item (unsuccessful communication). The experimenters noted the behavioural responses of the subjects to these levels of success in communication. Both Leavens et al. (2005b) and Cartmill and Byrne (2007b) found that apes responded depending on the success of their communicative bids and persisted in their communicative attempts when these failed, i.e. they continued to communicate when presented with a delivery of chow. Additionally, Cartmill and Byrne (2007b) observed that not only did subjects persist in their communicative attempts when faced with communicative failure, but they also modified their gestural communication flexibly to take into account the recipient’s state of comprehension when their goals were not met or only partially met. For instance, the orang-utans repeated the same gestures when faced with partially successful outcomes but used new gestures more often when they completely failed to communicate.

While such experimental studies have made an important contribution to our knowledge about cognitive processes underlying gestural communication by great apes, important empirical gaps still remain in our understanding of repetition and elaboration in gestural communication. One shortcoming of previous studies on persistence in communicative attempts is that they have used food or a food related tool (e.g. a stick needed to obtain honey from a dipping device, Russell et al., 2005) as the desired object. However, great apes are sensitive to the presence of food and an intense emotional response (including facial, vocal and visual behaviours) usually follows visual presentation of desirable food items in both captive and wild apes (see e.g. Goodall, 1986). Thus, it is reasonable to argue that when food is used as the stimuli for elicitation of persistence, emotional arousal may play a role in the expression of the ensuing communicative behaviours. For instance Russell et al. (2005) argued that when food is presented to the chimpanzees they make noises such as cage banging or attempts to reach towards unattainable food as result of excitement and frustration. However, such stereotypical behaviours are not used purposefully to influence the behaviour of the recipient to achieve desired goals. Instead, they represent involuntary expressions of arousal and anxiety in reaction to the inability to attain the desired food. Thus, the fundamental requirement of persistence, that the behaviour is intentionally produced towards achieving the desired goal, i.e. signallers direct their communication towards a recipient with a priori knowledge of the effect that the signal will have on the recipient (Bates et al., 1979, Bates et al., 1975) is not met in those analyses.

Moreover, this limitation of research on persistence is exacerbated by the fact that some authors included not only stereotypical but also non-communicative behaviours in their analyses; for instance, Cartmill and Byrne (2007b), included behaviours such as scratching, spitting through bars and yawning in the reported gestures. However, these behaviours cannot be interpreted by the recipients in terms of intentions and desires of the signaller or the state that he is in. That is because for a change in the behaviour of a recipient to occur, information has to be provided by the sender, the receiver can then subsequently use that information in deciding how to respond (Bradbury and Vehrencamp, 1998). Those behaviours do not provide the recipient with the information about the signaller's state because no alterations to recipient's behaviour can be observed following those signals to the benefit of a recipient or a signaller (see e.g. Paukner and Anderson, 2006 for detailed analyses of function of self directed yawning). Thus those behaviours do not entail any costs to the signaller and instead represent involuntary expressions of internal state with functions other than information transfer between signaller and recipient. Consequently, the fundamental requirement of intentional communication, i.e. that the signaller provides information to the recipient about the goal that he wants the recipient to obtain, is not evident in these analyses. Taking into consideration that both stereotypical and non communicative behaviours have been included in previous analyses, it is reasonable to argue that experimental studies require improved methods before the presence and nature of intentional persistence can be reliably demonstrated among our nearest living relatives.

The study of intentionality in gestural communication in wild chimpanzees may illuminate fundamental questions about evolutionary transition from pre-linguistic to linguistic communication in humans. Moreover it will help identify which cognitive abilities underlying human language evolution were present in the common ancestor of humans and chimpanzees and which were exclusive to humans. It aids us in understanding of language evolution and also addresses some important questions in about what chimpanzees know about their gestural communication. For instance, do wild chimpanzees understand the effects that their signals have on the recipient? Do they realise that they can influence comprehension states of their recipients to achieve their goals by communicative means? Do they know that they can use different means to the same end?

To address these important questions, we examined episodes of gestural communication in wild chimpanzees focusing on what happens when signallers fail to achieve their desired goals. Failure in communication occurs when signallers direct their gestures to the recipients but fail to achieve the desired response. For instance, recipients may misunderstand the signal and provide a response type which does not match the desired goal in any way, or only partially act in accordance with the signallers' expectations. Subsequent to failures in understanding, signallers may try to clarify the meaning of their initial signals and continue to signal in an attempt to achieve their goals. For instance, signallers might persist by repeating the original signals, or substituting the original signals until the desired outcome is obtained.

The study of gestural communication can provide information not only about whether chimpanzees engage in communicative repairs but also about the nature and complexity of the interactions. For instance, if wild chimpanzees persevere in their communicative attempts, do they simply repeat the original signals or are they capable of engaging in non-stereotypical repairs? If wild chimpanzee persistence is only an inbuilt reaction to a particular internal state, contingent upon changes in the availability of the goal itself, then only repetitions of the original signals should be expected to occur. If on the other hand chimpanzees are aware of the impact that their signals will have on the recipient and can modify their signalling flexibly contingent upon changes in the recipient's behaviour toward the goal, then they should demonstrate more complex communicative abilities such as ability to add and substitute original signals dependent upon the recipients' state of comprehension.

We examine these questions in the first systematic study into intentionality underlying gestural communication in wild chimpanzees. We complement previous research in captivity by addressing methodological problems in four important ways. Firstly, we aim to demonstrate communicative persistence across variety of contexts, i.e. including food and non food contexts, to exclude effects of frustration. Secondly, we aim to include in our analyses only those behaviours which could convincingly be classified as intentional, i.e. communicative behaviours accompanied by looking at a signaller and visual monitoring of response rather than behaviours effecting change in recipient by mechanical impact at a goal. Thirdly, we examine persistence with respect to an identifiable desired goal, which we determined observationally and statistically. Finally, we follow the behaviour of a recipient throughout the whole sequence production to determine more clearly whether the type of response by a recipient was a causal factor in production of sequences.

METHODS

Study site and subjects

One group of habituated East African chimpanzees was studied over three separate periods totalling eight months (September 2006, April - July 2007 and March - May 2008) at Budongo Conservation Field Station, Budongo Forest Reserve in Uganda (see Appendices 1 and 2 for maps of the study area). This study site is located in western Uganda on the edge of the western Rift Valley (1˚37'- 2˚00'N; 31˚22'- 31˚46'E) at the mean altitude of 1100 m (Eggeling 1947). The reserve area of 793 km^2 is composed of grassland, forest and semi-deciduous tropical forest with predominantly continuous forest cover of 428 km^2(see e.g. Eggeling, 1947, Reynolds, 2005 for detailed descriptions of floral composition of the study area). The chimpanzee community varied from 76 to 79 individuals during the study period (see Appendix 3 for a list of all community members). For the purposes of this study we chose six adult parous females and six adult males, selecting only those individuals who did not have limb injuries and who could be distinguished according to two rank categories (i.e. 3 high ranking and 3 low ranking males and females). All of the focal chimpanzees were habituated to humans and tolerated human observers at close distance of approximately 5 m (see Appendix 4 for additional details on the observed chimpanzee subjects).

Data collection and coding protocol

Quantitative continuous focal animal follows and opportunistic, qualitative *ad libitum* samples were taken to establish a complete inventory of gestures for each of the focal individuals. Focal subjects were chosen systematically, based on availability of individuals and their behaviour recorded during a standardised observation period of 20 minutes duration. Each focal individual was observed equally at different times of the day across study period with the aim of sampling each individual at least once every week to ensure an even distribution of samples throughout the day, and across the study period. In order to avoid dependency in the data set, at least 20 minutes was taken between consecutive samples of the same focal subject. Whenever possible, consecutive sampling of the same individual was avoided, by switching to a different focal subject after completing a focal follow. Such a sampling protocol enabled the collection of 250 hours of focal footage, of which mean (SD) of 17.21 (1.29) hours of independent focal data per each focal individual could be used for analyses, that is, footage with good to excellent visibility of focal subject and context.

During focal follows behaviour was recorded continuously using a digital video camera recorder (SONY DCR – HC18E and SONY DCR – HC32E), with the camera centred on the focal individual but also taking a wider view to include the recipient and other interactants within the visible presence of the focal individual. Whenever a recipient was out of range of video recording, but their behaviour could still be seen by the observer, all contextual information was described and spoken onto the camera.

As the first step in analyses, an inventory of gesture types and usage in chimpanzees was derived from video recordings. For each gesture event, the sender and recipient of a gesture were coded along with the behaviour of the recipient prior to and after initiating gesture. Behaviour was coded as an act of gestural communication if it was an expressive movement of the limbs or head and body posture which was mechanically ineffective (did not induce change in behaviour of recipient by exerting physical force upon a body part of a recipient), communicative (i.e. overall consistently produced change in the behaviour of recipient) and intentional. Behaviour was considered to be intentionally produced if consistently accompanied by goal directedness (i.e. the signaller looking at recipient during or after gesture production) (Bates et al., 1979). We grouped gestures into different gesture types quantitatively using an ethogram to code different morphological characteristics of each gesture event (i.e. number of hands performing the movement, type of arm movement, position of the arm relative to the body of the signaller, hand shape and position of hand relative to forearm). This ensured reliability of our repertoire analyses, i.e. classification of gestures into gesture types based on morphological resemblance.

The recipient was coded as the individual at whom the gesture was most clearly directed, i.e. an individual at whom the signaller was looking during or immediately after performing the gesture. The behaviour of recipient was scored as a response if the change in the state of recipient’s behaviour occurred within 30 seconds of gesture production and prior to any other context which might have led to a change in the behaviour of a recipient or signaller’s goal. All observable changes in the behaviour of recipient were labelled as a response, whereas the absence of observable change was marked as no response. Thus, presence of any behavioural change in the behaviour of a recipient was initially considered as a response to a gesture (see e.g. Genty et al., 2009 for similar approach).

A total of 199 video sequences of gestures were coded, consisting of 34 manual visual gesture types and their behavioural context (see Chapter 2 for detailed descriptions of repertoire and usage and Chapter 4 for ethograms of responses coded). For the purpose of these analyses, only those sequences where manual visual gestures were emitted first in the gestural sequences were included, to avoid dependent data. Thus any sequences where manual visual gestures occurred in the middle or towards the end of the gestural sequences were removed from the data set. This allowed us to exclude the potential confounding influence of preceding signals in the sequence on gesture usage. Moreover, any gesture type that was observed less than 6 times during the study period was either removed from the data set or combined with another logical category. This data pooling procedure applied only to various types of arm flap which were merged into one gesture type. Since other gesture types with only a few cases could not easily be combined with any other gesture type they were removed from the data set. This data reduction procedure greatly restricted the amount of data available for this study, but was necessary as it increased reliability of our contextual analyses, i.e. behavioural effects of signal production on recipient’s response.

Next, for each gesture event we noted any instances of repetition or substitution in gestures following the first gesture in a sequence. The gesture used to initiate an interaction (prior to response) was named the ‘first’ gesture in a sequence while all following gestures in a sequence were named consecutively as second, third, fourth and fifth gestures. Only gestures prior to a positive response by a recipient immediately or following the persistence sequence were considered part of the same sequence. Thus any gestures made by a signaller following no response, half successful response or wrong response by a recipient were also considered part of the same gesture sequence (see section below for a categorisation of different response types). Moreover, we noted any further gestures emitted by a signaller following a positive response by a recipient within 30 seconds of positive response production within the same behavioural context. For the analyses we only chose those sequences where the first gesture in a sequence was a visual manual gesture without any use of substrate or objects. This allowed us to exclude potential confounding effects of differences in effectiveness between gestures, i.e. influence of gesture type on number of gestures in persistence sequences. For example, tactile manual gestures are more effective than manual visual gestures at eliciting a positive response from a recipient at first or second attempt at communication. This in turn may result in higher frequencies of repetitions in persistence sequences. Thus to reduce the number of potential confounding factors in our analyses we examined manual visual gestures only. Following the first gesture in a sequence, all subsequent gesture types were coded in elaboration and repetition sequences. The presence of both manual visual gestures as well as any other gesture categories such as tactile manual gestures, manual gestures using objects, movements of legs or body directed at recipient were scored, including modality (visual, tactile or auditory), intensity (visual - less intense, tactile or auditory - more intense), duration between successive gestures in a sequence (see Table 3.1 for description of the communicative gestures coded in this study and most frequent context) and type of response to a final gesture in a sequence.

Finally, the specific responses to each gesture type were examined in more detail. The most commonly seen response type for each gesture type was selected from the data base and labelled ‘expected response’. We used ‘expected response’ as a proxy for a specific goal of each gesture type performed by our focal chimpanzees (see Results section for analyses whether the ‘expected response’ was the appropriate response type for the examined gestures). Without the assumption that gestures were used towards specific goals, inferences about the success or failure of communication could not be made (Golinkoff, 1986). Thus, each response matching an expected response was labelled as *positive response* and it constituted a successful communication attempt by a signaller. As such it provided a criterion against which all other responses were compared. A response matching positive response but failing to elicit the desired outcome fully (e.g. approaching only half way) represented only a partially successful communication attempt and was thus labelled as *a half-successful response*. Each change in the recipient's behaviour not matching the positive response in any way was labelled as a *wrong response* and represented a failure to communicate the goal by a signaller. Similarly, a lack of any observable response constituted lack of successful communication and was labelled as *no response*. Consequently, all responses to the first and last gesture within a sequence (the last gesture in a sequence was the final gesture emitted in a persistence sequence, following no response or wrong response by a recipient to a first gesture in a sequence) could be pooled into four categories denoting four main response types: positive response, no response, wrong response and half successful response.

Analyses

Manual visual gestures occur rarely, i.e. an average 0.6 of manual gestures per hour was recorded during our data collection period. Thus, because of the small sample size we conducted the analyses using a gesture as the unit of analyses and pooling across all of the individuals and dyads, taking care that both individuals and gestures contributed equally to the sample size of gestures analysed in this study (see Figures 3.1 and 3.2 for contribution of subjects and gestures respectively to the overall sample size per response type). These methods of analyses have reliably been used in the majority of recent gestural communication studies (see e.g. Genty et al., 2009, Pollick and de Waal, 2007). All statistical tests conducted in this study were non-parametric and two tailed. Non-parametric statistical tests were used because data were categorical and thus there was no normal distribution to apply parametrical tests. Effect size (r) in Mann-Whitney post hoc test is an objective and standardized measure of the magnitude of an observed effect. A coefficient of 0 would signify no effect, while a value of 1 would signify a perfect effect; values of 0.1, 0.3 and 0.5 signify small, medium and large effects, respectively. On the boxplot figures, the box (the shaded area) represents the inter-quartile range (50% of observations fall in this area). Thick horizontal line within box represents the value of a median. Asterisks and circles outside of the boundaries of the whiskers represent outliers on the box plot, placed above box plot of the pertinent response type.

Figure 3.1: Contribution to overall sample size of gestures per signaller

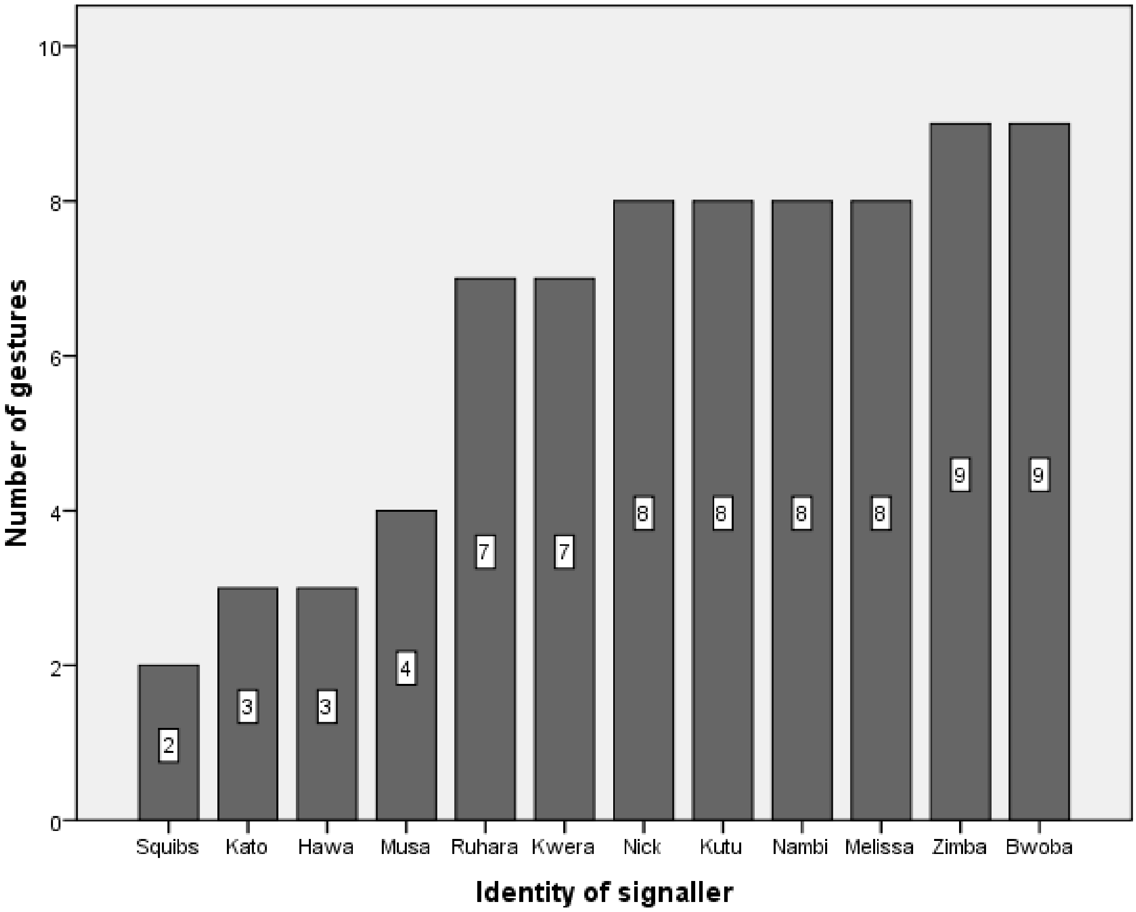


Figure 3.2: Contribution to sample size of gestures per gesture type

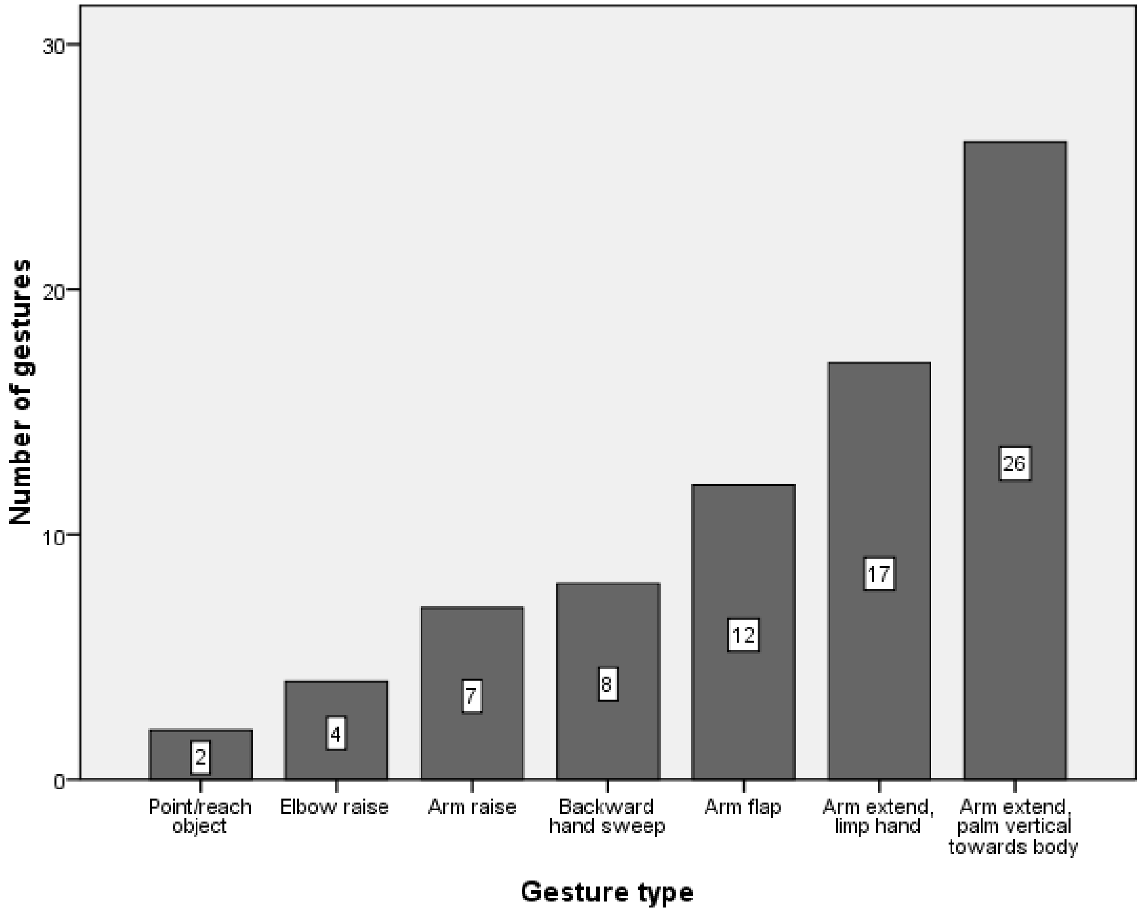


Table 3.1: Description of morphological features and the most frequently observed response for each gesture type

Gesture label	**Description of gesture morphological features**	**Expected response (most frequently observed)**
Elbow raise	One elbow raised upwards, arm fully flexed with hand directed downwards and placed towards centre of the body, while elbow extended sharply outward, gesture performed in single movement	Approach signaller
Reach object	One arm extended towards object without touching it, gentle flexion of hand towards body at wrist joint, whole cupped hand or only fingers move up and down vertically towards object extending fingers towards object at each upward swing, repetitive fast movement	Attend to external referent
Arm extend, palm vertical towards body	One or two hands extended with palm vertical directed towards signaller’s body, signaller directs inner part of arm and hand at the recipient, made as single movement	Approach signaller
Backward hand sweep	One hand extended vertically down towards behind the signaller’s body, hand makes a sweeping movement vertically backwards towards another individual, performed as single movement	Climb on signaller’s back
Arm flap	One hand raised upwards with palm facing down makes sharp, slapping movement towards the recipient from upwards to downwards, from either wrist joint or shoulder, no contact occurs but movement can be executed in close proximity and directed at particular body part of recipient, single movement	Move away from signaller
Arm extend, limp hand	One arm strongly flexed, upper arm in contact with body, forearm extended forward towards another individual, hand suspended limply at wrist joint, palm directed vertically towards signaller’s body or downwards, made as single movement	Expose body part for grooming
Arm raise	One arm raised high in the air with forearm above the head, hand suspended limply at wrist joint, palm directed vertically away from own body and towards the recipient, single movement	Receive groom
Hit object	Chimpanzee hits object with one hand with force	Stop activity/move away

Shake object	Chimpanzee shakes/pulls branch or vegetation with both hands simultaneously and repetitively	Defensive approach/move away
Brief touch another	Chimpanzee briefly touches another with one hand without exerting physical force to induce recipient’s movement	Approach/move body part towards signaller
Embrace another	Chimpanzee embraces recipient with one arm for short period of time, single movement	Approach/move body part towards signaller
Forward head move	Chimpanzee is in sitting stance, and moves head forward in single sharp movement	Stop activity/move away
Forward back move	From sitting stance, chimpanzee moves upper and lower back forwards and backward in sharp movement	Stop activity/move away
Bipedal bow	Whilst in bipedal stance and holding trunk, chimpanzee moves upper and lower back downwards	Approach signaller/stop displaying
Quadrupedal head bow	Whilst in quadrupedal stance and stationary chimpanzee gently flexes hind legs, whilst moving head and back downwards	Climb on back
Quadrupedal stare	Whilst quadrupedal and stationary, chimpanzee gently flexes hind legs and stares at recipient	Groom present/receive groom
Bipedal flexed run	Whilst bipedal and holding trunk, chimpanzee moves up the trunk with strongly flexed hind legs	Pass by/stop displaying
Bipedal flexed stationary	Whilst stationary and bipedal holding trunk chimpanzee strongly flexes the hind legs	Approach signaller/stop displaying
Leg stamp	Whilst in sitting position, chimpanzee stamps object with one leg	Defensive approach/move away

RESULTS

Factors influencing the occurrence of communicative persistence in chimpanzees

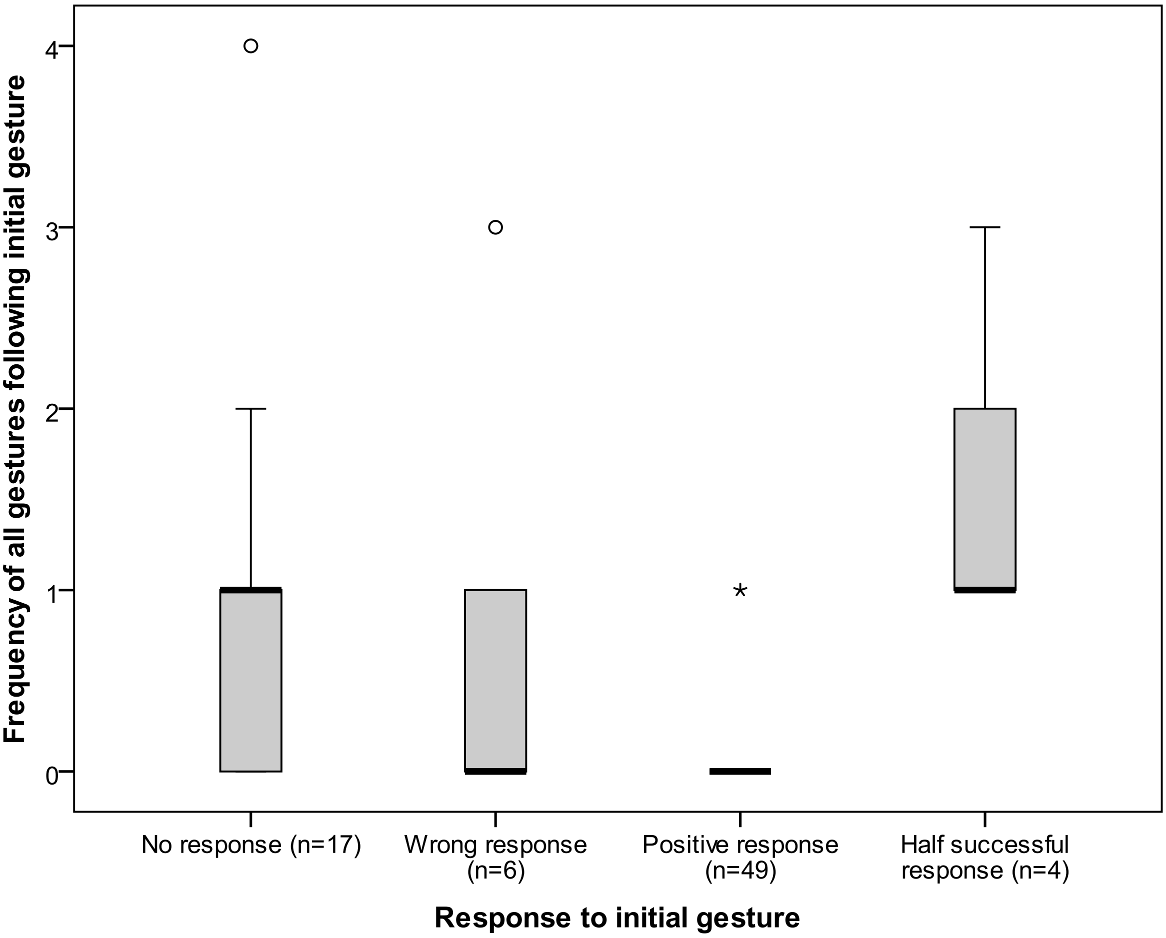
Only the recipient's response following the production of the first gesture had an effect on the propensity of a signaller to continue their communicative attempts by subsequently producing one or more gestures (Fisher's exact probability test, $p < 0.001$). There was no significant association between the number of gestures in a sequence and sex and age class of a recipient (N = 38 infant; N = 7 juvenile; N = 2 subadult male; N = 8 adult female; N = 21 adult male, Fisher's exact probability test, $p = 0.331$), the overall context of signal production (N = 1 unclear; N = 8 sex; N = 1 travel; N = 1 visitor; N = 1 rest; N = 14 breast feed; N = 4 clinging; N = 2 contact; N = 7 food; N = 24 groom; N = 13 ride; Fisher's exact probability test, $p = 0.189$), initiating gesture type (N = 4 elbow raise; N = 2 reach object; N = 26 arm extend, palm vertical towards body; N = 8 backward hand sweep; N = 12 arm flap; N = 17 arm extend, limp hand; N = 7 arm raise; Fisher's exact probability test, $p = 0.234$) or individual identity of a signaller (N = 8 NK; N = 2 SQ; N = 9 BB; N = 4 MS; N = 3 HW; N = 3 KT; N = 8 KU; N = 7 KW; N = 8 ML; N = 8 NB; N = 7 RH; N = 9 ZB; Fisher's exact probability test, $p = 0.246$).

Chimpanzees persist in their communicative attempts when faced with communicative failure

Chimpanzees act purposefully to correct misunderstandings when their goals are not met or only partially met (see Table 3.2 for all sequences of communicative persistence in wild chimpanzees). The total number of gestures varied significantly across the four response types to first gesture (Kruskal-Wallis test, H (3) = 43.44, $p < 0.001$), see Figure 3.3. We carried out Mann-Whitney post hoc test (Bonferroni correction $p < 0.016$) to reveal the differences between positive response, no response and half successful response types.

The total number of gestures following a positive response (*Mdn* = 0) was significantly lower than in no response condition (*Mdn* = 1, U = 129, r = -0.75, $p < 0.001$) and half successful condition (*Mdn* = 1, U = 1.5, r = -0.88, $p < 0.001$), with no significant difference between no response (*Mdn* = 1) and half successful conditions (*Mdn* = 1, U = 25, r = - 0.19, $p = 0.386$).

Figure 3.3: Median frequency of total number of gestures emitted by a signaller following different types of recipient response to first gesture



Frequency distributions indicate that signallers ceased their communication when receiving a positive response, i.e. in only one case (2%) out of 49 positive response cases did the signaller continue to gesture with one additional gesture. Out of 17 cases of no response, 29.4% (5 cases) were characterised by the absence of any further communicative attempts, while in 70.6% (12) of cases signaller persevered in their communicative attempts. Of these

17 cases, in 47.1% (8/17) of cases individuals continued to communicate with one additional gesture, two additional gestures were recorded in 13% (3/17) of cases and in one case out of 17 (5.9%) an individual produced a four gesture sequence to obtain their communicative goal. In all half-successful response cases individuals continued to communicate (in 4 out of 4 cases). In 75% of those cases (3/4), individuals emitted one further gesture and in one case out of 4 (25%), an individual emitted 3 additional gestures.

Table 3.2: Gesture type, the response obtained to initial gesture and details on any communicative repair sequences (N = number of cases). For definitions of gestures see Table 3.1

Response to first gesture	**Gesture type**	**N**	**Repair 1**	**Repair 2**	**Repair 3**	**Repair 4**	**Repetition**	**Elaboration**
Positive	*Arm extend, limp hand*	13	-	-	-	-	0	0
	Arm extend, palm vertical towards body	14	-	-	-	-	0	0
	Arm flap	8	-	-	-	-	0	0
	Arm raise	5	-	-	-	-	0	0
	Backward hand sweep	5	-	-	-	-	0	0
	Elbow raise	3	-	-	-	-	0	0
	Reach object	1	*Reach object*	-	-	-	1	0
Total		**49**	**1**	**0**	**0**	**0**	**1**	**0**
Half successful	*Arm extend, palm vertical towards body*	2	*Arm extend, palm vertical /body*	-	-	-	1	0
	Backward hand sweep	1	*Backward hand sweep*	*Backward hand sweep*	*Brief touch another*	-	2	1
	Elbow raise	1	*Elbow raise*	-	-	-	1	0
Total		**4**	**4**	**1**	**1**	**0**	**5**	**1**
Wrong	*Arm extend, palm vertical towards body*	1	-	-	-	-	0	0
	Arm extend, palm vertical towards body	1	*Quadrupedal head bow*	-	-	-	0	1
	Arm flap	2	-	-	-	-	0	0
	Arm flap	1	*Sitting head bow*	*Sitting back bow*	*Hit object*	-	0	3
	Arm raise	1	-	-	-	-	0	0

Response to first gesture	**Gesture type**	**N**	**Repair 1**	**Repair 2**	**Repair 3**	**Repair 4**	**Repetition**	**Elaboration**
Total		**6**	**2**	**1**	**1**	**0**	**0**	**4**
No response	*Arm extend, palm vertical towards body*	3	-	-	-	-	0	0
	Arm extend, palm vertical towards body	2	*Brief touch another*	-	-	-	0	1
	Arm extend, palm vertical towards body	1	*Embrace another*	-	-	-	0	1
	Arm extend, palm vertical towards body	1	*Bipedal bow*	*Bipedal flexed stationary*	-	-	0	2
	Arm extend, palm vertical towards body	1	*Leg stamp*	*Leg stamp*	*Leg stamp* *Shake/pull object*	*Shake/pull object*	0	4
	Arm extend, limp hand	1	-	-	-	-	0	0
	Arm extend, limp hand	1	*Quadrupedal stare*	-	-	-	0	1
	Arm extend, limp hand	2	*Arm extend, limp hand*	-	-	-	1	0
	Arm flap	1	*Arm flap*	-	-	-	1	0
	Arm raise	1	*Arm raise*	*Brief touch another*	-	-	1	1
	Backward hand sweep	1	-	-	-	-	0	0
	Backward hand sweep	1	*Bipedal flexed run*	-	-	-	0	1
	Reach object	1	*Reach object*	*Reach object*	-	-	2	0
Total		**17**	**12**	**4**	**1**	**1**	**6**	**12**
Overall		**76**	**19**	**6**	**3**	**1**	**12**	**17**

Chimpanzees persist in their communication to achieve specific goals

Examination of response types to all gestures in the gesture sequences demonstrates that signallers discontinued sequences when a positive response was achieved in all 10 out of 10 cases (Binomial test, N = 10, $p = 0.002$). Moreover, signallers were more likely to receive a positive response following persistence sequences than any other response type, with a prevalence of 83.3% (10/12) of positive response cases following persistence sequences compared to 16.6% (2/12) of responses other than expected response following persistence sequences (Binomial test, N = 12, $p < 0.05$).

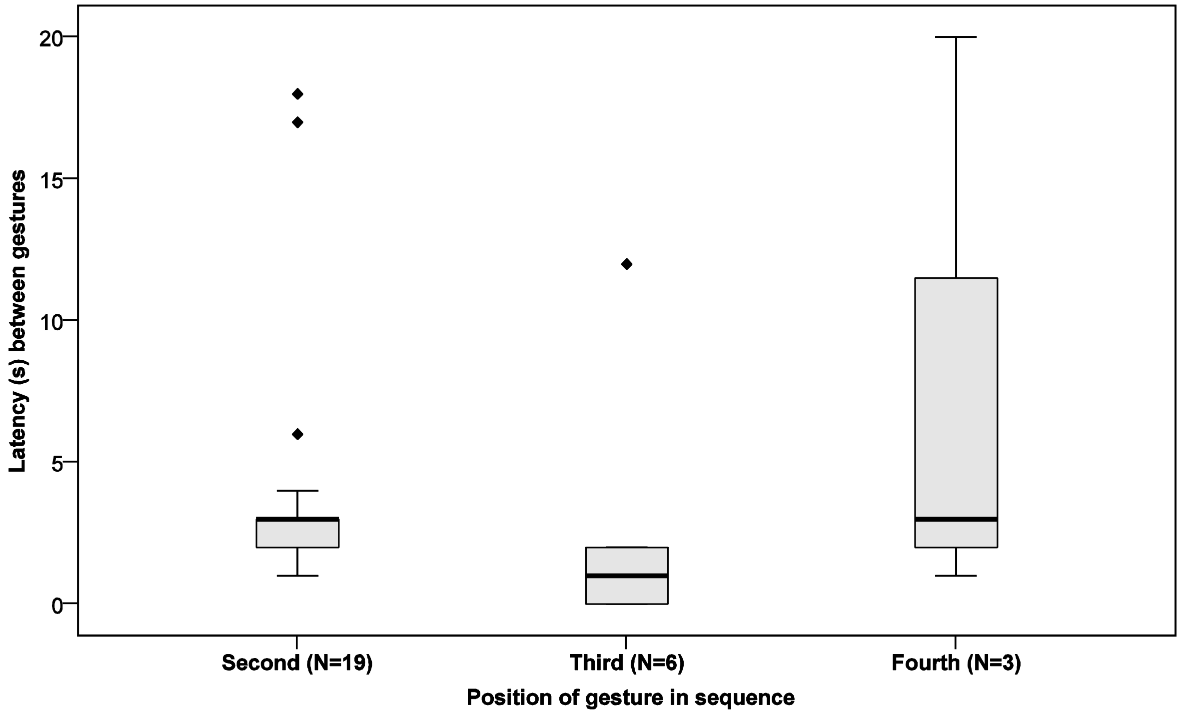
Chimpanzees view their recipients as autonomous agents which can be influenced by informative signals

Chimpanzees were significantly more likely to use communicative signals than perform a physical action to achieve their goal when not met with positive response. Following misunderstanding, on only 1 occasion did the signaller resort to physical action to achieve the goal whereas in 19 cases the communicative signal was used to repair this misunderstanding (Binomial test, N = 20, $p < 0.001$). This suggests that chimpanzees perceive others as autonomous agents who best respond to informative signals.

Intentional persistence in chimpanzees is not an effect of frustration

Differences in intensity and latency in relation to each gesture's position within a sequence may provide further indication as to whether signals are communicative or primarily affective responses in response to a failure (see e.g. Stout et al. 2003; Dickinson and Balleine 1994; Roberts 1981). Overall, individuals were no more likely to use more intense (tactile or auditory) gestures when substituting original signals than they were to use equally low intensity (visual) modality across elaboration sequences (Binomial test, N = 18, $p = 0.481$). Additionally, signallers did not progressively increase signal intensity; there was no significant difference in intensity between gesture type one, two and three within sequences (Friedman test, χ^2 (2) = 3, *p* = 0.667). Similarly, there was no evidence for an effect of frustration on the duration of the interval between the gestures emitted within a sequence. The inter-gesture interval did not decrease over time; in cases where three gestures were used in a sequence there was no significant difference in interval duration between gesture one and two (*Mdn* = 2 seconds) and between gesture two and three (*Mdn* = 1 second, Wilcoxon signed ranks test, T = 3.40, r = -0.39, *p* = 0.250, see Figure 3.4).

Figure 3.4: Latency (in seconds) between subsequent gestures (N represents number of cases) emitted within sequences



Chimpanzees engage in complex repairs homogenous in meaning

Chimpanzees modulated their repair sequences in terms of both the gesture type and modality in order to achieve their goals. For instance, in 52.9% of no response cases individuals replaced the original gesture with one other gesture type on 7 occasions (77%)

and with 2 gesture types on 2 occasions (22.22%). In the half successful response condition, in the single case of elaboration, one additional gesture type was used. A similar pattern of repairs emerges in relation to the number of changes in the modality of communication used within substitution sequences. For instance, in 58% (7/12) of cases in the no response condition and in 50% (2/4) of half-successful responses signallers changed gesture modality once.

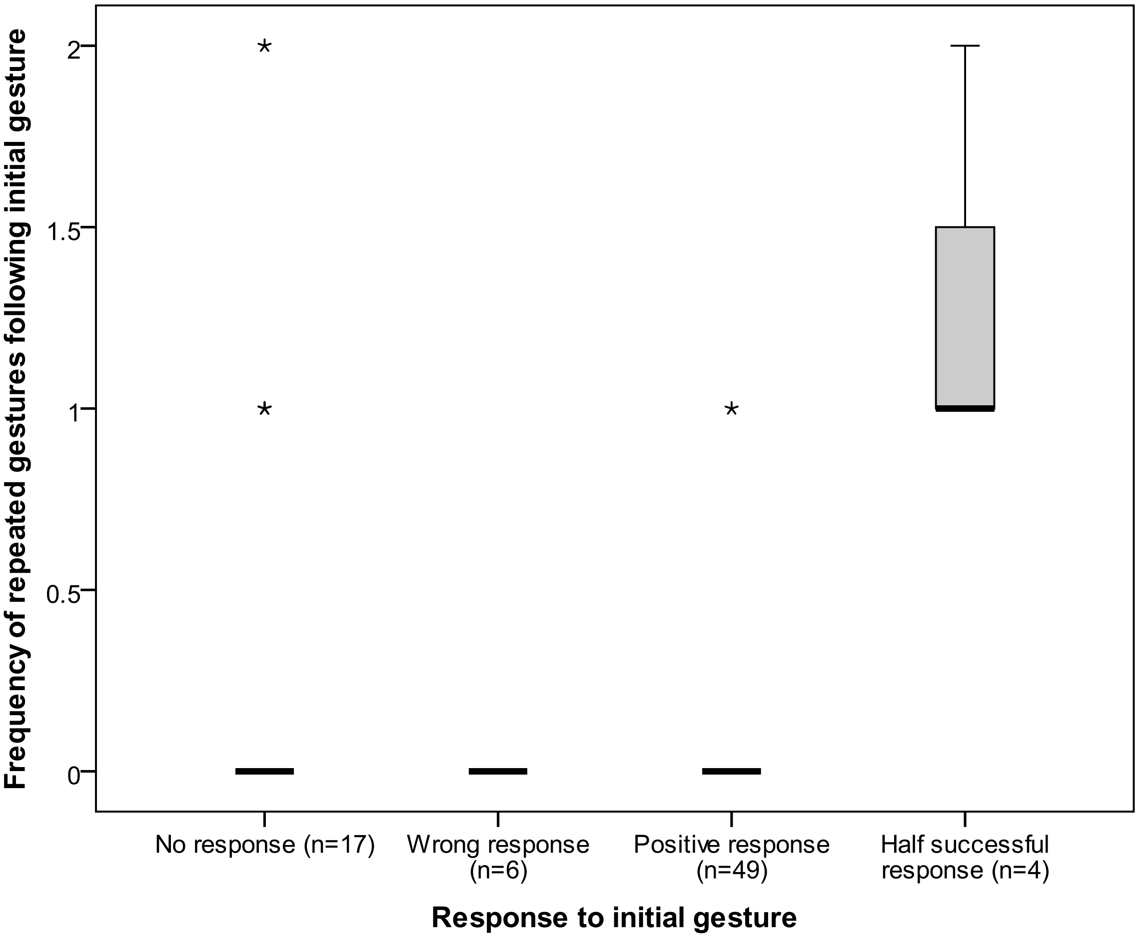
Overall, chimpanzees tended to replace original signals with signals with the same or related meaning. Across all sequences, gestures with the same or related meaning were used significantly more often (*Mdn* = 1) than gestures with unrelated meaning (*Mdn* = 0), Wilcoxon signed ranks test, T = 0, $p = 0.023$, r = -0.36. Thus, although substitution sequences show a degree of diversity in gesture type and number of modality changes, the diversity in meaning within elaboration sequences appears more limited.

Chimpanzees modulate repetitions of signals in relation to recipient's comprehension state

Chimpanzees modulate the frequency of their gestural repetitions according to the recipient's state of comprehension (see Table 3.2 for all cases of communicative repetition across different response types). The total number of repetitions varied significantly across response conditions following the first gesture (Kruskal-Wallis test, H (3) = 36.022, $p < 0.001$, see Figure 3.5). Mann-Whitney post hoc tests (Bonferonni correction $p < 0.016$ significance level) were used to examine differences between positive responses, no responses and half successful responses. The total number of repetitions following a positive response (*Mdn* = 0) was significantly lower than in no response condition (*Mdn* = 0, U = 326, r = -0.35, $p = 0.011$) and half successful condition (*Mdn* = 1, U = 1.500, r = -0.88, $p < 0.001$). No response (*Mdn* = 0) and half successful conditions (*Mdn* = 1) also differed significantly (U = 8, r = - 0.59, $p = 0.009$).

In the positive response condition on only one occasion out of 49 did an individual repeat the original gesture (2.04%). In 76.5% (13/17) of cases individuals did not repeat their gestures following no response from a recipient. While in 17.6% (3/17) of no response cases individuals continued to communicate by repeating the same gesture once, in 5.8% (1/17) of cases individual repeated the same gesture twice. In all cases of half-successful responses individuals continued repeating their gestures in the face of partial understanding; a single repetition in 75% (3/4) of cases and an additional repetition in the remaining case (25%).

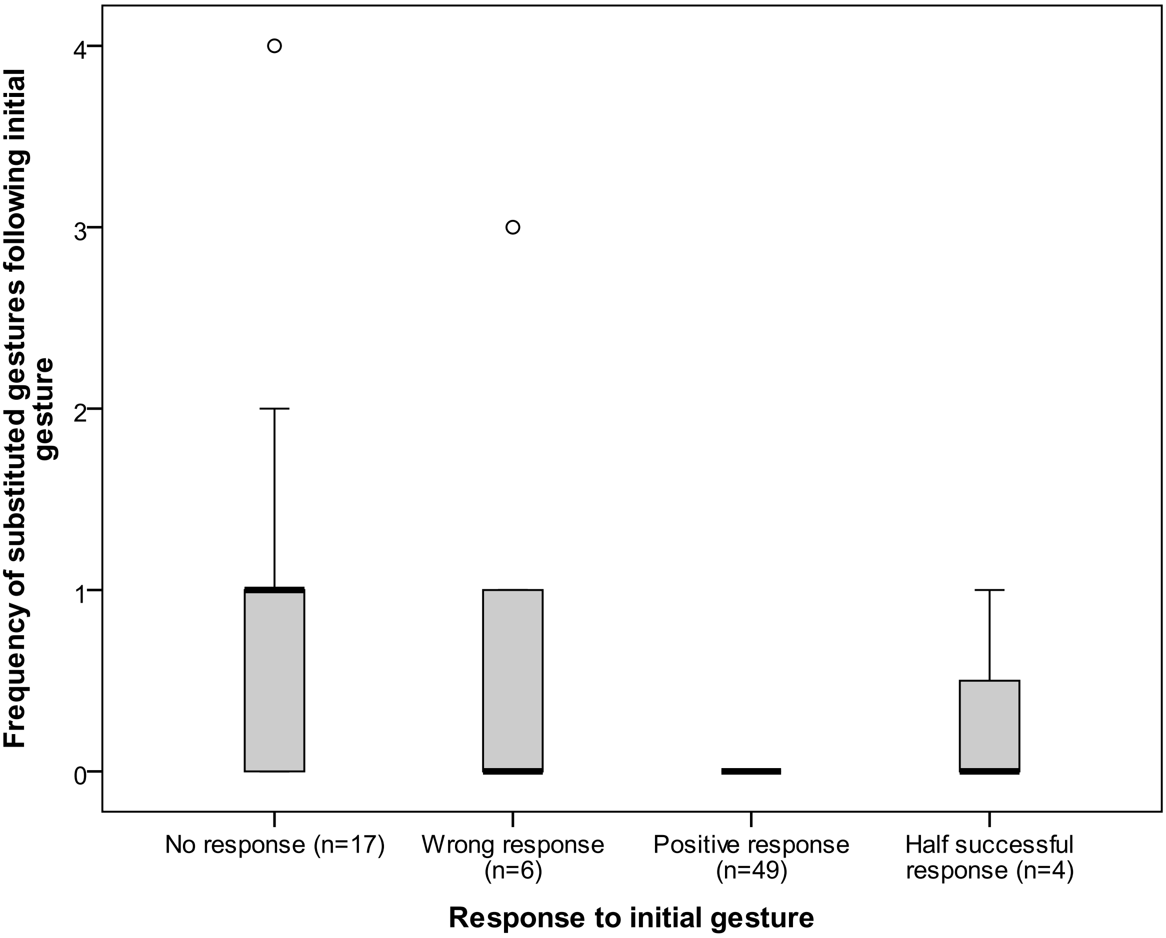
Figure 3.5: Median frequency of repetitions following all categories of recipients response to first gesture



*C*himpanzees elaborate their signals irrespective of audience comprehension

When the goal is only half met or not met at all, chimpanzees substitute their original signals in flexible ways (see Table 3.2 for examples of communicative substitution). The total number of elaboration gestures (those other than repetitions of initial gesture) varied significantly across responses to the first gesture (Kruskal-Wallis test, H (3) = 27.891, $p < 0.001$, see Figure 3.6). Mann-Whitney post hoc test ($p < 0.016$ significance level with Bonferroni correction) was applied to examine differences in the frequency of gestures other than repetitions between positive response, no response and half successful response conditions. The frequency of substitutions was significantly higher in no response condition (*Mdn* = 1) than the positive response condition (*Mdn* = 0, U = 196, r = -0.66, $p < 0.001$). However, there was no significant difference in total number of substitutions in the no response (*Mdn* = 1) and half successful conditions (*Mdn* = 0, U = 23.5, r = -0.22, $p = 0.428$).

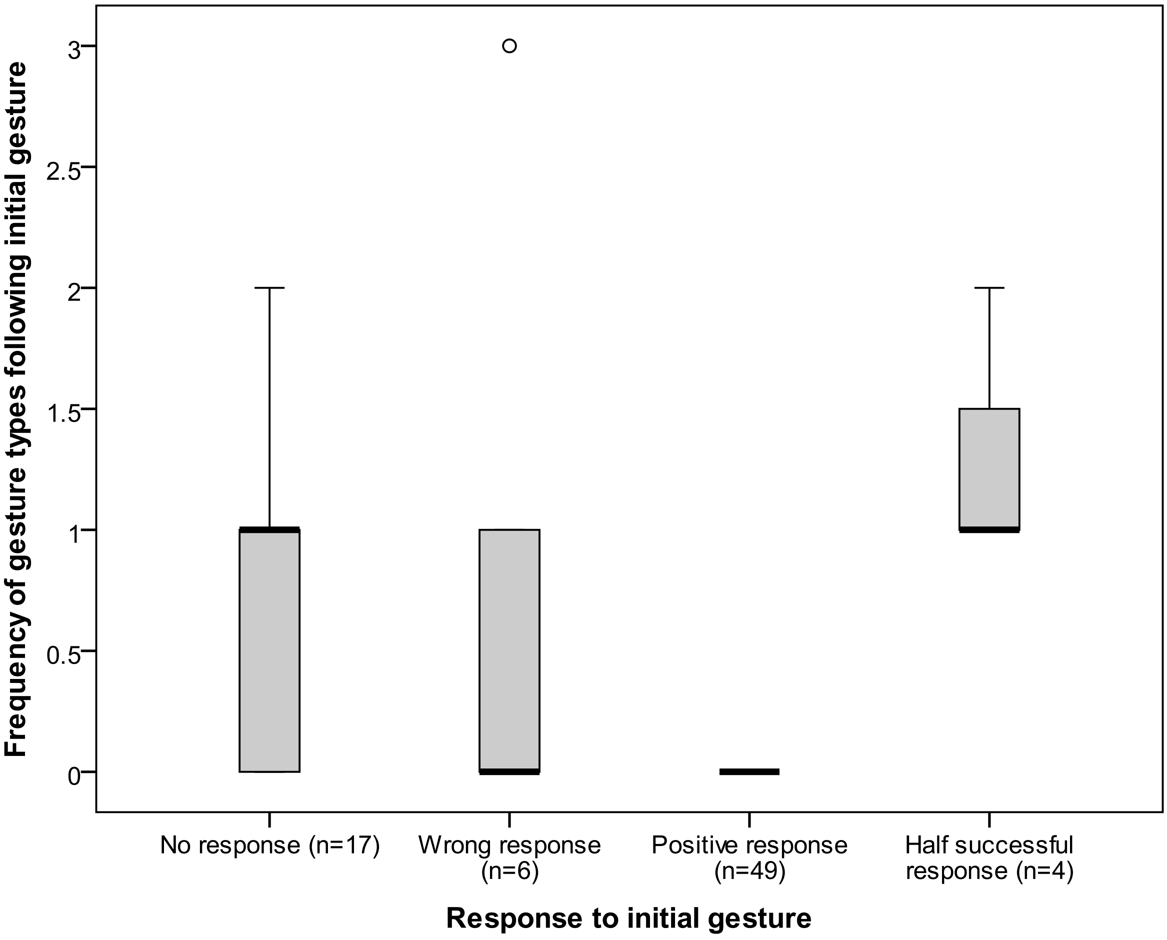
Figure 3.6: Median frequency of substitutions of original gesture with different gesture types following all categories of recipients response to first gesture



Frequency distributions for the total number of substitutions across the different response types show that signallers never emitted another gesture type if the response to the initial gesture was positive. Following no response from a recipient, in 47.05% (8/17) of cases individuals did not substitute their gestures. Of those gestures in the no response condition which were subsequently substituted, 41.17% (7/17) of gestures were substituted by one gesture, in 5.8% (1/17) of cases individuals substituted the first gesture twice and in 5.8% (1/17) individuals substituted their first gesture four times. In the half-successful condition, only one case out of 4 (25%) resulted in substitution of the original gesture.

A similar pattern of results is observed in the number of gesture types used to substitute the original signal. The total number of gesture types within substitutions varies significantly across conditions (Kruskal-Wallis test, H (3) = 47, *p* < 0.001), see Figure 3.7. Mann-Whitney post hoc tests (*p* < 0.016 significance level with Bonferroni correction) was used to determine differences between positive response, no response and half successful response in number of gesture types used for substitutions. The test shows that number of gesture types was significantly higher in no response condition (*Mdn* = 1) than the positive response condition (*Mdn* = 0, U = 122.5, r = -0.79, *p* < 0.001). However, there was no significant difference in total number of substituted gestures between no response (*Mdn* = 1) and half successful conditions (*Mdn* = 0, U = 24, r = - 0.21, *p* = 0.363).

Figure 3.7: Median frequency of gesture types different from first gesture following all categories of recipient's response to first gesture



DISCUSSION

Our research strongly suggests that chimpanzee gestural communication is cognitively complex in that it shows a priori awareness in the chimpanzees of the effects that the signals will have on a recipient, the realisation that marks the onset of verbal symbolic capacities in humans. While prior research on intentions underlying gestural communication amongst captive chimpanzees has suggested that chimpanzees adjust the modality of their gestures to the attention states of the recipient, our research shows that wild chimpanzees can go much further to achieve their communicative purposes when communicating with conspecifics. Wild chimpanzees in our study have shown that they have a definite goal in mind while communicating gesturally and persevere in the face of communicative failure by producing gestures in innovative and non-stereotypic ways. Chimpanzees reformulate the meaning of their signals by substituting old signals with the new ones while at the same time supplying a variably urgent gestural label by modulating the frequency of repetitions according to recipient’s level of comprehension. The episodes of gestural communication in wild chimpanzees when signallers fail to achieve their desired goals clearly illustrate these distinctions.

Chimpanzees ceased their communicative attempts when immediately successful at a goal and persevered in gestural communication when misunderstood by substituting and/or repeating the original signals. They discontinued their persistence sequences when understood and their persistence sequences achieved the expected goals more often than a different response type. This is in contrast with the research on gorillas by Genty and Byrne (2009) which suggests that gesture sequences are not orientated towards receiving the particular goal but instead are an information exchange where two individuals negotiate the goal and final outcome of an interaction in gesture sequences. For instance, Genty and Byrne (2009) reported that the number of gestures in a sequence did not have an influence on the probability of receiving a response and that using a sequence was rarely in response to communication failure.

However, the number of gestures in sequence in relation to likelihood of response may not be a good indicator for assessing whether sequences are formed in relation to communication failure. This is because the probability of a reaction to a gesture may not only depend on the number of gestures produced within a sequence but primarily on the motivation of a recipient to respond to a gestural message, i.e. while in some contexts signallers may need to repeat and augment original gestures several times (e.g. sexual), in others (e.g. nursing) one or two gestures may be sufficient to elicit the desired response from a recipient. Additionally, Genty and Byrne (2009) delimited the gesture sequences by a short time period within which the gestures were said to occur, i.e. within 1 second duration. However, it seems reasonable to assume that the goal should be a primary criterion in including the clusters of gestures in the sequences. For instance, in fast interactions such as play the goal of interaction may be changing as quickly as the gestures are emitted within sequences. This is important because when a sequence represents several goal changes it is difficult to assess when failure in communication has occurred and also whether signaller has made any repair attempts. The inclusion of many sequences emitted in a play context in Genty and Byrne's (2009) analyses may thus explain inconsistencies in findings. Further studies of gesture sequences using expected outcomes of gesture types as a proxy measure for the intended goal of a signal as the delimiting factor for sequence length may clarify differences in findings between our studies as to why sequences are formed.

The absence of significant differences in both the intensity of gestures and the rate of production of gestures, in relation to gesture position in a sequence, also suggests that the signaller emits the signal with an intentionally communicative purpose. Overall, chimpanzees were no more likely to use more intense (tactile or auditory) gestures when substituting original signals than they were to use less a intense (visual) modality type across elaboration sequences. Additionally, signallers did not increase the intensity of substituting gestures progressively across positions in a sequence, that is, there was no escalation in signal intensity over time. Similarly, there was no evidence for an effect of frustration on the rate of signal production in a sequence, i.e. the interval between subsequent signals did not decline over time. These results suggest that as signallers continued to receive no response, they neither lost interest nor became increasingly frustrated. These data are in accordance with previous work on intentional persistence in captive orang-utans (see e.g. Cartmill and Byrne, 2007b) and strengthen the conclusion that persistence is intentionally communicative about desired goals.

Furthermore, although chimpanzees used different gesture types within repair sequences, these tended to be homogenous in overall meaning. This is in contrast to current interpretations of means-ends dissociation phenomena and their implications for theories of language evolution. Tomasello and Call (1997 p. 243, see also Tomasello et al., 1994) explained intentional persistence thus: ‘alternative means may be used toward the same end, the same means may be used toward alternate ends, and some new exigencies may be flexibly accommodated’. While means ends dissociation has been specifically theorised in the context of intentional persistence (see e.g. Bates et al., 1979, Bruner, 1981, Piaget, 1952) several authors have taken that as an implication for overall flexibility in the meaning of gestures and dissociation between meaning and form in gestures, i.e. that gestures with different meanings can be used towards the same end and that different goals can be associated with variety of gesture types (see e.g. Liebal et al., 2004a, Liebal et al., 2004b, Liebal et al., 2006, Pika et al., 2003, Pika et al., 2005b, Pollick and de Waal, 2007, Corballis, 2003). However, our results indicate that while chimpanzees use different morphological gesture forms towards the same end, those forms nevertheless possess the same or closely related meanings. Recent data on the meaning of gesture sequences in other studies of great apes demonstrate similar findings. For instance, Genty and Byrne (2009) found that the probability for a gesture in a sequence to be followed by another with the same major function in western lowland gorillas was significantly higher than for the gesture to be followed by one with a different function.

One potential reason for inconsistent findings across studies may be that authors have used different levels of classifications for gestures. For instance, while Liebal et al. (2004a) and Pika et al. (2003) used relatively broad classifications, the categorisations used in our own and other studies (see e.g. Genty et al., 2009, Genty and Byrne, 2009) have been more fine grained. It is reasonable to assume that the level of classification may influence the number of functions ascribed to a gesture type because broader classifications may involve including larger number of contexts for each gesture type. Such gestures identified broadly would appear less context specific, simply because various gesture types have been pooled into one category, whereas those classified at a more fine grained level would be more context-specific. In sum, our findings suggest that while intentional persistence may show flexibility expressed in means-ends dissociation by gesture form, this cannot be interpreted in the same way when examining semanticity of gestures. Thus, while chimpanzee gestures are flexibly accommodated to the recipients' behavioural states, they nevertheless appear also goal-directed and function-specific. Studies of gesture meaning using statistically defined units of gesture type and how these gesture forms overlap with behavioural context may further elucidate whether gestures are referent-specific or whether meaning of gestures is defined by context.

Finally, chimpanzees substituted and reformulated meanings equally often when faced with both partial and complete misunderstanding. Simultaneously, when the behaviour of the recipient was indicative of a goal being only partially met (half successful), the chimpanzees repeated their original gestures more often, focusing on the original signals which have proved to work partially. On the other hand, when the recipient's behaviour was indicative of complete comprehension failure, the chimpanzees avoided use of repetition. The strategies employed by our chimpanzees differ from those implied by studies in captivity. For instance, Cartmill and Byrne (2007b) found that orang-utans alternate between repetitions and substitutions across different degrees of understanding, i.e. repeat gestures more often when partially understood and substitute gestures more often when completely misunderstood. One possible reason for this apparent variation in tactics employed by the subjects is that previous research considered a gesture quite broadly. For instance, Cartmill and Byrne (2007b) included behaviours such as yawning, reaching towards objects with a stick and spitting through bars. However, it is possible that these behaviours are an inadvertent reaction to internal emotional state rather than an attempt to influence the recipient's behaviour to achieve the desired goals. Moreover, it is possible that these behaviours do not hold informative value for the recipient and do not consistently affect recipient behaviour in predictable ways.

While structural differences between orang-utan and chimpanzee sequences may be explained by different methodological approaches, the chimpanzee and orang-utan sequences nevertheless fulfil the same functional objectives. For instance, they both signal content of the message while at the same time signalling failure of the recipient to decode the signal. When subjects realise that their signals have been ineffective in achieving the desired goal they replace the old signals rather than persisting with signals which have worked ineffectively. These tactics employed by both wild chimpanzees and orang-utans in captivity allow them to overcome misunderstandings more effectively.

These data are the first to give systematic insight into intentionality underlying gesture use in wild chimpanzees. In summary, the findings of this research are clear: chimpanzees communicate intentionally about desires and actions that they want recipients to undertake; they do not just express their emotions. They persist in communicative attempts when met with miscomprehension and adjust their communicative tactics to the comprehension states of their interlocutors. In particular, the chimpanzees repeated their gestures when the overall goal of the interaction was only partially met, and avoided repetition of gestures when the recipients' behaviour indicated a complete comprehension failure. Thus when signalling, chimpanzees flexibly adjust their use of gestures in light of the behaviour of the recipient, indicating an awareness of the effects of their gestures may have on the recipients' responses. This flexibility indicates that gesturing in wild chimpanzees is underpinned by a degree of cognitive complexity, in that they modify their gestural behaviour to reach an overall goal. Whether this cognitive complexity is based on an understanding that the recipients posses specific mental states of comprehension (comprehend, partially comprehend, do not comprehend), or is based a simpler reading of the recipient's behaviour, should be a focus of further research.

The results of this chapter have been submitted for publication:

Roberts, A.I.; Vick, S-J. & Buchanan-Smith, H.M. Communicative intentions in wild chimpanzees: Persistence and elaboration in gestural signalling.

Chapter 4: Contextually defined gesture comprehension in wild chimpanzees

INTRODUCTION

One of the central issues in the study of language evolution is examining features of cognition and communication in our closest primate relatives (Zuberbühler, 2005, Crockford and Boesch, 2003, Burling, 1993). One proposed modality of language evolution is that of manual gestural communication (Hewes, 1973, Corballis, 2003, Corballis, 2002). Primate manual gestures are more cognitively complex than vocalisations and display characteristics which are more similar to human language, such as flexible production and usage (Tomasello and Zuberbühler, 2002, Tomasello and Call, 2007, but see e.g. Genty et al., 2009 for alternative view). Contextually defined comprehension is one of the key components of human language and implies that signal perception is less tied to specific emotions, which may involve making informed choices based on mental representations (Tomasello and Herrmann, 2010). Contextually defined comprehension can be understood as comprehension of gestural signals where recipients understand the literal, semantic meaning of a gesture but also infer true intentions of the signaller in deciding how to respond (Grice, 1975, Levinson, 1983).

While previous research on signal perception explored whether primates comprehend the semantic meanings of gestures, little is known about whether primates are also capable of contextually defined comprehension. However, it is important to examine whether primates are capable of contextually defined comprehension. Language is a system of cognition and communication, which is primarily contextually understood (Hockett and Altmann, 1968b, Burling, 1993). Wild East African chimpanzees (*Pan troglodytes schweinfurthii*) are our closest living relatives (Olson and Varki, 2003) and display some cognitively complex behaviour in other domains of gestural communication such as intentional persistence and elaboration in signal use. It is therefore interesting to examine characteristics of their gestural communication in relation to the specific characteristics of human language, to shed some light onto what was the modality of language evolution in our hominid ancestors.

Several properties of human language have been investigated in studies of gestural communication with captive apes (see for example studies of flexibility by Pika et al., 2003, Pika et al., 2005b, Liebal and Tomasello, 2002, Liebal et al., 2006, Liebal et al., 2004a, Genty and Byrne, 2009, Genty et al., 2009). While these studies have shown that certain properties of language are present in the gestural domain, one central property which may be informative with regards to gesture as a potential modality of language evolution is contextually defined comprehension. The cognitive abilities underlying contextually defined comprehension are important because they suggest that individuals may be capable of shared intentionality and secondary representation, i.e. that recipients recognise the desired goal state of the signaller and draw and connect information from relevant sources to model hypothetical situations. Additionally, contextually defined comprehension is cognitively demanding because recipients have to attribute and entertain multiple mental states when inferring the signaller's goals and intentions (Tomasello and Herrmann, 2010).

Contextually defined comprehension is different from other types of signal comprehension such as semantic comprehension, where recipients understand the literal meaning of the utterance and do not take into account the broader context of a signal such as the signaller's true intentions (Bell, 1999). While contextually defined comprehension requires understanding of other's goals and intentions, semantic comprehension may reflect conditioned, automatic responses, with little cognitive processing involved (Tomasello, 2008). For instance, semantic comprehension has been shown in the vocal domain across a wide variety of species such as chickens (Evans and Evans, 1999), prairie dogs (Slobodchikoff et al., 1991) and marmots (Boero, 1992).

Previous studies have not conclusively shown whether gesture comprehension in primates is semantic or contextually defined. In terms of contextually defined comprehension, primate studies have operationalised contextually defined comprehension as the use of communicative signals where one signal type is associated with variety of contexts and one context is associated with variety of gesture types. For instance, studies have shown that the percentage of gesture types associated with more than one behavioural context was 48% in chimpanzees (Tomasello et al., 1985, Tomasello et al., 1984), 50% in bonobos (Pika et al., 2005b), 72% in gorillas (Pika et al., 2003) and 80% in orang-utans (Liebal et al., 2006). Across the gesture types associated with multiple contexts, there was variation in respect to how many contexts the gestures were associated with, for instance per gesture type, in chimpanzees up to 4 contexts were observed (Tomasello and Call, 2007), in bonobos up to 5 contexts (Pika et al., 2005b), in orang-utans up to 9 contexts (Liebal et al., 2006) and in gorillas up to 7 contexts were shown (Pika et al., 2003). Moreover, few contexts had gestures specific to them, and the context of play was associated with greatest number of gesture types. For instance, bonobos displayed 19 gesture types in play (Pika et al., 2005b); gorillas used all 33 gesture types (Pika et al., 2003) from the repertoire within the play context. Using these criteria of association between gesture and number of contexts and context with number of gestures, studies across all captive species of great apes have claimed that gesture comprehension is contextually defined and thus concluded that gestures have no specific meanings and responses are determined by recipient’s perception of overall context.

However, studies have also illuminated that gesture comprehension could also be semantic and that some gesture types reliably receive specific responses regardless of the context in which they are used. For instance Genty et al. (2009, 2009) have shown that in gorillas certain gesture types were given more often than all other response types combined. That is, a specific gesture seemed to invoke a specific response from the receiver on most occasions.

This conflicting view of the gesture comprehension system in primates suggests that relationship between neither context nor response in association with gesture type alone may be adequate for determining contextually defined comprehension, i.e. the mere context of gesture production alone cannot really tell us if recipients take into account the true intentions of the signaller in deciding how to respond. Additionally, looking at recipients' responses to gesture types, without taking into account the ultimate intentions of the signaller is not informative about how recipients interpret meanings of gestures.

We aim to address these shortcomings in the first systematic study of contextually defined comprehension in manual gestures of wild chimpanzees. This approach is novel in terms of examining recipients' responses to a gesture in light of the intended interaction goals of the signaller. We aim to determine whether gesture comprehension is best described as semantic or contextually defined and attempt to address fundamental questions about cognitive abilities underlying comprehension of gestural communication. For instance, can gestures convey specific meanings to the recipients? Are chimpanzees capable of producing responses to signals in a voluntary way? Is the interpretation of the meaning of gestures dependent upon accompanying context? Do recipients interpret meanings of signals in relation to true intended goals by a signaller?

We examine the characteristics of wild chimpanzee comprehension of gestures using an alternative approach to previous studies. First, we examine manual gesture types in wild chimpanzees, determined statistically as reliably different from other types. This allows us to avoid potential biases that may be present with more qualitative categorisations of gesture types and the inclusion of both contexts and meaning used to identify and categorise gesture. Second, we assess the potential semantic meanings of manual gestures as determined by prior work by looking in more detail at congruence of responses with the predicted meaning of a gesture and in relation to relative rank of the recipients. Taking into account the rank of a recipient in examining responses to gestures is important because it allows us to determine whether the response is congruent or incongruent with the predicted meaning of a gesture. For instance, whilst for a high-ranking recipient it is congruent to retaliate aggressively against an antagonistic gesture, such a response would be incongruent for a low-ranking recipient. Finally, we determine quantitatively the likely goals and intentions of the signaller, by looking at the types of behavioural outcomes observed at the end of communicative episodes. For instance, the gesture ‘arm extend, palm vertical towards body’, may initiate approach by a recipient towards the signaller, but the signaller’s goal/intentions may be grooming or copulation with the recipient. Based on this determination of signal meaning and signaller’s goals and intentions, we are able to examine how recipients interpret gesture requests in relation to the likely intended goals of a signaller.

METHODS

Study site and subjects

The manual gestures of one community of habituated East African chimpanzees were examined over three periods totalling an 8 month period (September 2006, April - July 2007 and March - May 2008) at Budongo Conservation Field Station, Budongo Forest Reserve in Uganda (see Appendices 1 and 2 for maps of the study area). The study area is situated in western Uganda on the edge of the western Rift Valley (1˚37’- 2˚00’N; 31˚22’- 31˚46’E) at the mean altitude of 1100 m (Eggeling 1947). The reserve area covers 793 km^2 and is composed of grassland; forest and semi-deciduous tropical forest with predominantly continuous forest cover of 428 km2 (see e.g. Eggeling, 1947, Reynolds, 2005 for detailed descriptions of floral composition of the study area).

The chimpanzee community under study varied from 76 to 79 individuals, habituated to humans and tolerating human observers at distances of approximately 5 m (see Table 1 in appendix for additional details on the observed chimpanzee subjects). In this study the gestural behaviour of 12 adult individuals was examined (see Appendix 3 for list of all community members of Budongo) who did not have limb injuries and who could be distinguished according to two rank categories (i.e. 3 high-ranking and 3 low-ranking males and females). All females selected as focal subjects in this study were parous (see Appendix 4 for details on life history of all focal individuals). Additionally, *ad libitum* data on subadult subjects was collected in non-play contexts to expand the data set of gestures in food and locomotion contexts. The data set on subadult subjects was obtained via focal follows during pilot phase of the study and contributed a small number of observations, i.e. 19 gesture events in total.

Data collection

Quantitative focal continuous individual follows and opportunistic, qualitative *ad libitum* samples were taken to establish a complete inventory of gestures for each of the focal subjects. The focal individual was followed for a standardised period of 20 minutes duration, sampling each individual in the group equally at different times of the day and study period.

Behaviour was recorded continuously using a digital video camera recorder (SONY DCR – HC18E and SONY DCR – HC32E), with the camera focusing on the focal subject but also taking a wider view to include interactants and context. Whenever the context of signal production, i.e. eliciting context, recipient's response and signaller's goal was out of range of video recording but still visible to the observer, the context was described and spoken into the camera. This sampling protocol enabled collecting 250 hours of focal footage, where the mean (SD) observation duration used for analyses per focal subject was 17.21 (1.29) hours of good visibility, independent focal data.

Video analysis

As the first step in analyses, an inventory of gesture types and accompanying context in chimpanzees were derived from video recordings. Two hundred and eighteen manual gestures were extracted from video recordings where the quality of footage allowed accurate coding of morphological details. For each gesture event, the following data were recorded: the sender and recipient of a gesture were identified; morphological details of each gesture; the context; the response if the behaviour of recipient following a gesture involved change relative to its behaviour prior to the gesture event and signaller's goal. Additionally, sequences were examined in relation to signaller's goal (see chapter 3 for complete description of data collection, video analysis and statistical analysis of gesture sequences).

The signaller was identified as an individual performing a gesture. The recipient of a gesture was coded as the individual at whom the gesture was most clearly directed, i.e. an individual at whom the signaller was orientated with head or a body or at whom signaller was looking during or immediately after performing the gesture. Behaviour was scored as a manual gesture if it was an expressive movement of the limbs which was visual and mechanically ineffective (did not touch recipient or any object and did not effect behaviour change in the recipient by any mechanical means; see Pollick and de Waal, 2007 for detailed definition of manual gesture). Additionally, these behaviours were considered to be a gesture if they were communicative (i.e. overall consistently induced a change in the behaviour of the recipient) and intentional. Behaviour was considered intentionally produced if consistently accompanied by goal directedness (i.e. the signaller was looking at the recipient during or after gesture production) or persistence and elaboration in gesture use in the face of a lack of response from a recipient (Bates et al., 1979). The units of manual gestures were first identified qualitatively but then precise categories of gesture types were identified statistically using an ethogram with multistate categorical elements (based on combinations of morphological attributes, see Chapter 2 for coding scheme and methods of gesture coding) by means of a hierarchical cluster analysis. Hierarchical cluster analysis identified the most significant clusters of gestures and classified morphological components into 30 gesture types. Additionally discriminate function analysis was used to validate the gesture units identified by hierarchical cluster analysis (see chapter 2 for the results of this classification). Cross-validation procedures of discriminate function analysis allowed us to identify 20 gesture types, which were reliably different morphologically from other gesture types.

In order to determine the context of gesture production, all new environmental conditions that might have lead to the production of gestures were coded, i.e. any new conditions that confronted the signaller before and during the production of a gesture. These included for instance, any physical or communicative actions of the recipient towards the signaller, or a third party to which the signaller was visually oriented and seemed to be responding gesturally, or concurrent behaviours seen during the production of a gesture by a signaller, such as the presence of other bodily gestures, vocalisations, facial expressions or autonomic behaviour (see Table 4.1 for eliciting context categories coded in this study).

Table 4.1: Categories of context types eliciting manual gestures

Context label	**Context description**
Groom	The recipient is involved in grooming with the signaller and producing other groom signals such as scratching whilst looking at the signaller
Travel	Travelling, pausing for listening whilst travelling, observing other individuals travelling or hearing travelling noises from others
Contact	The recipient produces contact communication, such as soft whimper, pout or gentle touch, towards the signaller prior to and during a gesture
Food feed	The recipient is feeding on or handling desirable food items, such as meat, fruit or bark
Food observe	The recipient is looking intently at food, or the other individual feeding on desirable food item, and reaching towards food
Mutual sex	The signaller, the recipient or both, displaying signs of sexual motivation towards the other, or copulating with each other
Recipient sex	The recipient is displaying signs of sexual motivation towards a third party, or is copulating with a third party
Signaller sex	The signaller is displaying signs of sexual motivation towards a third party, or is copulating with a third party
Submission	The recipient is stationary, or approaching submissively, such as cowering behaviour and pant grunts, towards the signaller, prior to and/or during a gesture
Recipient aggression signaller	The recipient is stationary, or approaching aggressively, such as producing directed visual threats, physical aggression, undirected pant hoots or drums, towards the signaller prior to and/or during a gesture
Recipient aggression other	The recipient is stationary or approaching aggressively, such as producing directed visual threats, physical aggression, undirected pant hoots or drums, towards a third party prior to and/or during a gesture
Signaller aggression recipient	The signaller is stationary or approaches aggressively, such as producing directed visual threats, physical aggression, undirected pant hoots or drums, towards the recipient prior to and/or during a gesture
Signaller aggression other	The signaller is aggressive, such as producing directed visual threats, physical aggression, undirected pant hoots or drums, towards a third party prior to and/or during a gesture
Other aggression recipient	Third party aggression, such as directed visual threats, physical aggression, undirected pant hoots or drums, directed towards the recipient prior to and/or during a gesture
Other aggression signaller	Third party aggression, such as directed visual threats, physical aggression, undirected pant hoots or drums, directed towards the signaller prior to and/or during a gesture

Moreover, to examine the effect of a gesture on a recipient, any changes in the behaviour of the recipient immediately after the signal were coded for each gesture event. The behaviour of the recipient was scored as a response if a) the change in the recipient's behaviour state occurred within 30 seconds of the initial gesture production, and b) occurred prior to any other context which might have led to a change in the recipient's behaviour, including any events in the environment or any additional signals made by a signaller such as gestures, vocalisations or facial expressions. Additionally, when there was no response to a gesture and the signaller persisted with gestural communication until the desired response was achieved by a signaller, the final response to a sequence was also classified for analysis as a response to the first signal in the sequence. Types of behaviours considered as a response include: changes in proximity relative to signaller or other subjects; changes in activity patterns; onset of communication; changes in possession of a resource (see Table 4.2 for information on response categories coded in this study).

Table 4.2: Categories of response types to manual gestures

Broad response category	**Response label**	**Definition of response type**
APPROACH	Referent approach	The recipient moves towards a referent in relaxed manner, the approach is directed towards a referent previously indicated by a signaller
	Neutral approach	The recipient moves towards a signaller in a relaxed manner, signalled by lack of visible signs of autonomic arousal and a lack of defensive or offensive communication, such as pant grunt or branch shake. The approach is performed towards a signaller in general, and prior to any other gesture preceding the activity or interaction with the signaller
	Defensive approach	The recipient is stationary, approaching or following, and directs defensive behaviour, such as whimpering; pant grunts or screaming or other appeasement behaviour, towards the signaller
	Offensive approach	The recipient is stationary, approaching or following produces offensive behaviour such as physical aggression or agonistic gestures
	Stop approach	The recipient is moving towards a signaller in a relaxed, inoffensive manner and then stops moving towards a signaller
LEAVE	Neutral leave	The recipient moves away from a signaller in a relaxed, inoffensive manner signalled by a lack of visiual signs of autonomic arousal and a lack of defensive or offensive behaviours
	Defensive leave	The recipient moves away from the signaller, accompanied by defensive behaviour such as crouching, screaming or running away
	Offensive leave	The recipient moves away their body part, or leaves signaller in rejection of the requested behaviour, accompanied by offensive behaviour such as stiff posture
	Pass by	The recipient continues their approach and passes by the signaller
OBJECTS/ ITEMS	Give item	The recipient gives a food item or object to the signaller, by transferring it with their hand or dropping it from their mouth
	Reach item	The recipient reaches towards or takes food or an object from a signaller
ATTENTION	Attention referent	The recipient redirects their visual attention towards the external object
	Attention signaller	The recipient redirects their visual attention towards the signaller
GROOM	Groom present	The recipient moves the body part indicated by a signaller
	Give groom	The recipient moves strands of hair with the fingers to remove dirt or parasites

Broad response category	**Response label**	**Definition of response type**
		from the signaller's body
	Receive groom	The recipient accepts the signaller's actions, where the signaller moves pieces of hair to remove dirt and parasites from the recipient's coat
INFANTS	Breast feed	An infant feeds on breast milk directly from the signaller's breast
	Climb back	The recipient climbs on signaller's body where he reaches the back and sits there holding back of a signaller
OTHER	Copulation	The recipient engages in sexual contact, where the male penis enters a female reproductive tract and thrusting occurs, followed or not by ejaculation
	Inspection	The recipient manipulates the genital area of a signaller by inserting fingers inside the reproductive tract, or manipulating the area on the outside of genitals with the hands or mouth
	Play	The recipient engages in activity with a signaller, where he playfully touches the signaller, accompanied by laughing, tumbling, tickles, chases and other play behaviours
	Pant hoot	The recipient emits a call where he begins with low-pitched hoots which make transition into quicker, higher-pitched in and out pants, building into a loud climax
NO RESPONSE	No response	The recipient does not produce any change in activity, communication or autonomic state in response to signaller's gesture

The responses to each gesture type were examined in more detail to establish their meaning. The most commonly seen response type for each gesture type was selected from the database. We used the most commonly seen response as a proxy for a meaning of a gesture. Additionally, the signaller's persistence and elaboration in communication until the most common response was attained, helped to clarify the meaning of signals in those cases when the response to a gesture was not immediately produced by a recipient (see Chapter 3 for complementary determination of meaning of gestures using persistence and elaboration in communication). This method of studying goal-directed signalling in primates is one of the best ways of determining meaning of signals (see e.g. Golinkoff, 1986, Cartmill and Byrne, 2010).

Furthermore, the observed responses were scored according to whether these were congruent and incongruent with the dominant meaning responses. Congruence was determined by taking into account the predicted meaning of a gesture (derived from most commonly seen response type to a gesture) but importantly also the rank of the recipient in relation to the rank of the signaller (ranks were taken from published accounts, see Appendices 8 and 9). Thus, responses which matched the most commonly seen response type to a gesture would be scored as congruent, 'accept request' responses. If a gesture functions as a communicative signal, acceptance responses should occur above chance levels. However, some reject or ignore responses may also be considered congruent with gesture meaning when taking into account the rank of a recipient making a response. For instance, when a signaller performs an arm flap in order to induce a recipient to move away, a lower ranking individual might accept the request, i.e. move away from a signaller, while a matched or higher-ranking recipient might accept or reject the request, i.e. ignore it or retaliate aggressively against the signaller. Thus, consideration of relative rankings of the signaller and recipient is crucial to a full understanding of response types being either congruent or incongruent with the meaning of a gesture. Specifically, the categorisation of congruence and incongruence is made by scoring each response to a gesture against the prediction that for lower ranking recipients it would be incongruent with a gesture meaning to perform neutral or offensive, ignore or reject request responses, but congruent to accept or defensively ignore or reject request responses. On the other hand, for matched or higher ranking recipients, it would be congruent to make accept, neutral or offensive ignore or reject responses, but incongruent to make defensive ignore or reject request responses (see Table 4.3 for congruence scoring of all response types to gesture types).

Table 4.3: Congruence of recipient's response with predicted gesture meaning

Manual gesture	**Predicted meaning**	**Recipient rank**	**Response type**	**Response category**	**Congruent response?**	**N**
arm extend, limp hand	to request groom present of specific body area	lower	Groom present	accept	yes	9
arm extend, limp hand	to request groom present of specific body area	lower	Receive groom	ignore/reject	no	2
arm extend, limp hand	to request groom present of specific body area	same or higher	Defensive leave	ignore/reject	no	1
arm extend, limp hand	to request groom present of specific body area	same or higher	Groom present	accept	yes	8
arm extend, limp hand	to request groom present of specific body area	same or higher	No response	ignore/reject	yes	1
arm extend, limp hand	to request groom present of specific body area	same or higher	Receive groom	ignore/reject	yes	3
arm extend, palm upwards, hand cupped	to request handing over of an item	lower	Give item	accept	yes	1
arm extend, palm upwards, hand cupped	to request handing over of an item	lower	Reach item	ignore/reject	yes	1
arm extend, palm upwards, hand cupped	to request handing over of an item	same or higher	Give item	accept	yes	3
arm extend, palm upwards, hand cupped	to request handing over of an item	same or higher	No response	ignore/reject	yes	3
arm extend, palm upwards, hand cupped	to request handing over of an item	same or higher	Offensive leave	ignore/reject	yes	1
arm extend, palm vertical towards body	to request approach by a recipient towards self	lower	Attention signaller	ignore/reject	no	1
arm extend, palm vertical towards body	to request approach by a recipient towards self	lower	Breast feed	accept	no	2
arm extend, palm vertical towards body	to request approach by a recipient towards self	lower	Defensive approach	accept	yes	2
arm extend, palm vertical towards body	to request approach by a recipient towards self	lower	Neutral approach	accept	yes	26
arm extend, palm vertical towards body	to request approach by a recipient towards self	lower	No response	ignore/reject	no	6
arm extend, palm vertical towards body	to request approach by a recipient towards self	same or higher	Attention signaller	ignore/reject	yes	1
arm extend, palm vertical towards body	to request approach by a recipient towards self	same or higher	No response	ignore/reject	yes	1
arm extend, palm vertical towards body	to request approach by a recipient towards self	same or higher	Pass by	accept	no	1
arm flap	to request moving away by a recipient	lower	Defensive approach	ignore/reject	yes	2
arm flap	to request moving away by a recipient	lower	Defensive leave	accept	yes	5
arm flap	to request moving away by a recipient	lower	Stop approach	accept	yes	2

Gesture type	**Predicted meaning**	**Recipient rank**	**Response type**	**Response category**	**Concordant response?**	**N**
arm flap	to request moving away by a recipient	same or higher	Defensive leave	accept	no	3
arm flap	to request moving away by a recipient	same or higher	No response	ignore/reject	yes	1
arm flap	to request moving away by a recipient	same or higher	Offensive approach	ignore/reject	yes	1
arm raise	to request grooming	lower	Give groom	accept	yes	3
arm raise	to request grooming	lower	Neutral leave	ignore/reject	no	1
arm raise	to request grooming	lower	Receive groom	accept	yes	5
arm raise	to request grooming	same or higher	No response	ignore/reject	yes	1
backward hand sweep	to request climbing on back by a recipient	lower	Climb back	accept	yes	9
elbow raise	to request approach by a recipient towards self	lower	Neutral approach	accept	yes	7
fingers sweep	to request cessation of aggression by a recipient	same or higher	Give groom	accept	yes	1
fingers sweep	to request cessation of aggression by a recipient	same or higher	Offensive approach	ignore/reject	yes	2
fingers sweep	to request cessation of aggression by a recipient	same or higher	Offensive leave	accept	yes	1
fingers sweep	to request cessation of aggression by a recipient	same or higher	Pass by	accept	yes	1
hand bend	to request cessation of aggression by a recipient	lower	Pass by	accept	no	1
hand bend	to request cessation of aggression by a recipient	same or higher	Give groom	accept	yes	1
hand bend	to request cessation of aggression by a recipient	same or higher	Inspection	accept	yes	1
hand bend	to request cessation of aggression by a recipient	same or higher	Pass by	accept	yes	14
hand bend	to request cessation of aggression by a recipient	same or higher	Stop approach	accept	yes	1

Finally, in order to examine how recipients decide how to respond to individual gestures, the signaller’s goal for each gesture was coded. The signaller’s goal is best defined as the behaviour of signaller following the first response to a gesture by a recipient - for example, backward hand sweep may initiate climbing by the recipient onto signaller’s back and subsequent travel of signaller. In the presence of more gestures in the sequence, the signaller’s goal is the behaviour of the signaller following the response by a recipient to a last gesture in a sequence. For instance, a signaller with an erect penis may gesture to a female with a sexual swelling to initiate approach towards him. After unsuccessful attempts at attracting a female, the female may finally approach; the signaller may then copulate with the recipient. If the sequence of events did not lead to any observable outcome, such as when an approach invitation gesture in a grooming context elicited approach but no other interaction, the most frequently observed change of behaviour of signaller for combination of context with a gesture was assumed to be the desired outcome for a signaller. The types of behaviours considered as signaller’s goals could be initiation of travel, copulation, and nursing, acquisition of a resource such as desirable food (see Table 4.4 for information on signaller’s goals categories coded in this study). Outcomes were classified into two categories, i.e. competitive and cooperative outcomes based on whether the outcome was mutually beneficial to the interactants or unequally beneficial to one interactant.

Table 4.4: Categories of signaller's goals coded in this study

Label	**Signaller's goal description**
Groom	Signaller grooms recipient
Travel	Signaller travels
Cling	Signaller carries recipient by holding
Copulate	Signaller copulates with recipient
Nurse	Signaller breastfeeds recipient
Gain sex	Signaller gains access to sexual female previously engaged with another male
Embrace	Signaller embraces recipient
Gain food	Signaller gains possession of desirable food
Maintain travel	Signaller maintains route of travelling
Maintain copulation	Signaller continues copulating regardless of interruption
Maintain food	Signaller continues to feed on undivided desirable food such as piece of meat
Maintain groom	Signaller continues exclusive grooming of desirable groom partner
Avoid sex	Signaller avoids copulation with recipient
Avoid redirected aggression	Signaller avoids redirected aggression previously directed at another individual
Avoid direct aggression	Signaller avoids aggression directed at himself
Avoid support aggression	Signaller avoids aggression from supporters of individuals whom signaller previously challenged
Maintain status	Signaller maintains status in the social hierarchy (coded if there was no obvious reason for dispute)

Statistical analysis

Data selection procedure

Due to the small sample size, observations from all individuals were pooled together for analyses. This methodology is in accordance with other research on gestures in captivity where low rates of gesture production prevented use of subjects as a unit of analysis (see e.g. Pollick and de Waal, 2007, Genty and Byrne, 2009, Genty et al., 2009). All analyses were performed only on gesture types which were identified by hierarchical cluster analysis and validated above chance level by discriminate function analysis. In all analyses only those gesture types were examined where we had at least 5 cases of an independent gesture events per gesture type and 6 cases for Binomial tests. Additionally, data were excluded if there was no response to a gesture even after persistence sequences, with the exception of congruence of responses analysis, where ‘no response’ cases were taken into account. This data selection procedure restricted the amount of data examined, but was necessary to better ensure validity and reliability of the contextual analyses.

Data analysis

All tests were non-parameteric due to nature of the data, which was categorical. All data analyses were performed using statistical package SPSS 17.0. Additionally, with the exception of gestural sequence data analysis, all nonparametric tests were two-tailed.

RESULTS

Did signallers convey specific information to the recipients in their gestures?

If chimpanzees convey specific information in their gestures, then gestures should be associated with a limited number of responses, specific to a gesture type. There was variation as to how many response types each gesture was associated with. Two gesture types (22%) were associated with one response type, i.e. backward hand sweep was responded to by climbing on signaller's back, and elbow raise was associated with a neutral approach by a recipient. Seventy-eight percent of gesture types (N =7) were associated with 3 or more response types. These gestures were associated with 3 responses (43% of gesture types, N=3), 4 responses (43% of gesture types, N=3) and 6 response types (14% of gesture types, N=1). For instance, arm extend palm vertical towards body was associated with responses including: recipient redirecting attention towards signaller, breast feeding, approaching defensively or neutrally, refraining from antagonism or not responding.

Whilst gestures were associated with a variety of responses, these responses were specific to gestures both overall (Fisher's exact test, $p < 0.001$) as well as within most of the gesture types. In other words, with the exception of elbow raise ($p = 0.385$), all gestures were significantly associated with specific responses, hand bend ($p < 0.001$); fingers sweep ($p = 0.005$); backward hand sweep ($p < 0.001$); arm raise ($p < 0.001$); arm flap ($p < 0.001$); arm extend, palm vertical towards body ($p < 0.001$); arm extend, palm upwards, hand cupped ($p < 0.001$) and arm extend, limp hand ($p < 0.001$).

Additionally, among the responses that were specific to a gesture type, most gestures elicited one particular response type more often than all other response types, i.e. elbow raise was associated with neutral approach (7/7 cases, $p = 0.016$), backward hand sweep was associated with climb back response (9/9 cases, $p = 0.004$), hand bend was primarily associated with stop antagonism response (16/19, $p = 0.004$); in 26 out of 33 cases arm extend, palm vertical towards body was associated with neutral approach ($p = 0.001$); in 17 out of 23 cases arm extend, limp hand was associated with groom present response ($p = 0.035$). Only three gesture types were not significantly associated with one type of response, these were gesture types for which the sample size of gesture events was particularly small, i.e. arm raise ($p = 1$); arm flap ($p = 0.581$) and arm extend, palm upwards, hand cupped (p

=0.688). Thus, whilst a variety of responses was seen across gesture types, those responses were tightly associated with particular gestures.

Moreover, variability in responses could be considered in terms of congruence of responses with the predicted meaning of a gesture and accounting for relative dominance ranks. Gestures associated with solely congruent responses accounted for 44% of all gesture types. These gestures were associated with 1 congruent response (22% of solely congruent gesture types), 3 responses (22% of solely congruent gesture types), 4 congruent with meaning responses (44% of solely congruent gesture types) and 5 congruent responses types (11% of solely congruent gesture types). For instance, arm flap was responded to by five congruent responses such as defensive approach, defensive leave and stop approach by lower ranking individual as well as no response and offensive approach by same and higher ranking individuals. In terms of incongruent with meaning responses; 56% of all gesture types were associated with incongruent responses. These were: one incongruent response (33.3% of gesture types associated with incongruent responses), two incongruent responses (11% of gesture types associated with incongruent responses), or four incongruent responses (11% of gesture types associated with incongruent responses). For instance, arm extend, limp hand was observed to occur with incongruent responses such as receive groom by a lower ranking recipient and defensive leave by same or higher ranking recipient.

Whilst most gesture types received both congruent and incongruent responses, overall most gestures elicited responses which were congruent with meaning of a gesture significantly more often than responses which were incongruent with meaning combined (Binomial test, $p<0.001$). This relationship was also significant when data were considered per gesture type alone, i.e. in 7 out of 7 cases elbow raise was a request for approach towards self ($p = 0.016$); in 17 out of 18 cases hand bend was a request for cessation of aggression by a recipient ($p < 0.001$); in 9 out of 9 cases backward hand sweep was a request for climbing onto back by a recipient ($p = 0.004$); in 9 out of 10 cases arm raise was made to request grooming ($p = 0.021$); in 30 out of 40 cases arm extend, palm vertical towards body was an effective request for an approach from a recipient ($p = 0.002$); in 9 out of 9 cases arm extend, palm upwards, hand cupped was a request to hand over an item such as food or body part ($p =0.004$); in 21 out of 24 cases arm extend, limp hand was a request for groom present of a specific body area by the recipient ($p < 0.001$). Only a single gesture, arm flap (which nonetheless approached significance, $p = 0.057$), did not follow this pattern of results.

Finally, this association of gestures with both a single response and a congruent response can be illustrated by the specificity of gestures for one response type and congruent with meaning response type. Specificity of gestures for eliciting a single response type is defined by the percentage of cases where each gesture type elicited its most common response type. The average signal specificity for a single response type was high, 73%, ranging from 40% for fingers sweep in eliciting offensive approach to 100% for both elbow raise in eliciting neutral approach and for backward hand sweep gesture in eliciting climb on back response (see Table 4.5 for specificity of responses across gesture types). Furthermore, the most common response specificity for each response type's dominant gesture type (percentage of cases when the dominant response type was elicited by its designated gesture type) was higher, at 81%. For example, a receive groom response was elicited in 50% of cases by both arm raise and arm extend, limp hand; groom present was elicited by arm extend, limp hand in 100% of cases, as was a climb on back response elicited by backward hand sweep gestures.

The specificity of gestures for congruent with meaning responses is defined by the percentage of cases where a specific gesture type elicited its congruent with meaning response type. The average signal specificity for congruent with meaning responses across all gesture types was high, i.e. mean = 92%, ranging from 100% for four gesture types, i.e. backward hand sweep; elbow raise and fingers sweep to 75% for arm extend, palm vertical towards body gesture (see Table 4.6 for specificity of congruent responses across gesture types). Congruent with meaning response specificity, which is the percentage of cases in which a congruent with meaning response type was elicited by its most common gesture type, was marginally lower. The average congruent response specificity across all gesture types was 89%, ranging from 100% for meanings of gestures such as: request groom present of specific body area; request grooming bout; request moving away by a recipient; request climbing on back; request handing over of an item such as food or presenting a body part and indicate an object, to 77% for meanings of gestures such as a request for cessation of aggression by a recipient. In conclusion, whilst some gesture types were highly specific to responses elicited in the recipients (i.e. backward hand sweep), other gesture types (i.e. arm extend, palm vertical towards body, arm flap) displayed a more loose association. Overall, gesture requests conveyed highly specific information and there was little flexibility in the way recipients were able to interpret fixed meanings of gestures.

Table 4.5: Index of response specificity for manual gestures

Response type	**Frequency of cases per gesture type**									**Response specificity (%)**
	Arm extend, limp hand	**Arm extend, palm upwards, hand cupped**	**Arm extend, palm vertical towards body**	**Arm flap**	**Arm raise**	**Backward hand sweep**	**Elbow raise**	**Fingers sweep**	**Hand bend**	
Defensive leave	1	-	-	**8**	-	-	-	-	-	**88.9**
Offensive leave	-	1	-	-	-	-	-	1	-	-
Neutral leave	-	-	-	-	1	-	-	-	-	-
Reach item	-	1	-	-	-	-	-	-	-	-
Defensive approach	-	-	2	2	-	-	-	-	-	-
Neutral approach	-	-	**26**	-	-	-	**7**	-	-	**78.8**
Offensive approach	-	-	-	1	-	-	-	**2**	-	-
Pass by	-	-	1	-	-	-	-	1	**16**	**88.9**
Attention signaller	-	-	2	-	-	-	-	-	-	-
Attention referent	-	-	-	-	-	-	-	-	-	-
Referent approach	-	-	-	-	-	-	-	-	-	-
Groom present	**17**	-	-	-	-	-	-	-	-	**100**
Receive groom	5	-	-	-	**5**	-	-	-	-	**50**
Stop approach	-	-	-	2	-	-	-	-	1	-
Breast feed	-	-	2	-	-	-	-	-	-	-
Climb back	-	-	-	-	-	**9**	-	-	-	**100**
Give item	-	**4**	-	-	-	-	-	-	-	-
Give groom	-	-	-	-	**3**	-	-	1	1	**60**
Inspection	-	-	-	-	-	-	-	-	1	-
Signal specificity (%)	**73.9**	**66.7**	**78.8**	**61.5**	**55.6**	**100**	**100**	**40**	**84.2**	

Note: dominant response type for each gesture type and dominant gesture type for response type are in bold, specificity only reported for samples of gestures with N>5

Table 4.6: Index of congruent with meaning response specificity for manual gestures

Meaning type	**Frequency of cases per gesture type**									**Congruent response specificity for signal (%)**
	arm extend, limp hand	**arm extend, palm upwards, hand cupped**	**arm extend, palm vertical towards body**	**arm flap**	**arm raise**	**backward hand sweep**	**elbow raise**	**fingers sweep**	**hand bend**	
Request groom present of specific body area in recipient	**21**	-	-	-	-	-	-	-	-	**100**
Request handing over of an item such as food or body part	-	**9**	-	-	-	-	-	-	-	**100**
Request approach by a recipient towards self	-	-	**30**	-	-	-	**7**	-	-	**81**
Request moving away by a recipient	-	-	-	**11**	-	-	-	-	-	**100**
Request grooming	-	-	-	-	**9**	-	-	-	-	**100**
Request climbing on back by a recipient	-	-	-	-	-	**9**	-	-	-	**100**
Request cessation of aggression by a recipient	-	-	-	-	-	-	-	**5**	**17**	**77**
Other function (incongruent response)	3	-	**10**	3	1	-	-	-	1	**56**
Signal specificity for meaning (%)	**88**	**100**	**75**	**79**	**90**	**100**	**100**	**100**	**94**	

Note: dominant meaning type for each signal type and dominant signal type for each meaning type are exposed in bold type

Is the specific information conveyed by gestures influenced by context or signaller's goals?

Whilst gestures considered alone display specificity for particular response types, it is possible that context may have influence on the meanings of gestures, as illustrated by association between immediate responses, eliciting contexts and signaller's goals within gesture types. In general, gestures were associated with a variety of contexts and signaller's goals. The mean (SD) number of contexts the gestures were associated with was 3.33 (2.12). The mean (SD) number of signaller's goals the gestures were associated with was 2.77 (2.04). Whilst gestures were associated with a variety of contexts and signaller's goal types, these contexts and goals had limited influence on responses to gestures. When considering percentage of cases when gesture/ context combination shared most common to a gesture type response type, it is evident that the influence of context or communication outcome was comparatively small.

On average gesture/context combinations shared a single most common for a gesture response type 75% of the time, whilst congruent response for a gesture type 98% of the time. Similarly, gesture/ signaller's goal combinations shared most common for a gesture response type 73% of the time, whilst congruent response for a gesture type 98% of the time. This association between gesture and response type regardless of context or signaller's goal was significant. When considering the influence of context on responses to gestures, combinations of gestures with context share a single most common response type to a gesture significantly more often (*Mdn* = 2) than any other response type combined (*Mdn* = 1, Wilcoxon signed ranks test, T = 1.5, p=0.047, r = -0.53). Similarly, combinations of gestures with context shared congruent with meaning of a gesture response type significantly more often (*Mdn* = 2) than incongruent response types combined (*Mdn* = 0, Wilcoxon signed ranks test, T = 0, p=0.04, r = -0.63). However, when considering the influence of signaller's goal on responses to gestures, combinations of gestures with signaller’s goals did not share the most common response type to a gesture significantly more often (*Mdn* = 2) than other response types combined (*Mdn* = 1, Wilcoxon signed ranks test, T = 2, p=0.125, r =-0.48). On the other hand, combinations of gestures with signaller’s goals had congruent with a meaning of a gesture response type significantly more often (*Mdn* = 2) than incongruent response types combined (*Mdn* = 0, Wilcoxon signed ranks test, T = 0, p=0.04, r = -0.63). For instance, arm extend, palm vertical towards body elicited the same neutral approach response type when combined with sexual behaviour in the signaller, such as penile erection, as when combined with fearful and aroused behaviour from a signaller, such as bipedal run forward, scream and piloerection, or when the signaller was engaged in defensive behaviour, such as quadrupedal with forelegs and hind legs flexed (see Tables 4.7 and 4.8 for indication of response and congruent response types across combinations of gestures with context). Similarly, arm extend, palm vertical towards body elicited the same neutral approach from the recipient most often, whether the perceived signaller’s goal was copulation or nursing (see Tables 4.9 and 4.10 for indication of response and congruent response types across combinations of gestures with signaller’s goals).

Table 4.7: Index of response specificity for combinations of gestures with context

Gesture	Context	Attention signaller	Breast feed	Climb back	Defensive approach	Defensive leave	Give groom	Give item	Groom present	Inspection	Neutral approach	Neutral leave	Offensive approach	Offensive leave	Reach item	Receive groom	Pass by	Stop approach	Specificity Index
Af	Food observe					**4**													
Af	Groom																	**1**	
Af	Mutual sex					**2**													
Af	R sex				**1**	**1**													
Af	S aggression R												**1**						
Af	S sex					**1**													
Af	Submission				**1**													**1**	
Ap	Food feed							**3**						1	1				**60**
Ap	Food observe							**1**											
Ar	Groom						2					1				**5**			**63**
Ar	Contact						1												
Bs	Travel			**9**															**100**
Er	Contact										**6**								**100**
Er	Travel										**1**								
Fs	O aggression R						**1**												
Fs	R aggression S																**1**		
Fs	S aggression O												**2**	1					
Hb	R aggression O																**3**		
Hb	R aggression S						1			1							**13**	1	**81**
Lh	Groom					1			**13**							3			**76**
Lh	R aggression O								**1**										
Lh	R aggression S															**2**			
Lh	Submission								**1**										
Lh	Contact								**2**										
Pv	Contact		2								**16**								**89**
Pv	Mutual sex				1						**2**								

Gesture	**Context**	**Attention signaller**	**Breast feed**	**Climb back**	**Defensive approach**	**Defensive leave**	**Give groom**	**Give item**	**Groom present**	**Inspection**	**Neutral approach**	**Neutral leave**	**Offensive approach**	**Offensive leave**	**Reach item**	**Receive groom**	**Pass by**	**Stop approach**	**Specificity Index**
Pv	O aggression R										**5**								**100**
Pv	O aggression S										**1**								
Pv	R aggression S	**1**															**1**		
Pv	Travel	1			1						**2**								
Specificity index				**100**		**44**	**60**		**88**		**48**					**50**	**72**		**84**

Note: in bold responses most common for gesture/context combination, in grey highlight most common response types for gesture/context combination matching most common response type for a gesture alone. Abbreviations CONTEXT: S – signaller, R - recipient, O – third party; Abbreviations GESTURE: Af (arm flap), Ap (arm extend, palm upwards, hand cupped), Ar (arm raise), Bs (backward hand sweep), Er (elbow raise), Fs (fingers sweep), Hb (hand bend), Lh (arm extend, limp hand), Pv (arm extend, palm vertical towards body)

Table 4.8: Specificity index of congruent responses with the meaning of gesture alone for gesture/context combinations

Gesture	**Context**	**Congruent responses**	**Incongruent responses**	**Specificity index**
arm extend, limp hand	Contact	2		
arm extend, limp hand	Groom	15	3	**83**
arm extend, limp hand	Recipient aggression third party	1		
arm extend, limp hand	Recipient aggression signaller	2		
arm extend, limp hand	Submission	1		
arm extend, palm upwards, hand cupped	Food feed	8		**100**
arm extend, palm upwards, hand cupped	Food observe	1		
arm extend, palm vertical towards body	Contact	16	4	**80**
arm extend, palm vertical towards body	Mutual sex	3	2	**60**
arm extend, palm vertical towards body	Third party aggression recipient	5	1	**83**
arm extend, palm vertical towards body	Third party aggression signaller	1		
arm extend, palm vertical towards body	Recipient aggression signaller	1	1	
arm extend, palm vertical towards body	Travel	3	2	**60**
arm flap	Food observe	4		
arm flap	Mutual sex	0	2	
arm flap	Recipient aggression third party	1		
arm flap	Recipient sex	1	1	
arm flap	Signaller aggression R	1		
arm flap	Signaller sex	1		
arm flap	Submission	3		
arm raise	Contact	1		
arm raise	Groom	8	1	**89**
backward hand sweep	Travel	9		**100**
elbow raise	Contact	6		**100**
elbow raise	Travel	1		

Gesture	**Context**	**Congruent responses**	**Incongruent responses**	**Specificity index**
fingers sweep	Third party aggression recipient	1		
fingers sweep	Recipient aggression signaller	1		
fingers sweep	Signaller aggression third party	3		
hand bend	Recipient aggression third party	3		
hand bend	Recipient aggression signaller	14	1	**93**
Average specificity				**85**

Table 4.9: Specificity index of response for combination of gesture with signaller’s goal (def = defensive, Offens = offesnive, App = approach, SI = specificity index

Gesture	Signaller’s goal	Attend signaller	Breast feed	Climb back	Def App	Def leave	Give groom	Give item	Groom present	Inspect	Neutral App	Neutral leave	Offens App	Offens leave	Reach item	Receive groom	Pass by	Stop App	SI
Lh	Avoid direct aggression															**2**			
Lh	Avoid redirected aggression								**1**										
Lh	Groom					1			**16**										94
Ap	Gain food							**4**						1	1				67
Pv	Avoid direct aggression	**1**															1		
Pv	Cling										**3**								
Pv	Copulate				1						**2**								
Pv	Embrace										**5**								100
Pv	Nurse		2								**13**								87
Pv	Travel	1			1						**3**								60
Af	Avoid sex					2													
Af	Gain sex				1	1													
Af	Maintain copulation					1													
Af	Maintain food					**4**													100
Af	Maintain groom																	1	
Af	Maintain status												1						
Af	Maintain travel				1													1	
Ar	Groom						3					1				**5**			56
Bs	Travel			**9**															100
Er	Nurse										**6**								100
Er	Travel										1								
Fs	Avoid direct aggression																1		

Gesture	Signaller’s goal	Attend signaller	Breast feed	Climb back	Def App	Def leave	Give groom	Give item	Groom present	Inspect	Neutral App	Neutral leave	Offens App	Offens leave	Reach item	Receive groom	Pass by	Stop App	SI
Fs	Avoid redirected aggression						1												
Fs	Avoid support aggression												**2**	1					
Hb	Avoid direct aggression						1			1							**13**	1	81
Hb	Avoid redirected aggression																3		
SI of response for gesture/signaller’s goal																			84

Note: in bold responses most common for gesture/signaller’s goal combination, in grey highlight most common response types for gesture/signaller’s goal combination matching most common response type for a gesture alone. Abbreviations gesture: Af (arm flap), Ap (arm extend, palm upwards, hand cupped), Ar (arm raise), Bs (backward hand sweep), Er (elbow raise), Fs (fingers sweep), Hb (hand bend), Lh (arm extend, limp hand), Pv (arm extend, palm vertical towards body)

Table 4.10: Specificity index of congruent responses with the meaning of gesture alone for gesture/signaller's goal combinations

Gesture	Signaller's goal	Congruent response	Incongruent response	Specificity index %
arm extend, limp hand	Avoid direct aggression	2	0	
arm extend, limp hand	Avoid redirected aggression	1	0	
arm extend, limp hand	Groom	18	3	**86**
arm extend, palm upwards, hand cupped	Gain food	9	0	**100**
arm extend, palm vertical towards body	Avoid direct aggression	1	1	
arm extend, palm vertical towards body	Groom	1	0	
arm extend, palm vertical towards body	Travel	4	1	**80**
arm extend, palm vertical towards body	Cling	3	2	**60**
arm extend, palm vertical towards body	Copulate	3	2	**60**
arm extend, palm vertical towards body	Nurse	13	3	**81**
arm extend, palm vertical towards body	Embrace	5	1	**83**
arm flap	Maintain travel	2	0	
arm flap	Gain sex	1	1	
arm flap	Maintain copulation	1	0	
arm flap	Maintain food	4	0	
arm flap	Maintain groom	1	0	
arm flap	Avoid sex	0	2	
arm flap	Maintain status	1	0	
arm flap	Avoid redirected aggression	1	0	
arm raise	Groom	9	1	**90**
backward hand sweep	Travel	9	0	**100**
elbow raise	Travel	1	0	
elbow raise	Nurse	6	0	**100**
fingers sweep	Avoid direct aggression	1	0	
fingers sweep	Avoid redirected aggression	1	0	
fingers sweep	Avoid support aggression	3	0	
hand bend	Avoid direct aggression	14	1	**93**

Gesture	**Signaller's goal**	**Congruent response**	**Incongruent response**	**Specificity index %**
hand bend	Avoid redirected aggression	3	0	
Average specificity				**85**

Finally, to explore the influence of context and signaller's goal on the responses to gestures, we examined whether gesture specificity for one response type and congruent response would decrease when a gesture is considered in combination with a particular context or signaller's goal. That is, whether the combination of gesture with context or signaller's goal elicited the most common response type for that specific combination more frequently than when the most common response to a gesture was considered without the accompanying context or signaller's goal.

When considering the ongoing behavioural context, the average signal specificity for a response was higher when gestures were considered in combination with their context, i.e. when gesture/context was considered in combination, the specificity of gesture/context combination for most common response to gesture/context combination type increased from 73% for specificity of most common response for gesture alone, to 84% for specificity of gesture in combination with context. Additionally, when the specificity of gesture/ context was considered for congruent with meaning of a gesture response, it decreased from the original 92% for gesture alone to 85% for gesture/context combination.

When gestures were considered in combination with the signaller's goal, the average signal specificity of responses followed a similar pattern, i.e. the specificity of gesture/ signaller's goal combination for most common response to gesture/ signaller's goal combination type increased from 73% for specificity of most common response for gesture alone, to 84% for specificity of gesture in combination with signaller's goal. Additionally, when specificity of gesture/ signaller's goal was considered for congruent with meaning of a gesture response, it decreased from the original 92% for gesture alone to 85% for gesture/ signaller's goal combination. Thus, whilst chimpanzees understood meanings of gestures regardless of contexts and signaller's goals, at times they ignored the specific meanings of gestures and instead acted upon meanings of the signaller's goals itself.

Did recipients respond to gesture requests flexibly in relation to the perceived signaller's goal?

Whilst chimpanzees understood the gestures specifically and inflexibly, they were also able to respond to the gestures flexibly by inferring the goal of the signaller from the combination of gesture and context. Primarily, there were differences between gesture types in the proportion of cases when gesture requests were accepted and rejected by the recipients (Fisher's exact test, p = 0.011). For instance, while arm extend, palm upwards, hand cupped received 44.4% accept and 55.6% reject responses; arm flap received 71.4% accept and 28.6% reject responses. Whilst there were differences between gesture types in how often requests were accepted and rejected by the recipients, those frequencies varied across different contexts within gesture types, suggesting that chimpanzees were aware a priori what a particular combination of gestures with context was likely to mean in terms of the signaller's goals. Analysis of the distribution of frequency of accept and reject responses across different combinations of outcomes and gesture types shows that overall recipients rejected and accepted gesture requests differently across different outcomes and gesture types (Fisher's exact test, p=0.001). For instance, when considering responses to arm extend, palm vertical towards body, there were more acceptance (93%) and fewer rejection (7%) responses in relation to a nursing outcome when compared with accept (60%) and reject (40%) responses to a copulation outcome. Thus, while the meaning of a gesture was determined by the gesture itself, recipients were able to accept or reject gesture requests based on something more, such as the perceived signaller's goal.

Did recipients persist in their responses in light of the perceived signaller's goal?

Chimpanzees also continued to ignore and reject subsequent persistence and elaboration attempts by the signaller in relation to the signaller's different goals, as evidenced by the differences in the length of sequences across cooperative and competitive outcomes.

Cooperative outcome sequences were significantly shorter than competitive outcome sequences, in which it took recipients significantly longer to negotiate and adhere to gesture requests made by a signaller (Mann-Whitney test, U = 343, r=-0.22, p=0.028). The mean (SD) number of gestures in sequences leading to cooperative outcomes was 0.28 (0.62), compared to 0.81 (1.22) for sequences with competitive outcomes. Additionally, signallers elaborated more across competitive rather than cooperative outcomes when trying to achieve their desired goals with the recipients (Mann-Whitney test, U = 371, r=-0.19, p=0.041). The mean (SD) number of elaborations on initial gestures in sequences with cooperative outcomes was 0.16 (0.41), compared to 0.63 (1.20) for sequences with competitive outcomes. However, signallers did not repeat the same gestures more in competitive than collaborative outcomes (Mann-Whitney test, U = 445, r= - 0.03, p=0.389. The mean (SD) number of repetitions of the initial gesture in sequences with cooperative and competitive outcomes was 0.12 (0.38) and 0.19 (0.54) respectively. Thus recipients understood that the signallers had a goal and pursued their actions until they achieved their desired outcomes. These data suggest that the recipient's perception of a signaller's goal takes into account the recipient's own interests in relation to desired outcome types, and leads to the diversity of lexicon of the gestural repertoire.

Do recipients make choices about signaller's goals based on their own interests?

Recipients accepted and rejected gesture requests differently across different contexts (Fisher's exact test, p=0.025) and signaller's goals (Fisher's exact test, p=0.007). When faced with cooperative goals chimpanzees accepted gesture requests more readily and rejected them less frequently (44.1% and 8.8% respectively). On the other hand, when faced with competitive goals, the frequency of reject responses increased whilst frequency of accept responses declined (34.6% and 12.5% respectively). Thus, chimpanzees took their own interests into account when making decisions about how to respond.

Does recipient's choice to respond to signaller's goals differ according to relative rank?

There was an effect of rank of the recipient relative to signaller on the likelihood of engaging in negotiating towards the signaller's goal. Overall, higher ranking recipients accepted significantly fewer and rejected significantly more gesture requests than lower ranking individuals (χ^2 (1) = 4.91, p=0.032). Low ranking subjects accepted 85% and ignored 15% of requests, whereas high ranking subjects accepted 69% and ignored 31% of all requests. Whilst for higher or equal ranking recipients there was variation across outcomes and gesture types (Fisher's exact test, p = 0.001), there was no such variation for lower ranking recipients in how likely they were to accept or ignore the requests (Fisher's exact test, p=0.158). Instead, lower ranking individuals accepted gesture requests significantly more often than they rejected them (Binomial test, p > 0.001), regardless of the perceived outcomes. Thus, while the intended outcome of the interaction was transparent to recipients, from the combination of gesture with context, higher ranking individuals displayed greater flexibility than lower ranking individuals in accepting or ignoring gesture requests.

DISCUSSION

Our research suggests that chimpanzee gestural communication is a strong candidate for precursor to human language in that it shows cognitive abilities in many ways similar to those capacities underlying language comprehension in humans. Although previous research on signal comprehension in captive apes has suggested that apes understand gesture meanings semantically, our research shows that gesture comprehension in wild chimpanzees is much more complex than that. Wild chimpanzees in our study have shown that they can make decisions about how to respond to individual gestures by taking into account signaller's goals and inferring these from combinations of gestures with context. Whilst chimpanzees understand the gestures specifically, they respond to them flexibly in light of perceived signaller's goals.

Firstly, wild chimpanzees attached specific meanings to gestures. They produced a set of specific response types to different gestures, congruent with meaning of a gesture, with one response type more frequently produced than all other response types combined. The responses to gestures were not reliably influenced by eliciting context or signaller's goals, but were relatively fixed in that whatever the response type, it was always congruent with the meaning of a gesture. This is in agreement with previous research on gesture comprehension in captive gorillas, which showed that recipients produce specific responses to the gestures (Genty and Byrne, 2009). Additionally, this further supports findings that wild chimpanzees persist and elaborate their gesture requests until they elicit correct response types in the recipient (see Cartmill and Byrne, 2010 for similar findings in captive orangutans).

On the other hand, the present findings are in disagreement with previous studies on contextually defined usage which implied that great ape gestures are devoid of specific meanings and instead purely contextually understood (see e.g. Pika and Tomasello, 2002, Pika et al., 2005b, Pika et al., 2005a, Liebal et al., 2004b, Liebal et al., 2006). One reason for this discrepancy in findings may be that previous research has primarily focused on the broad context of gesture production, lumping together eliciting context for a gesture as well as responses to signals. For instance, in Pollick and de Waal (2007), agonistic context was categorised as giving or receiving of threats, reconciliation and support behaviours. However, it is conceivable that taking context alone as a proxy for meaning does not give the most accurate picture of the likely meanings of gestures. For instance, while the eliciting context could be antagonistic for one gesture, the function of a gesture made in response to that antagonism could be either appeasement or retaliation, as indicated by either subsequent neutral behaviour by the recipient or escalation of the antagonism, respectively.

Additionally, the limitation of previous research on contextually defined usage is exacerbated by the fact that manual gestures are often included with other bodily movements. However, it is important to distinguish manual gestures from other bodily movements because they are neurologically distinct in both production and comprehension. While there is evidence that manual gestures are intentionally used (see e.g. Chapter 3), it is conceivable that bodily movements reveal specific emotions of signaller but are not meant to change the behaviour of recipient. One piece of evidence for this is that manual gestures that communicate what actions signaller wants a recipient to perform may elicit specific responses from the recipient towards the signaller, a third party or an object. On the other hand, bodily movements that inform others about emotions of the signaller may produce inconsistent responses, not directed at any particular entity. For instance, Cartmill and Byrne (2010) classified gestures broadly as both manual and bodily movements. They report that while some gesture types possessed specific and semantic meanings, some others were ambiguously understood and produced unspecific responses.

Previous research did not distinguish between age classes when investigating comprehension of gesture signals, studies primarily examined usage of gestures in sub-adult subjects (see e.g. Liebal et al., 2004a, Plooij, 1978, Plooij, 1979). However, it is important to distinguish gesture use by adults from that used by subadults because flexibility in use of gestures in sub-adult subjects may be a product of ontogenetic processes. For example, in the vocal domain, young individuals over-generalise eliciting stimuli and only gradually learn to produce vocalisations in appropriate contexts (Fischer et al., 2002, Fischer et al., 2000). Thus, our research suggests that when examining specificity in gesture comprehension, certain confounding effects need to be taken into account, i.e. that too broad a classification of contexts may not reliably predict response types to gestures, bodily movements not associated with specific responses towards specific entities may not be intentionally produced, and communication in young individuals may be influenced by ontogenetic processes.

Moreover, whilst chimpanzees understood gestures specifically, they were able to respond to the gestures flexibly by inferring the goal of the signaller from the combination of gesture and context. Whilst there were differences between gesture types in how often gesture requests were accepted and rejected by the recipients, the frequencies varied across different contexts within gesture types, suggesting that chimpanzees were aware a priori what a particular combination of gesture with context meant in terms of signaller’s goals. This is supported by a small albeit detectable influence of context and signaller’s goal type on response types by the recipients to combinations of gestures. For instance, there was higher specificity for the most commonly seen response type of gesture/signaller’s goal combinations than gesture alone, and some incongruence between meanings of gestures and meanings of gesture/signaller’s goal combinations. Whilst there is currently some controversy over whether great apes understand the intentional actions of others (see e.g. Povinelli and Vonk, 2003), more recent research suggests that chimpanzees are able to infer and act upon the goals of the interactants in negotiation games over desirable resources. For instance Hare et al (2000, 2001b) examined the behaviour of pairs of chimpanzees, who were contrasting in rank and who were placed in a competitive situation over food, with some food visible to both interactants and some only visible to the subordinate individual. Hare et al (2000, 2001b) found that subordinates most frequently chose to access the food which was hidden from the dominant’s view. They suggested that subordinates knew what dominant subjects were able to see and that they were able to infer what this perception meant for future goal-directed action of the dominant, i.e. that it would attempt to get seen food for itself. Our results support Hare et al’s (2000, 2001b) findings and crucially advocate that chimpanzees are capable of inferring goals of others in their usage of gestural communication.

Additionally, these results suggest that whilst inferring the goal of the signaller, recipients also understood the pursuit of goals by the signaller across long sequences of interaction. Chimpanzees segmented actions of the signaller in light of the signaller’s overall goal, rather than only considering goals of each separate action individually. They continued to ignore and reject separate persistence and elaboration attempts of signaller appropriately in relation to the type of signaller’s goal, as evidenced by the differences in length of the sequences across cooperative and competitive outcomes. While signallers persisted and elaborated in response to recipients actions, recipients evaluated each step of the interaction in light of the goal that both signaller and recipient commonly understood (see also Chapter 3 for understanding of one’s own goals by wild chimpanzees). This understanding that others have goals and can behave towards them persistently is in agreement with what previously has been argued in captive chimpanzees. For instance, Call et al. (2004) showed that chimpanzees understand when others are trying to achieve a certain goal. Captive chimpanzees continued responding more to experimenters who were unsuccessfully trying to give food to them as compared to when an experimenter was unwilling to give food. Our results support these findings with data on gestural comprehension by wild chimpanzees and suggest that capacity to understand pursuit of action by a signaller is more common than previously suggested.

Finally, whilst chimpanzees understood the goal and pursuit of the action of the signaller towards a commonly understood objective, they took their own interests into account when making decisions about sharing the goal with the signaller. When faced with cooperative goals, chimpanzees accepted gesture requests more readily and rejected them less frequently than when relating to competitive goals. On the other hand, when faced with competitive goals, the frequency of reject responses increased whilst the frequency of accept responses declined. It is also of interest in this context to consider the effect of rank of the recipient relative to signaller, in terms of how likely recipients were to engage in obtaining a goal with the signaller. Higher ranking recipients displayed greater flexibility in that they accepted fewer and rejected more gesture requests. On the other hand, lower ranking recipients were less flexible, they invariably accepted more often and seldom rejected the requests of the signaller. These results are in agreement with previous research on cooperative intentions, which suggested that chimpanzee intentions are primarily competitively motivated and chimpanzees perform better at tasks structured as competition rather than cooperation (see e.g. Hare and Tomasello, 2004). Thus, our results support previous findings and suggest that chimpanzees are selfish negotiators in their decision making about signallers goals and make calculated choices about whether to adhere to signallers requests. Whilst chimpanzees may infer signallers goals, having common ground for the interaction is not cooperatively motivated, but instead has a competitive basis at least in our community of wild chimpanzees.

These data provide the first systematic insight into contextually defined comprehension of gestures in wild chimpanzees. The findings of this research suggest the following: chimpanzees understand the content of their gestures specifically, but take into account goals of the signaller in deciding how to respond, and infer the common goal of the signaller from the combination of gesture with a specific context. While semantic comprehension may be cognitively simple, understanding of others' goals or intentions is cognitively complex and provides an interpretive matrix for understanding interactions. For instance, while one utterance such as 'it's hot in here' may relate to a true/false statement about the temperature of the room, the ability to understand the speaker's goals and intentions may lead to a number of different interpretations including 'open the window', 'let's go outside', etc. Thus, chimpanzees selectively ignoring parts of the message that aren’t appreciated in light of what they perceive as signaller’s goal, display similar characteristics to humans using language. These observations support previous research on flexibility in gesture use and suggest that manual gestures of wild chimpanzees are an important model for ancestral human language evolution. Future larger scale studies could adopt this more fine grained approach to exploring the potential meaning and interpretations of gestures in relation to context, response and signallers intentions, in order to better understand the precise nature of the flexibility and intentionality identified in great ape gestural communication.

The results of this chapter have been submitted for publication:

Roberts, A.I.; Vick, S-J. & Buchanan-Smith, H.M. Meanings of wild chimpanzee manual gestures: Contextually inferred or semantic?

Chapter 5: Referential and intentional use of gestural communication in language trained chimpanzees

INTRODUCTION

An important objective in elucidating the evolution of cognitive skills underlying communication is to examine how different rearing conditions affect cognition in our closest living relatives (Call and Tomasello, 1996). The amount of contact with humans during ontogeny is important for primate cognition because humans interact with captive apes in different ways than conspecifics, for instance by attempting to direct primate attention towards self or third party objects or events (Tomasello and Call, 2004). In particular, enculturation during extensive language training is important, such as training in the symbolic use and comprehension of lexigram symbols arranged on a panel to indicate a word (Call and Tomasello, 1994). Language-trained apes display cognitive abilities in their communication not displayed by other captive or wild populations and show many communicative and cognitive features which are characteristic of human language. For instance, language trained chimpanzees use various semantic categories of signs such as qualities, actions and traits, and employ these signs flexibly by combining, repeating or elaborating to ensure effective communication (Gardner and Gardner, 1969).

Whilst language-trained chimpanzees display complex cognitive abilities in their learned sign communication that are not displayed by other captive or wild chimpanzees (e.g. Gardner and Gardner, 1969, Matsuzawa, 1985, Premack, 1971, Rumbaugh, 1977, Savage-Rumbaugh, 1986, Terrace, 1979), we know very little about how language training might also affect the chimpanzee's natural system of communication, or which cognitive abilities chimpanzees might display in their natural communication system given exposure to language training. It is important to investigate how language interaction affects natural great ape communication. Language interaction plays a crucial role in the emergence of complex cognitive skills in human infants, such as understanding that others have goals and intentions different from one's own, which in turn are foundational capacities for the development of the referential abilities of language (Garfield et al., 2001).

One important element in examining how language training affects cognitive abilities in captive apes is to explore the cognitive skills that underlie the human capacity to communicate referentially. Referential communication is a basic characteristic of human language and can be understood as a system of communication which is intentionally produced and which has a specific structure, selectively produced in a specific context, and which elicits a specific response from recipients (Marler et al., 1992, Crockford and Boesch, 2003). Additionally, it is important to determine the cognitive skills that underlie the ability to communicate intentionally. Intentionality can be defined as the use of communicative signals, where the signaller has a specific goal and acts flexibly in the means of attaining it. A potential evolutionary precursor to intentional, referential human communication can be seen in primate non-vocal referential signals which, similarly to human language, redirect the attention of social agents to distal entities and provide reliable information about the presence of objects and events (Corballis, 1991). These acts of non-verbal reference involve the signaller's usage of deictic gestures, such as pointing, visual orienting behaviour and tactile or auditory attention getting behaviour (Leavens et al., 2004).

Some readers have explored the cognitive skills underlying use of deictic gestures and attention-getting behaviour in apes reared in typical captive conditions, that is without the extensive enculturation of language training. According to those studies of great apes in captivity, manual gestures such as pointing are used to reliably communicate about distal objects (Blake, 2004, Call and Tomasello, 1994, Leavens et al., 2004, Leavens et al., 2005b). For instance, in an experimental study captive chimpanzees reliably pointed to the location of a hidden object when presented with an experimenter who was naive about its location (Leavens et al., 2004). Furthermore, there is now extensive empirical evidence that great ape gestures are produced intentionally and show the flexible usage that distinguishes them from stereotyped behaviours and involuntary expressions of internal emotional states (Russell et al., 2005).

Several behavioural criteria for defining intentionality in non-verbal communication of human infants have been examined in captive apes, such as the influence of the attentional status of an observer on the propensity to exhibit gestures. For example, Leavens et al. (2004) observed that the rate of gesture production decreased significantly when an experimenter was absent compared to when experimenter was present (in full view) of the chimpanzees. Leavens et al. (2004) also found that the rate of gesture production increased when an experimenter was looking at the chimpanzees. Krause and Fouts (1997a) have shown that chimpanzees used attention-getting behaviours such as vocalisations and auditory gestures to attract the experimenter’s attention before employing pointing or other visual gestures.

Another set of supporting data for intentional communication in great apes comes from studies of persistence and elaboration in communicative attempts in face of ineffective communication. For instance, Leavens et al. (2005b) showed that chimpanzees exhibited persistence and elaboration in gestures and vocalisations when an experimenter failed to deliver the desired object. Cartmil and Byrne (2007a) showed that captive orang-utans alternated between persistence and elaboration across various degrees of communicative miscomprehension; the experimenter delivered a visible, desirable food item after a predetermined interval (comprehension), or only a part of the item (partial comprehension), or a less desirable food item (no comprehension).

Whilst we now have a relatively good understanding of the cognitive skills underlying natural gesture systems in apes reared in normal conditions of captivity, we know relatively little about cognitive skills underlying natural communication system in language-trained apes. However, it is important to understand how extensive linguistic interaction might shape the cognition that underlies primates' use of natural, species-specific gestures. Linguistic enrichment seems to play a fundamental role in development of the understanding that others have goals and intentions that differ from one's own and that attaining others goals and intentions can often be achieved by alternate means.

The current study examines how language-trained chimpanzees communicate with human interactants in a food recovery task, where the chimpanzees direct a naive experimenter towards hidden food items in the parkland surrounding their enclosure. This interactive communication task (the task can only be solved by cooperation between chimpanzee and human) is more complex than the previously used paradigm in which the food item was close and visible and the experimenter's behaviour was restricted to the delivery of an item following a short delay (e.g. after 30 seconds). In our task, the experimenter points and moves to various locations in search of the hidden object and the chimpanzees respond to the relative success of these attempts by either correcting or supporting the experimenter's actions, using pointing gestures, other manual gestures, bodily movements and vocalisations. The experimenter responds to the chimpanzee's communication and modifies his search behaviour for the hidden object until it is found. These components of chimpanzee and experimenter communicative behaviours provide us with information about how chimpanzees employ their referential and intentional abilities (seen in their lexigram use) in their natural system of communication, and how the abilities of language trained chimpanzees compare with those of other captive chimpanzee populations, with no training in lexigram or sign language use.

The first goal of this study was to examine the repertoire of the chimpanzees' responses to the experimenter's actions, with a special focus on pointing and its communicative meaning. In terms of the repertoire, individual variation may be examined to inform our understanding of possible strategies used by chimpanzees when communicating with humans. Gestures commonly understood as pointing are generally produced with the hands and possess specific patterns of movement, whereby the body part which carries out the pointing gesture is moved in a linear path and aimed at a specific distal target (Kendon, 2004). A few studies suggest that how a human pointing gesture is done may make a difference to its meaning. For instance, Kendon (1988) observed that among the Warlpiri and Warumungu tribes in Australia, the angle of the arm is altered depending on how far the object to which it is pointed at is deemed to be. Despite evidence in human pointing that referential distinctions made via deictic words (such as 'this' and 'that' or 'near' and 'far') are also present in pointing gestures, the idea that similar distinctions could also be made by great apes has never been explored. In our study, we looked at the chimpanzee's use of the angle of the arm (such as arm vertical and horizontal) when pointing, to explore whether there are systematic differences in how different arm angles are used in pointing, in relation to experimenter's behaviour, to convey communicative meanings.

A second aim of this research was to examine the chimpanzees' sensitivity to an audience in terms of the mode of communication production. Hosetter, Cantero and Hopkins (2001) examined this question in a study with captive chimpanzees that were required to gesture to food in the presence and absence of visual attention from a human experimenter. Chimpanzees used more visual gestures and facial expressions when the experimenter was looking at the chimpanzee, as opposed to looking away. Furthermore, chimpanzees produced their first vocal behaviour (of the vocal bout) and spat sooner when the experimenter was looking away compared to when the experimenter was not looking (i.e. the chimpanzee engaged in attention getting behaviours).

Our study aims to replicate these findings in language trained chimpanzees and examine which chimpanzee communicative signals are intentional. For instance, if chimpanzees exhibit a higher frequency of visual gestures such as pointing when the experimenter's visual attention is directed at the chimpanzees, then we might conclude that these communicative attempts are intentional. Furthermore, if chimpanzees exhibit a higher frequency of auditory gestures and vocalisations when the experimenter's attention is not directed at them then we would conclude that those behaviours may serve as intentional attention getters to establish visual contact with the experimenter (Hosetter et al., 2001, Russell et al., 2005). Alternatively, if there is no relationship between the experimenter's attention and frequency of gestures and vocalisations then we would assume that those behaviours do not carry communicative intent on the part of a signaller, but may reflect more basic emotional responses, such as frustration.

A final aim of this research was to examine whether chimpanzees intentionally elaborate and persist in the use of communicative gestures in the face of communicative failure. Leavens et al. (2005b) addressed this question with captive chimpanzees. The researchers presented chimpanzees with both desirable (banana) and undesirable food (chow) items and administered three different conditions: successful (delivery of banana); partially successful (delivery of half banana) and unsuccessful communication (delivery of chow). Subjects exhibited a higher frequency of vocalisations, food begging and hold hand out gestures, cage banging and barter attempts after unsuccessful as compared to successful communication. Furthermore, chimpanzees elaborated their communication in both half-successful and unsuccessful conditions, suggesting that chimpanzees communicate intentionally.

Our study addresses this question in language trained chimpanzees by examining their persistence and elaboration in intentional behaviour alone (as identified by sensitivity to visual attention), excluding the influence of potentially confounding factors of involuntary expressions such as vocalisations, cage bangs and barter attempts. For instance, if chimpanzees exhibit a higher frequency of intentional gestures after unsuccessful (experimenter pointing in another direction than where the food object is located) compared to successful communication (experimenter pointing in the hidden object direction), then we might assume that the chimpanzees intentionally persist in their communicative attempts. Furthermore, if the gesture types (e.g. rapid and slow pointing) vary in relation to type of miscomprehension (e.g. right and wrong indication of distance to object) then we might conclude that chimpanzees intentionally elaborate their communicative attempts.

METHODS

Participants

The subjects were two chimpanzees (*Pan troglodytes)* - Panzee (female, 18 years of age) and Sherman (male, 30 years of age). Both chimpanzees had been reared from an early age by human caregivers and given extensive exposure to spoken English and 256 lexigrams in the everyday contexts of travel, play, food, which they use in everyday interactions with humans. Their rearing and experimental histories are described by Brakke and Savage-Rumbaugh (1995, 1996). Both chimpanzees had been involved in cognitive research in topics such as language acquisition, long-term memory and numerical competence (Rumbaugh, 1977, Savage-Rumbaugh, 1986). The current task is used to examine spatial memory in chimpanzees (see Menzel, 1999 for details), but the communication strategies used had not previously been examined systematically.

Environment and Apparatus

Panzee and Sherman were housed in indoor and outdoor enclosures connected by a 1m long tunnel. The indoor enclosure was visually isolated from both the outdoor enclosure and the area surrounding the outdoor enclosure. The outdoor enclosure measured 8m by 9m. The test objects were concealed in an area of woodland measuring approximately $160m^2$ adjacent to the outdoor enclosure (see Appendix 10 for the map of the enclosure and surrounding area). The chimpanzees were provisioned with fruits, vegetables, chow, grains and nuts and were not food deprived during trials. The indoor and outdoor enclosures each contained a lexigram keyboard, with a total of 256 different lexigrams per board.

Design and Procedure

Each chimpanzee was tested individually in the outdoor enclosure. The study consisted of 3 trials. Panzee took part in two trials – in one of these trials peanuts were hidden, in the other trial a pear was hidden. Sherman took part in one trial, in which a banana was hidden. Each trial had three phases: hiding phase, recruitment phase and the response phase. During the hiding phase, the first person (Experimenter 1) made certain the subject was watching, held up the food item then walked to a predetermined hiding place and placed the object under natural cover, so that the object was entirely concealed from view. The object was concealed from 45 to 35 meters from the outdoor cage in surrounding parkland. In each trial the food item was hidden in a different location. After hiding the food item, Experimenter 1 left the area.

During the response phase, in order to obtain the hidden item, the chimpanzee had to recruit a second person (Experimenter 2) who did not know what the object was or where it was located, or when a trial may be conducted. This ‘uninformed person’ had worked with the chimpanzees prior to the experiment, and thus was familiar with the subjects’ gestures, vocalisations and behaviour patterns. The chimpanzees interacted with Experimenter 2 in the indoor area and directed Experimenter 2 to the food item.

All interactions relating to this object location task were initiated by the chimpanzees. If one of the subjects recruited Experimenter 2 outdoors, the chimpanzee’s gestures, vocalisations and use of the lexigram keyboard were videotaped. A second camera recorded the behaviour of the experimenter. If the chimpanzee guided the Experimenter 2 to the hidden food item, this experimenter uncovered the food item, took it indoors and offered it to the chimpanzee.

Behavioural Coding

Videotapes of the trials were analysed using the Power DVD DX video software and statistical package SPSS 17.0. The two videos (experimenter and chimpanzee focus) were synchronised and edited to allow a split screen view of the two sides of the interactions to be seen simultaneously.

Chimpanzee behaviour

Behavioural responses of the chimpanzee to the experimenter’s pointing gestures were coded. A response started immediately after the pointing gesture of the experimenter was made (with a 1.5m stick) and ended when the experimenter made another pointing gesture, started walking or searching through the ground with the stick. The following types of behavioural responses made by the chimpanzee were coded:

Indicative behaviour

Indicative gestures made by the chimpanzees included: pointing (pattern of movement where the arm, forearm and hand is moved in a linear path which appears to be aimed at specific distal target), outward beckon (subject moves its whole arm rapidly and outwardly, using open palm to indicate object location), iconic (subject points towards lexigram or makes iconic symbolic gesture to represent the hidden object).

The morphology of all indicative gestures made by the chimpanzees towards the hidden object was described using following modifier classes:

a) Speed of gesturing: slow gesture (subject moves its forearm forward and retains it in a pointing position for a few seconds), rapid gesture (subject moves its forearm forward in rapid movement singly or repeatedly).

b) Arm, forearm and finger positions: indicate up (arm, forearm and finger directed vertically up), indicate down (arm, forearm and finger directed horizontally or down).

For all indicative gestures, hand shape of gestures was recorded using the following categories: index finger pointing (index finger extended, other digits adducted); open hand spread (all digits adducted and spread); open hand closed (all digits extended and together). Additionally, direction of gesturing was recorded using the following categories: object (pointing in the direction of the object), experimenter (pointing in the direction of the experimenter), other (pointing in other direction than the direction of object or the experimenter) and lexigram (pointing to the symbol on a lexigram board).

Non indicative behaviour

Chimpanzee manual gestures other than pointing were recorded and defined as arm shake (subject shakes its one or both hands repeatedly with rapid movements upwards), hand shake (subject extends the back of its flexed wrist upwards and shakes it repeatedly with rapid movements), hand swing (subject swings hand or whole arm repeatedly with rapid movements, with the hand positioned vertically or horizontally relative to his own body). Additionally, bodily gestures were recorded such as bob (subject bobs and weaves with head or whole body in bowing position upwards or forwards), rocking (subject stands or sits and rocks its body from side to side or from forwards to backwards). Two additional behavioural responses were also recorded: scratch (using nails of own hand to rake through own hair and skin repeatedly) and vocalisation (sound made with the vocal tract).

Experimenter behaviour

The experimenter's pointing behaviour (with the stick) was recorded when the experimenter was standing in one place. All pointing gestures made by experimenter whilst walking were ignored because they were not responded to by the chimpanzees and it was not possible to reliably determine the accuracy of these pointing gestures. Each time the experimenter made a pointing gesture, the following data were recorded:

1. Distance of the experimenter to the hidden object in meters, determined from a map of the area of woodland (see Appendix 10 for the map of the enclosure and surrounding area). Objects in this study were hidden 45 meters (Panzee peanuts), 40 meters (Panzee pear) and 35 meters (Sherman banana) away from the experimenter at the start of the trial. The exact distances during the trial were subsequently pooled and categorised as close (0 – 10 meters distance between experimenter and the object) and far (45 – 10 meters distance between experimenter and the object).

2. The experimenter's direction of pointing gestures was coded using the following categories: point towards the object (experimenter pointing in the direction of a hidden object, which is within the experimenter's field of vision; the hidden object would be placed on the line which could be visually or physically extended from end of the pointing stick), point elsewhere (experimenter pointing in the direction other than hidden object; the hidden object would not be placed on the line which could be visually or physically extended from end of the pointing stick)

3. The experimenter's accuracy at indicating distance to the object, as evidenced by the height at which experimenter held the end of pointing stick relative to object's location, was scored as either correct (end of stick accurately determined the location of the object; the hidden object would be placed on the diameter of the circle which could be visually or physically drawn by the stick on the ground); or too far (the hidden object would be placed within the diameter of the circle which could be visually or physically drawn by the stick on the ground); or too close (the hidden object would be placed beyond the diameter of the circle which could be visually or physically drawn by the stick on the ground).

4. The experimenters' success at identifying steps bringing him closer to the goal relative to previous steps taken was also coded: bring closer (experimenter's pointing decreased the distance between the experimenter and the object relative to previous location); or bring further (experimenters pointing increased distance between experimenter and the object relative to experimenter's previous location)

For a second set of analyses, the experimenter's visual attention was coded continuously using the following categories: look at chimpanzee (head orientated towards the chimpanzee, which is in the experimenter's field of vision) and not attending (experimenter's head is turned away from the chimpanzee). Additionally, the presence of the object was coded as object absent (object hidden in the external environment), object found (object located by the experimenter). For the analyses of the rates of behavioural responses, in relation to visual attention and presence of object, the data on behavioural responses of the chimpanzees was recorded regardless of the experimenter's locomotion or pointing. A trial ended when the experimenter disengaged from the chimpanzee and left the area.

Analyses

Given the small sample size, simple non-parametric statistics were used in all analyses. Due to the limitations of the small sample size, data from the two Panzee trials was pooled for analysis. These two trials were pooled for analyses although because the two trials varied in terms of object used, the location where the object was hidden and experimenter's behavioural patterns. A similar approach was taken to those of other gestural studies, where the number of available subjects displaying the abilities of interest is a restrictive factor and precludes use of more robust statistical procedures.

Each subject was analysed separately and for each one the behaviour in different conditions was analysed separately within the trials, e.g. experimenter attending and not attending. However, when the behaviour patterns were compared within condition (e.g. rates of upward and downward pointing when distance to object was far), the data were treated as dependent. On all Mann-Whitney U tests, mean was reported if median for both independent groups was 0, see also Chapter 3, statistical analyses section for explanation of values of effect size (r) and boxplots. All tests performed here were non-parametric, due to the nature of data collected, which was categorical, tests were set at the .05 level of significance.

RESULTS

Repertoire of behavioural responses

The chimpanzees used a diverse repertoire of behaviours to communicate with the experimenter about the location of a hidden object. They used manual indicative gestures (i.e. pointing to the object and lexigram, outward beckoning in the direction of object), manual non-indicative gestures (i.e. swinging hand, hand shaking and arm shaking), bodily gestures (i.e. forward and upward bobbing with head and body, rocking horizontally and vertically), scratches and calls. Figure 5.1 presents the rate of each behaviour category by the subjects. Panzee showed a higher rate of manual indicative gestures, bodily gestures, scratches and vocalisations than Sherman, whereas Sherman displayed higher rates of non-indicative manual gestures than Panzee (see Figure 5.2 for rates of broad behaviour categories).

Figure 5.1: Rates of behavioural responses per subject

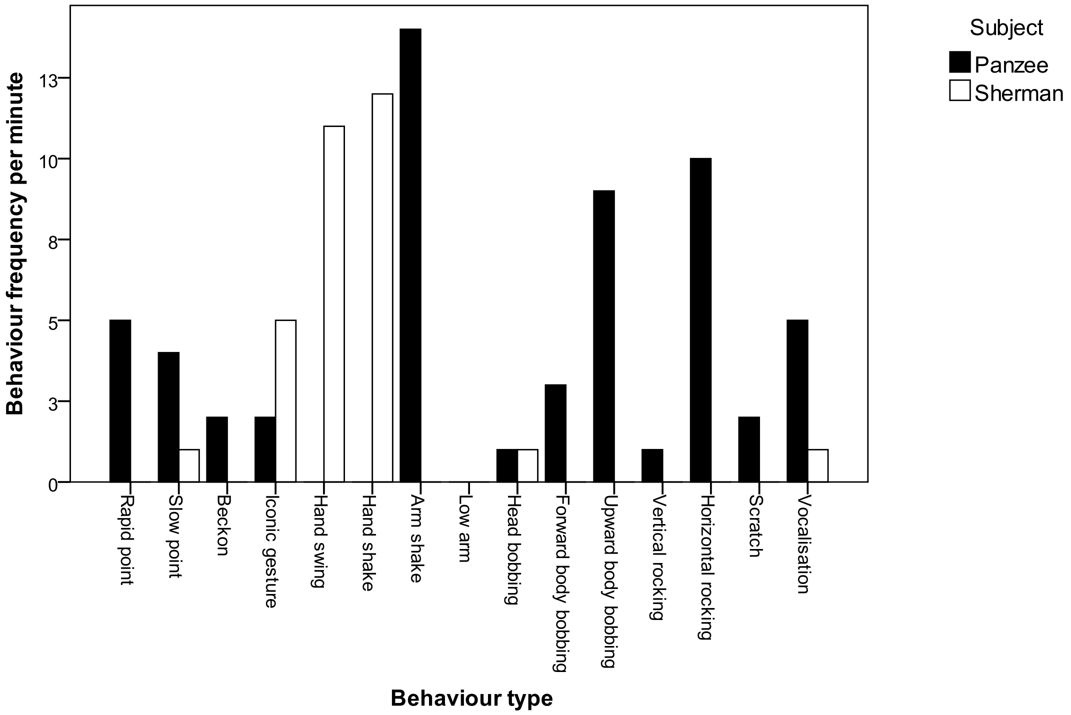
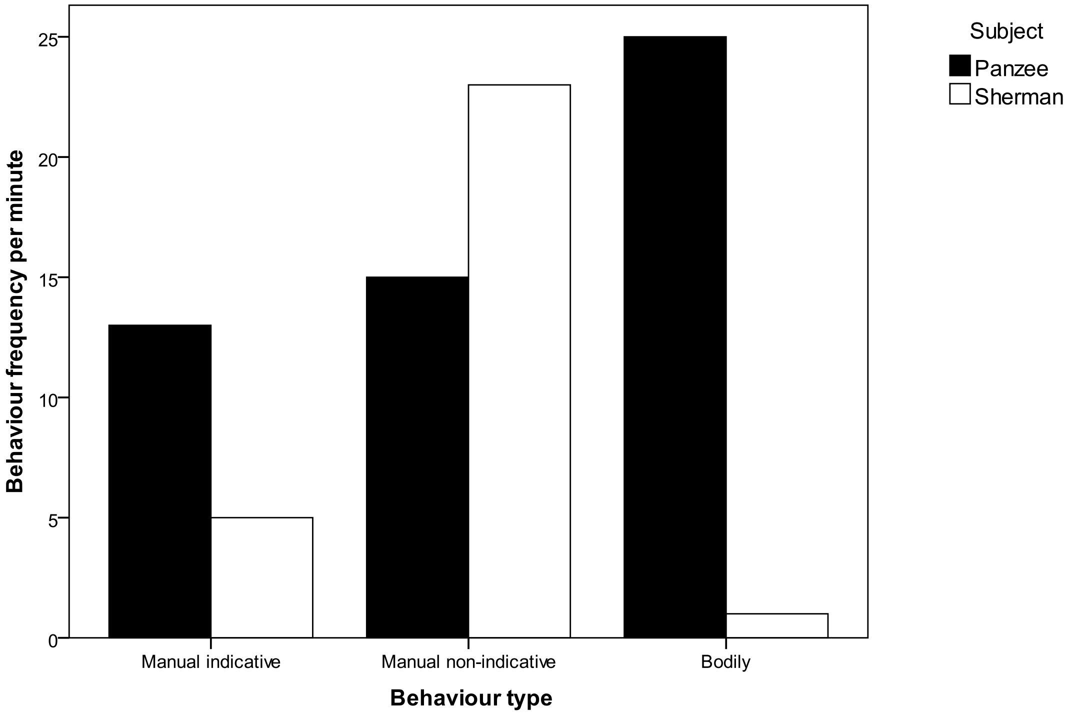


Figure 5.2: Rates of broad behaviour categories per subject



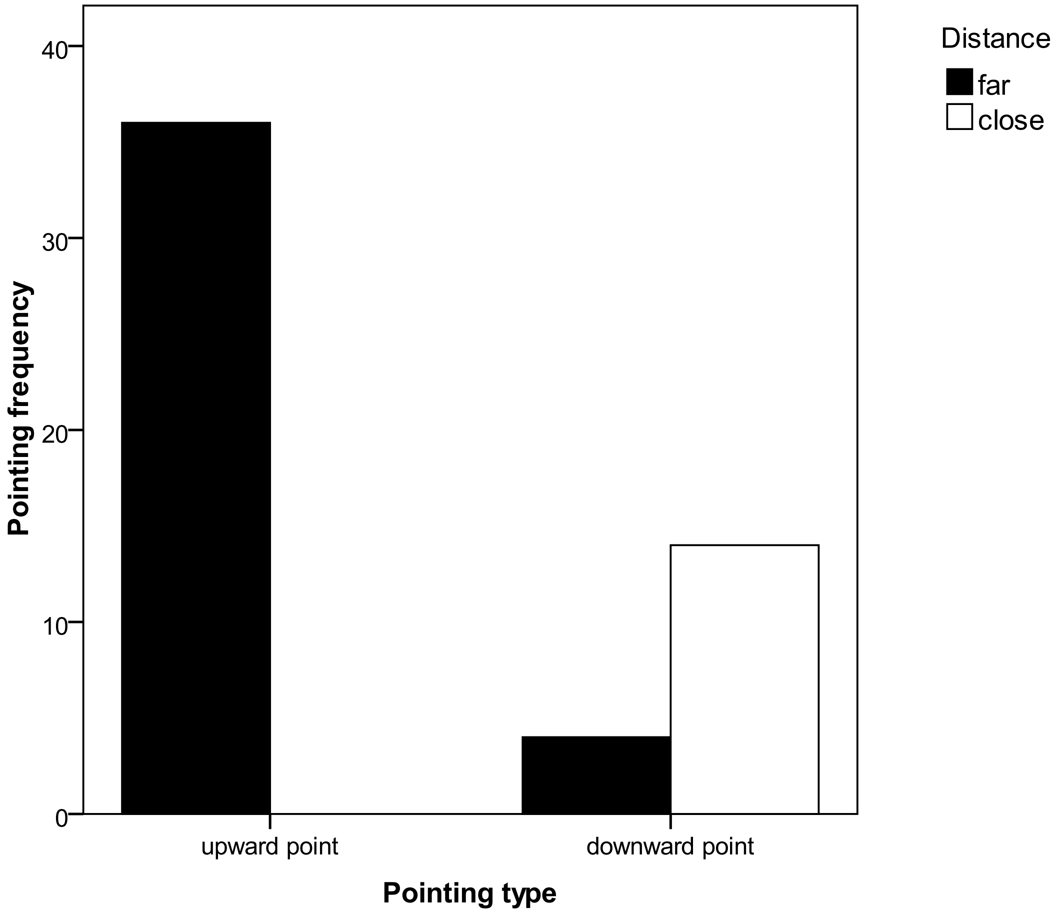
There were differences in the type of hand positions used by the subjects in indicative gestures. Panzee demonstrated the higher percentage of index finger pointing (79% of all indicative gesture events and 100% of all pointing events) followed by beckoning with open hand with fingers adducted and spread (21% of all indicative gestures). Sherman showed a preference for pointing with open hand with all fingers extended and together (86%) with a small percentage of iconic gestures pointing at lexigram, displaying index finger pointing morphology (14%).

Referential use of indicative gestures

There was a significant difference in the number of indicative gestures directed towards the object by Panzee. Panzee pointed or beckoned in the object direction 53 times out of 54 indicative gesture events. For Sherman, there was no difference in the number of pointing gestures directed towards object or elsewhere; out of 2 pointing gestures performed to indicate the object in the external environment, Sherman pointed twice in a direction other than the object's location.

The chimpanzees flexibly signalled to the experimenter his distance to the hidden object. There was a significant difference in morphology of Panzee pointing and beckoning gestures when the experimenter was close to the hidden object, compared to when the experimenter was further away (see Figure 5.3). If the experimenter was far from the object, Panzee produced points and beckoning gestures directed vertically up in terms of arms, forearms and fingers. In contrast, when the experimenter was close to the object the arms and fingers were positioned horizontally or down (Fisher's exact test, $p < 0.001$). There was insufficient data to perform this analysis for Sherman's pointing gestures, but the two points that Sherman produced to indicate object location did not differ in their morphology according to the experimenter's distance to the hidden object.

Figure 5.3: Frequency of type of pointing gestures across distance categories from object to experimenter by Panzee



Intentionality in communication use

Influence of attention of experimenter

For both subjects, there were significant differences in the rate of indicative manual gestures (such as pointing and outward beckoning) when the experimenter was attending to the chimpanzee, as compared to when the experimenter was not attending. Panzee had a significantly higher rate of manual indicative gestures when the experimenter was attending (*Mdn* = 17), compared to when the experimenter was not attending (*Mdn* = 0, Mann-Whitney U test: U=127, z = -4.7, p <0.001, r = -0.64, see Figure 5.4 for overall rates of indicative gestures on Panzee's trials). Sherman also had a significantly higher rate of manual indicative gestures when the experimenter was attending (*Mdn* = 3), compared to when the experimenter was not attending (*Mdn* = 0, Mann-Whitney U test: U=62, z = -2.6, p = 0.013, r = -0.47, see Figure 5.5 for overall rates of indicative gestures on Sherman trial).

A similar pattern was seen for the frequency of non-indicative manual gestures (i.e. hand shaking, arm shaking, and hand swinging) in relation to the visual attention status of the experimenter. Panzee showed a significantly higher rate of manual non indicative gestures when the experimenter was attending (*Mdn* = 12), compared to when the experimenter was not attending (*Mdn* = 0, Mann-Whitney U test: U=206, z = -3.1, p = 0.001, r = -0.43, see Figure 5.4 for overall rates of manual non-indicative gestures on Panzee trial). Similarly, Sherman used manual indicative gestures significantly more frequently when the experimenter was attending (*Mdn* = 30), compared to when not attending (*Mdn* = 0, Mann-Whitney U test: U=44, z = -2.8, p = 0.003, r = -0.52, see Figure 5.5 for overall rates of manual non-indicative gestures on Sherman trial).

The pattern for rates of bodily gestures in relation to experimenter attention was less clear. In terms of bobbing gestures (i.e. forward and upward bobbing of body or head) Panzee had a significantly higher rate of bobbing gestures when the experimenter was attending (*Mdn* = 19.4), than when not attending (*Mdn* = 0, Mann-Whitney U test: U=148, z = -4.13, p <0.001, r = -0.56, see Figure 5.4 for overall rates of bobbing gestures on Panzee trial). However, for Sherman the difference between rate of bobbing when the experimenter was attending (*Mdn* = 0) and not attending (*Mdn* = 0) was not significant (Mann-Whitney U test: U=105, z = -1, p = 1, r = -0.18, see Figure 5.5 for overall rates of bobbing gestures on Sherman trial). For rocking gestures (vertical and horizontal rocking of body and head), Panzee did not differ in the rate of rocking gestures when the experimenter was attending (*Mdn* = 0), compared to not attending (*Mdn* = 0, Mann-Whitney U test: U=327, z = -0.6, p

=0.54, r = -0.08, see Figure 5.4 for overall rates of rocking on Panzee trial). Sherman did not produce any rocking gestures during his trial.

Scratching behaviour did not systematically vary according to the experimenter's state of attention. For Panzee's trials there was no significant difference in the rate of scratches when the experimenter was attending (*Mean* = 0.54) and when he was not attending (*Mean* = 3.39, Mann-Whitney U test: U=311, z = -1.18, p =0.253, r = -0.16, see Figure 5.4 for overall rates of scratching on Panzee trial). Sherman did not perform scratching behaviour during his trial.

Vocalisations did not systematically vary according to attention of the experimenter in either subject. For Panzee the rate of vocalisations when the experimenter was attending (Mean = 7.3) did not differ from the rate when he was not attending (Mean = 7.4, Mann-Whitney U test: U=309.5, z = -1.01, p = 0.313, r = -0.13, see Figure 5.4 for overall rates of vocalisations on Panzee trial). Similarly, Sherman showed no significant difference in the rate of vocalisations when the experimenter was looking (Mean = 2), compared to not looking (Mean = 0, Mann-Whitney U test: U=90, z = -1.8, p=0.224, r = -0.32, see Figure 5.5 for overall rates of vocalisations on Sherman trial).

Figure 5.4: Rates of behaviour in relation to visual attention by the experimenter for Panzee trials

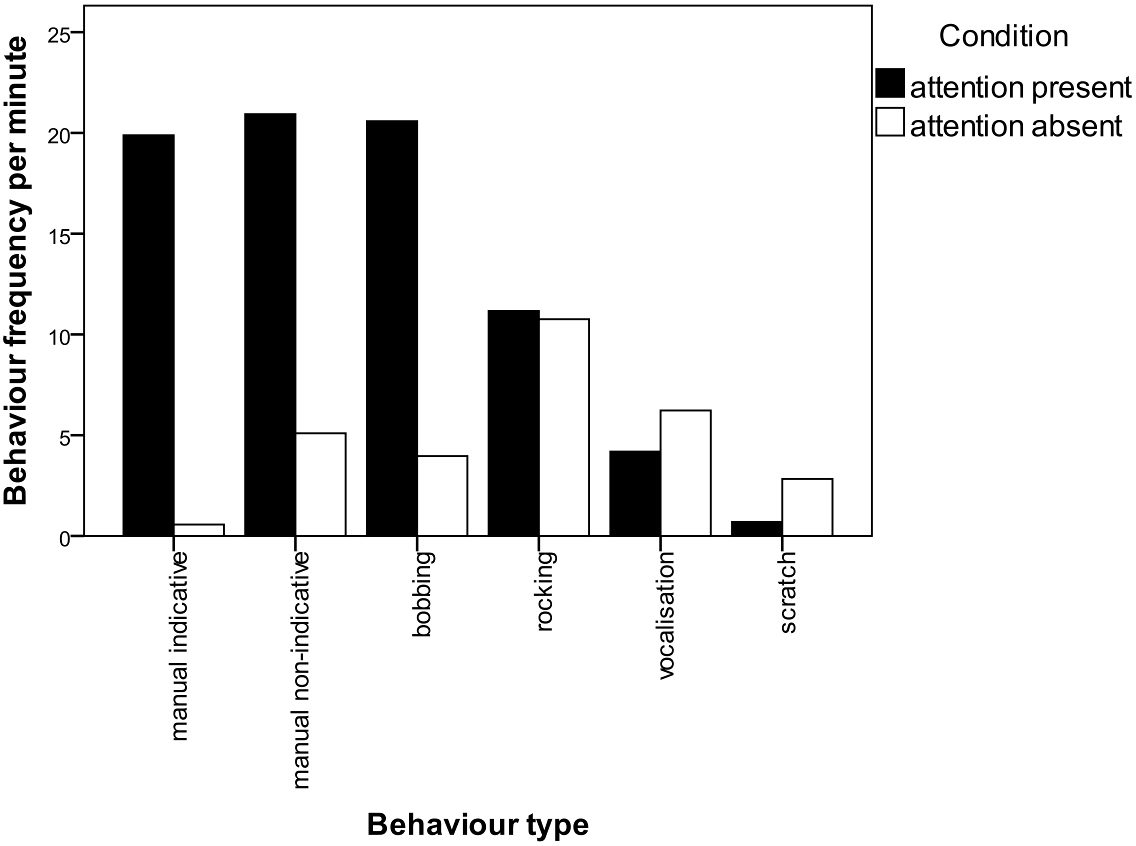
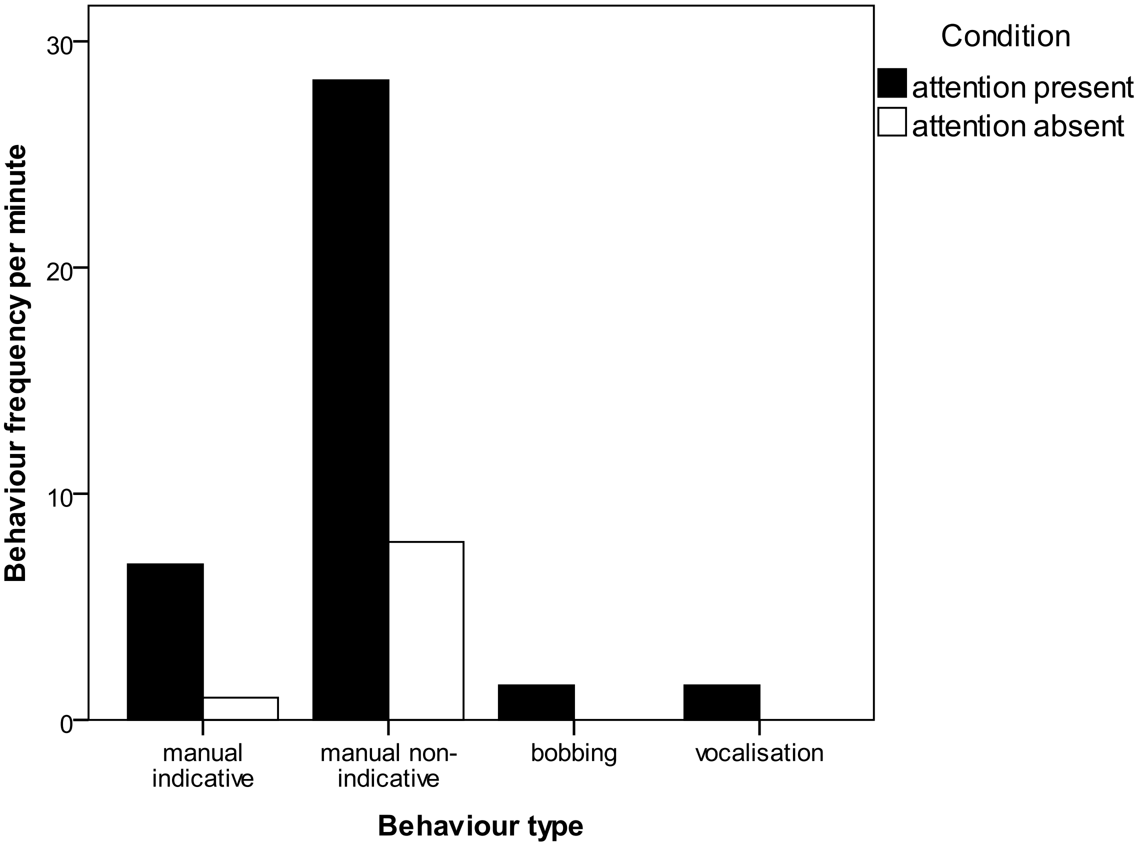


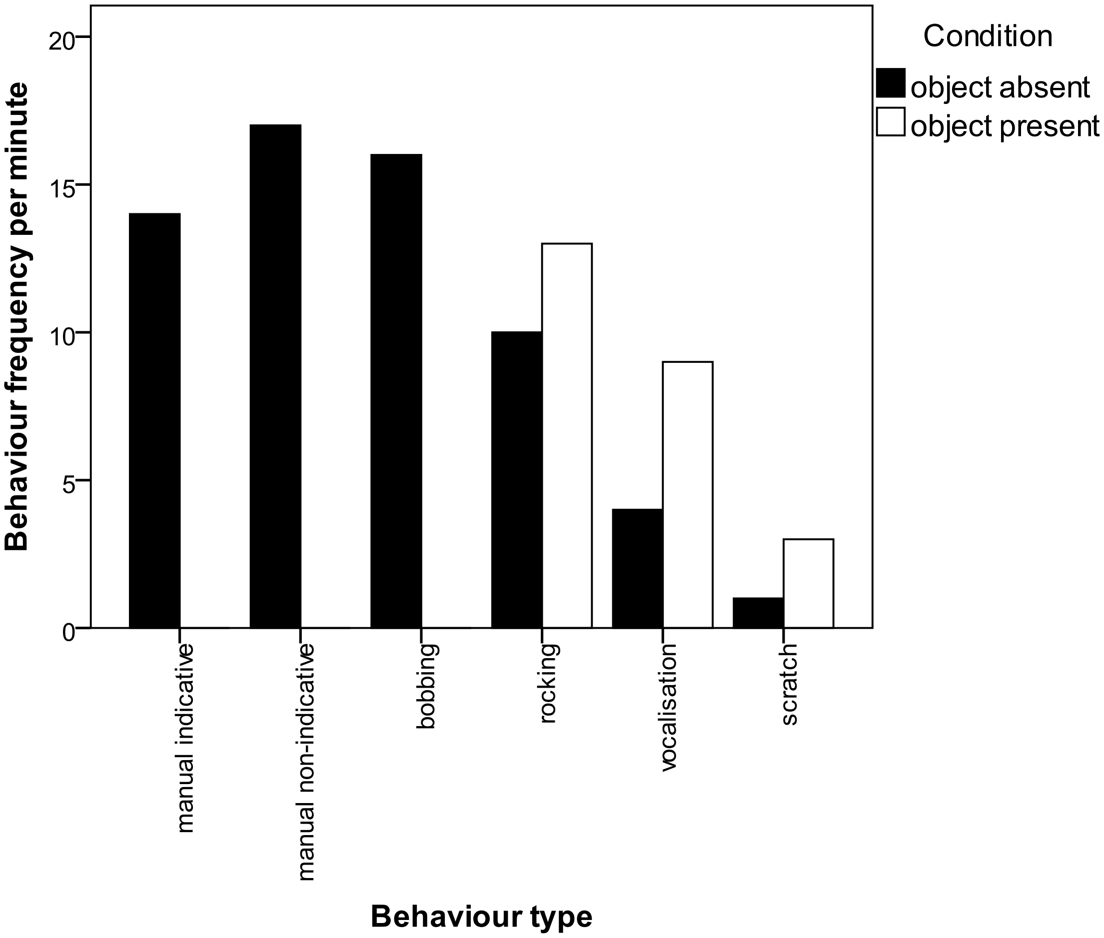
Figure 5.5: Rates of behaviour in relation to visual attention by the experimenter for Sherman trials



Influence of object presence

Figure 5.6 presents the rate of all communicative behaviours in the object hidden and object found phases. There were sufficient data to produce this figure only for Panzee’s trials because Sherman’s trial did not lead to a successful outcome (i.e. the item was not successfully located). This figure shows a higher rate of indicative manual gestures, non-indicative manual gestures and bobbing during the object hidden section of the trial than following a successful outcome. In contrast, rates of scratch, vocalisations and rocking behaviour were higher in object found condition.

Figure 5.6: Rates of behaviour categories per object in absent and object found conditions for Panzee



Influence of distance to object

There were differences between chimpanzees in the rate of indicative manual gestures such as pointing when the experimenter was close to the object, compared to when the experimenter was far from the object. Panzee had a significantly higher rate of manual indicative gestures when the experimenter was far from the object (*Mdn* = 60), than when the experimenter was close to the object (*Mdn* = 0, Mann-Whitney U test: U=262.5, z = -5.01, p <0.001, r = -0.54). However, for Sherman this difference in the rate of indicative manual gestures between object far from experimenter (*Mdn* = 0) and object close to experimenter conditions (*Mdn* = 0) was insignificant (Mann-Whitney U test: U=198.5, z = -0.591, p = 0.581, r = -0.08).

The opposite pattern of results was found for manual non-indicative gestures in relation to distance between experimenter and the object. Panzee had a significantly lower rate of manual non-indicative gestures when the experimenter was far from the object (*Mean* = 0), than when he was close to the object (*Mean* = 32.2, Mann-Whitney U test: U=484, z = -2.87, p =0.005, r = -0.30). However, for Sherman there was no significant difference in the rate of non-indicative manual gestures when the experimenter when far from the object (*Mean* = 74.8), as compared to when experimenter was close to the object (*Mean* = 32.2, Mann-Whitney U test: U=182, z = -0.798, p = 0.433, r = -0.11).

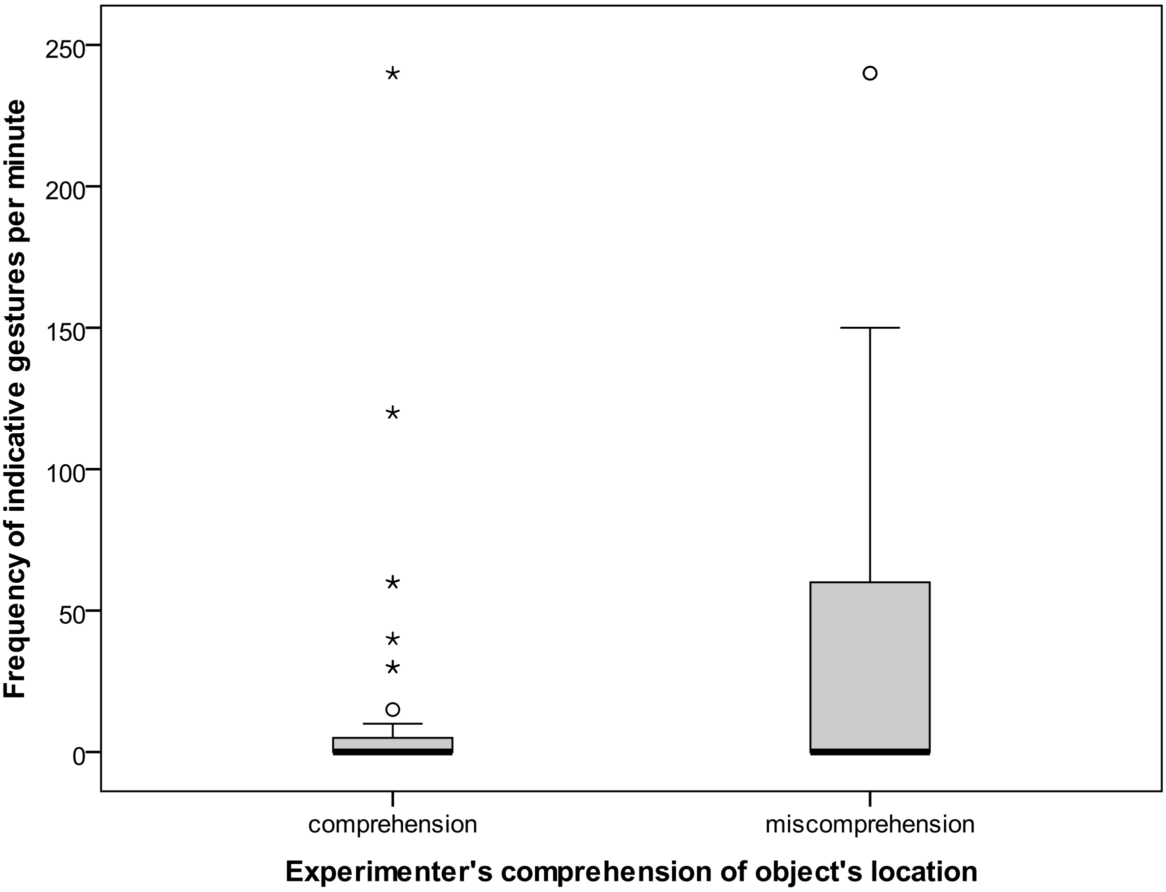
Similarly, when comparing frequency of non-indicative gestures other than manual gestures (such as bobbing, rocking and vocalisations), the rate was lower when the experimenter was further away from the object as opposed to when he was close. However, none of these differences were significant for Panzee (Mann-Whitney U test: U=667, z = -0.295, p = 0.772, r = -0.03, *Mean* object close = 51.9, *Mean* object far = 48.6) or for Sherman (Mann-Whitney U test: U=211, z = -0.199, p = 0.849, r = -0.02; *Mean* object close = 2, *Mean* object far = 3).

Influence of experimenter’s comprehension

There were differences between chimpanzees in the rate of indicative manual gestures when the experimenter comprehended the object’s location, compared to when the indication of the object location by the experimenter was wrong (see Figure 5.7). Panzee showed a significantly higher rate of manual indicative gestures when the experimenter miscomprehended the object’s location (*Mdn = 0*), compared to when experimenter’s pointing indicated comprehension (*Mdn = 0,* Mann-Whitney U test: U=688, z = -2.005, p =

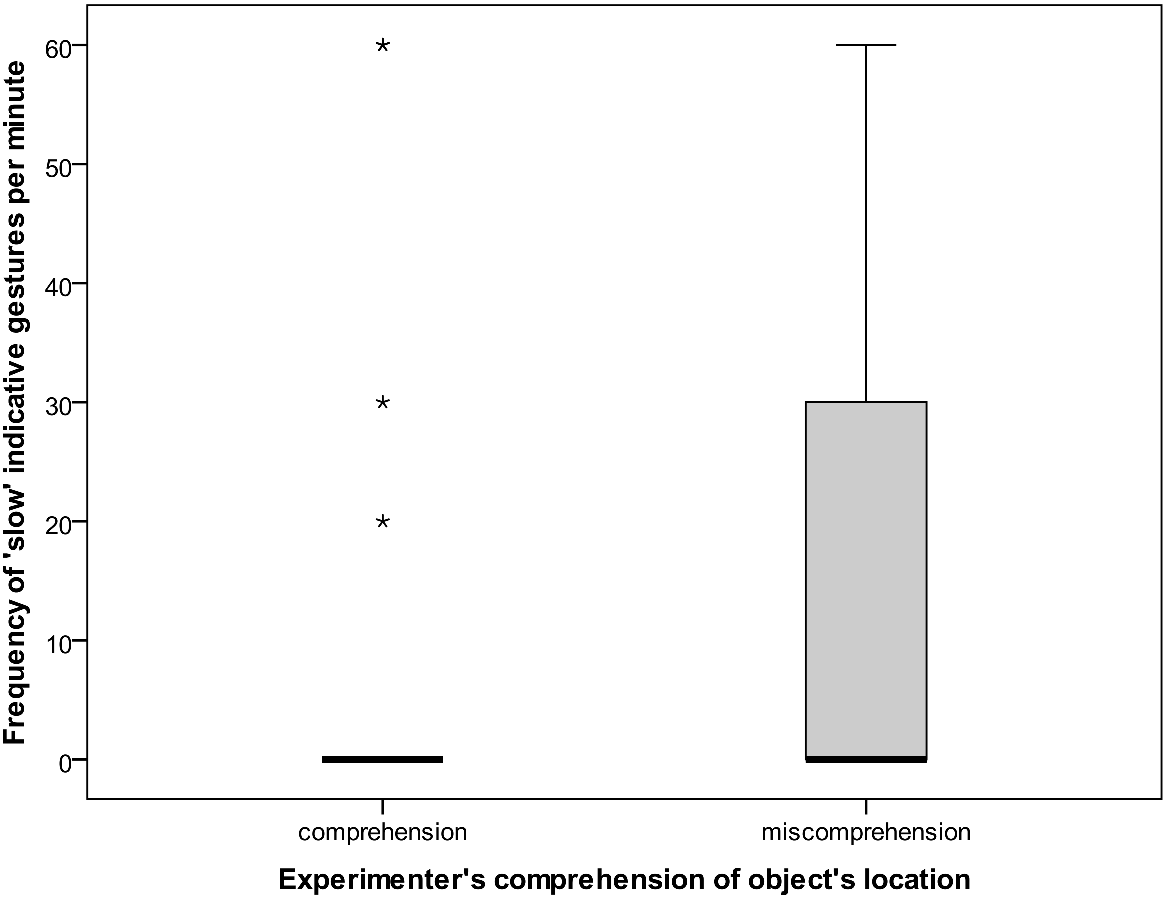
0.045, r = -0.21, see Figure 5.7 for median rates of indicative gestures per experimenters' state of comprehension). However, for Sherman there was no significant difference in the rate of indicative manual gestures between right (*Mdn = 0*) and wrong comprehension by the experimenter (*Mdn = 0,* Mann-Whitney U test: U=226, z = -0.489, p = 0.675, r = -0.07).

Figure 5.7: Median rates of indicative gestures per experimenters' state of comprehension for Panzee



Additionally, there were differences in the type of indicative gestures used by the chimpanzees in relation to the experimenter's comprehension, i.e. the experimenter's comprehension of the direction and distance to the hidden object. Chimpanzees used slow pointing gestures to correct the experimenter's understanding of direction (see Figure 5.8). Panzee used slow pointing gestures more frequently (*Mean* = 12.72) when the experimenter misunderstood the direction in which object than when he pointed in the right direction (*Mean* = 5.90, Mann-Whitney U test: U=726, z = -2.03, p = 0.046, r = -0.22). However, for rates of rapid pointing, this difference between experimenter's correct (*Mean* = 21.28) and incorrect comprehension of object's direction (*Mean* = 12.39) was not significant (Mann-Whitney U test: U=832, z = -0.888, p = 0.383, r = -0.09).

Figure 5.8: Median rates of 'slow' indicative gestures per experimenter's state of comprehension of direction of object's location for Panzee trials



On the other hand, chimpanzees used rapid pointing gestures to correct the experimenter's understanding of the distance to the hidden object. When the experimenter misunderstood the distance to hidden object, Panzee used rapid pointing more frequently in order to correct miscomprehension (*Mean* = 39.47), than when the experimenter pointed in the right direction, or past the object's location (*Mean* = 9.85, Mann-Whitney U test: U=456, z = -2.78, p = 0.004, r = -0.30). For slow pointing gestures, there was no significant difference between correct responses (*Mean* = 8.48) and misunderstanding of the distance to the hidden object (*Mean* = 13.42, Mann-Whitney U test: U=529, z = -1.39, p = 0.195, r = -0.15).

Moreover, there were differences in the morphology of hand and arm positions used when correcting the experimenter's comprehension of the distance to the hidden object. When the experimenter's pointing indicated that the object was closer than where it was actually hidden, chimpanzees corrected this miscomprehension by directing their pointing gestures vertically up in terms of arms, forearms and fingers more frequently (*Mean* = 46.5) than downwards (*Mean* = 6.32, Wilcoxon signed rank test, T = 11, p = 0.023, r = -0.50, see Figure 5.9). Additionally, when the experimenter's pointing indicated that the object was further away than where it actually was, chimpanzees used gestures positioned horizontally or down more often (*Mean* = 19.35) than pointing gestures which were positioned upwards (*Mean* = 0.97, Wilcoxon signed rank test, T = 3, p = 0.012, r = -0.45, see Figure 5.10).

Figure 5.9: Median rates of 'upward' indicative gestures per experimenter's state of comprehension of distance at which object was located on Panzee trial

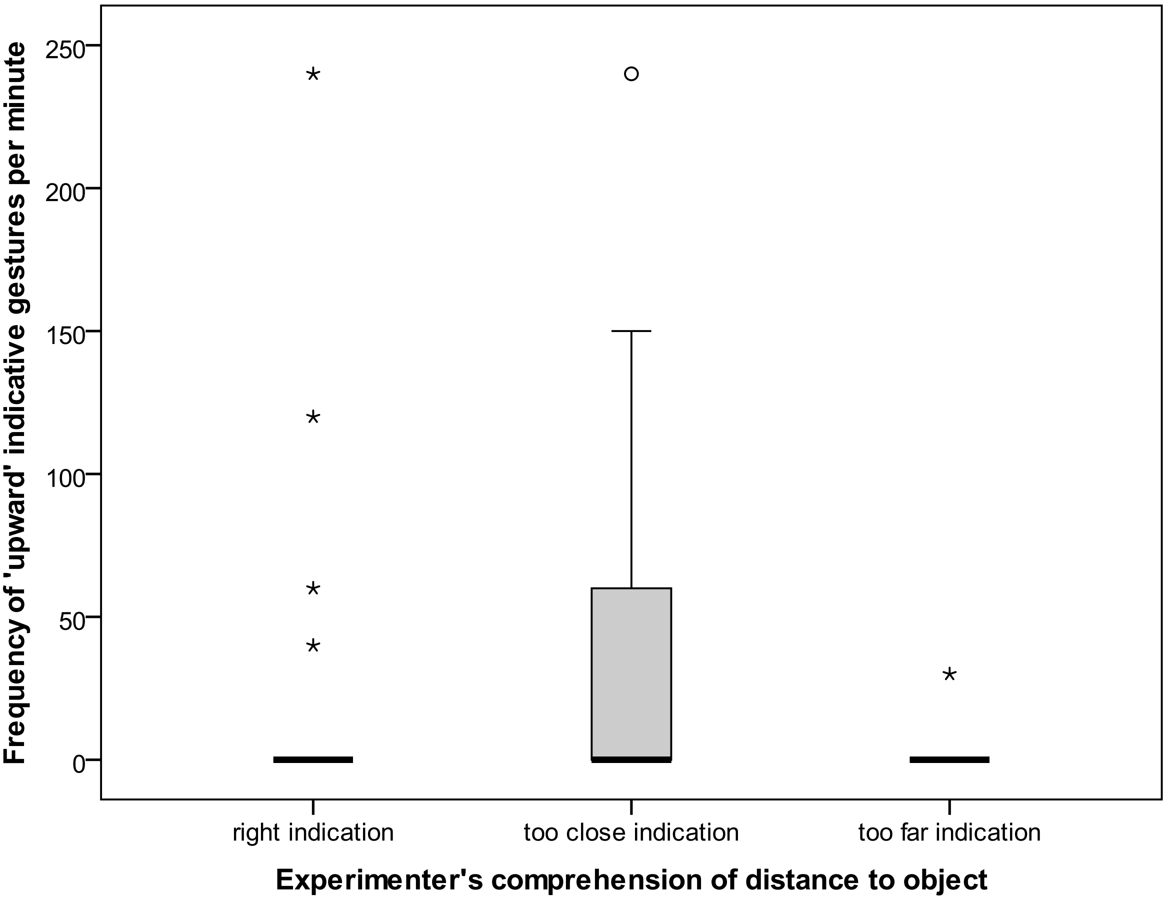
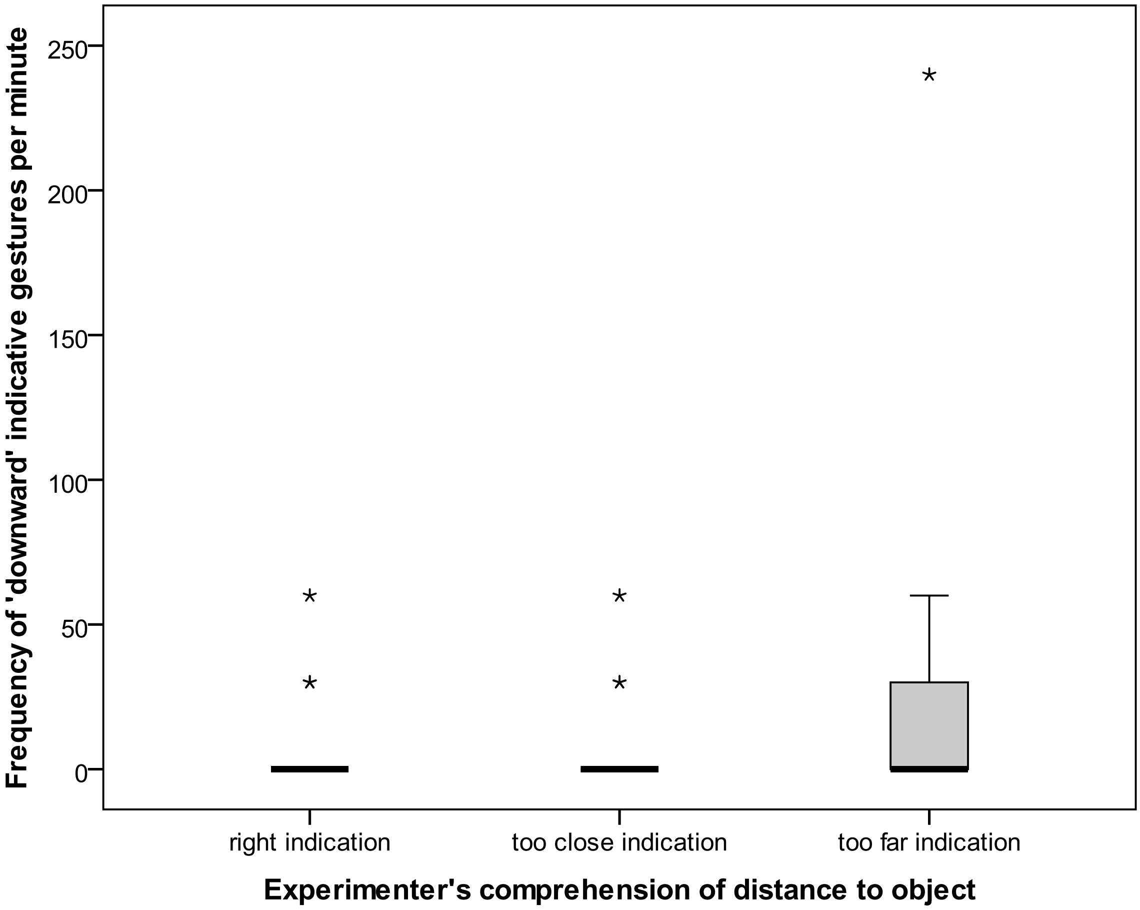


Figure 5.10: Median rates of 'downward' indicative gestures per experimenter's state of comprehension of distance at which object was located on Panzee trial

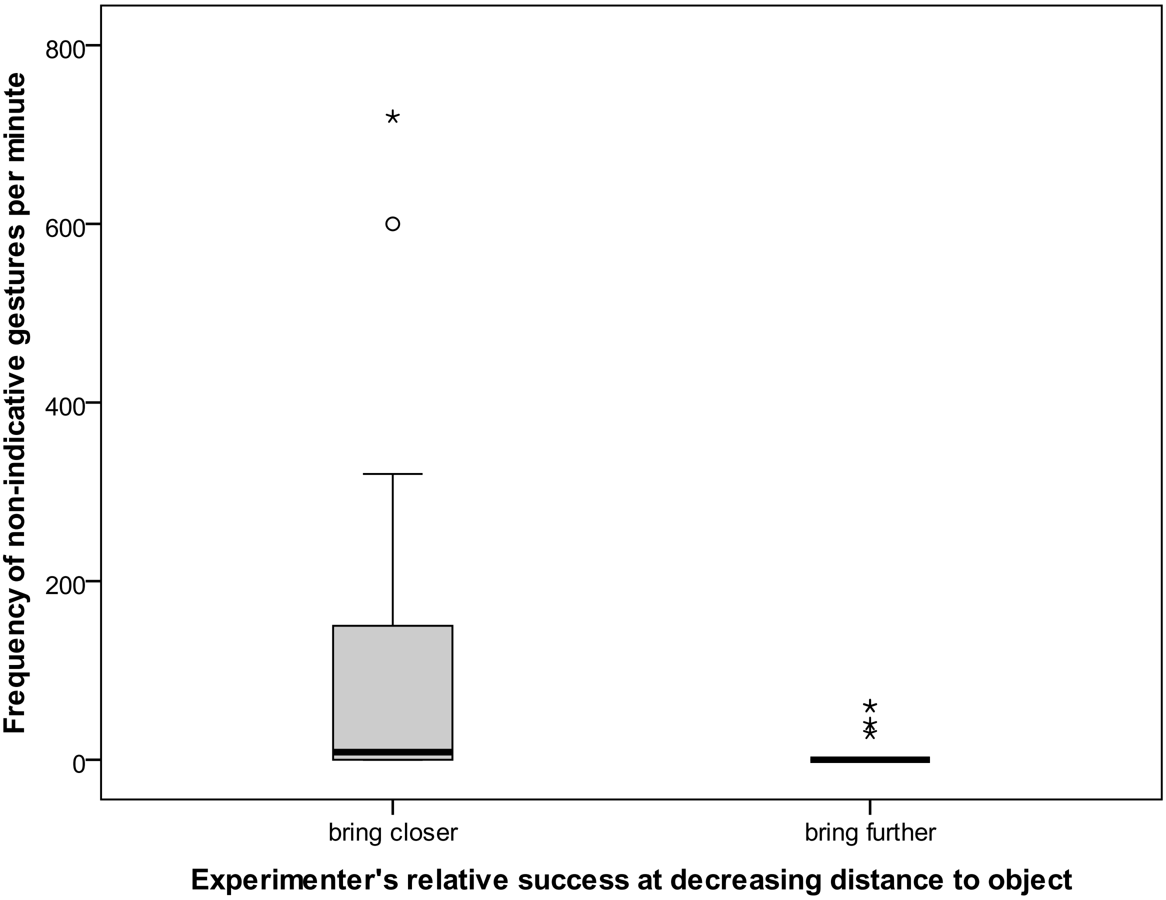


For Sherman, none of the differences between rate of slow and rapid pointing and experimenter's direction and distance comprehension were significant (rate of slow pointing vs. experimenter comprehension of direction: comprehension right, *Mean* = 0, comprehension wrong, *Mean* = 0.05; Mann-Whitney U test: U=238, z = -0.766, p = 1, r = -0.11; rate of rapid pointing vs. experimenter comprehension of direction: comprehension right, *Mean* = 0, comprehension wrong, *Mean* = 1.03; Mann-Whitney U test: U=238, z = -0.766, p = 0.1, r = -0.11; rate of slow pointing vs. experimenter comprehension of distance: comprehension right, *Mean* = 0.04, comprehension wrong, *Mean* = 0; Mann-Whitney U test: U=117, z = -0.387, p = 0.1, r = -0.05; rate of rapid pointing vs. experimenter comprehension of distance: comprehension right, *Mean* = 0, comprehension wrong, *Mean* = 5; Mann-Whitney U test: U=100, z = -2.5, p = 0.130, r = -0.38). Similarly, there were no differences between rates of high and low pointing gestures in relation to the experimenter's distance comprehension for Sherman (experimenter point too close: *Mean* upwards = 0, *Mean* downwards = 5, Wilcoxon signed rank test, T = 0, p = 1, r = -0.40; experimenter point too far: *Mean* upwards = 0, *Mean* downwards = 0.06, Wilcoxon signed rank test, T = 0, p = 1, r = -0.51; experimenter point at right distance: *Mean* upwards = 0, *Mean* downwards = 0, Wilcoxon signed rank test, T = 0, p = 1, r = 0)

A contrasting pattern of results was found for non-indicative gestures which displayed a degree of voluntary control by the chimpanzee, i.e. manual and bobbing gestures. Panzee did not display a significantly higher rate of non-indicative gestures when the experimenter comprehended object location (*Mean* = 68.2), compared to when his pointing indicated miscomprehension (*Mean* = 42.5, Mann-Whitney U test: U=737, z = -1.544, p = 0.124, r = -0.16). Similarly, Sherman did not discriminate in his non-indicative gestures between the experimenter's comprehension (*Mean* = 79.5) and miscomprehension (*Mean* = 55.7, Mann-Whitney U test: U=205, z = -0.755, p = 0.458, r = -0.11).

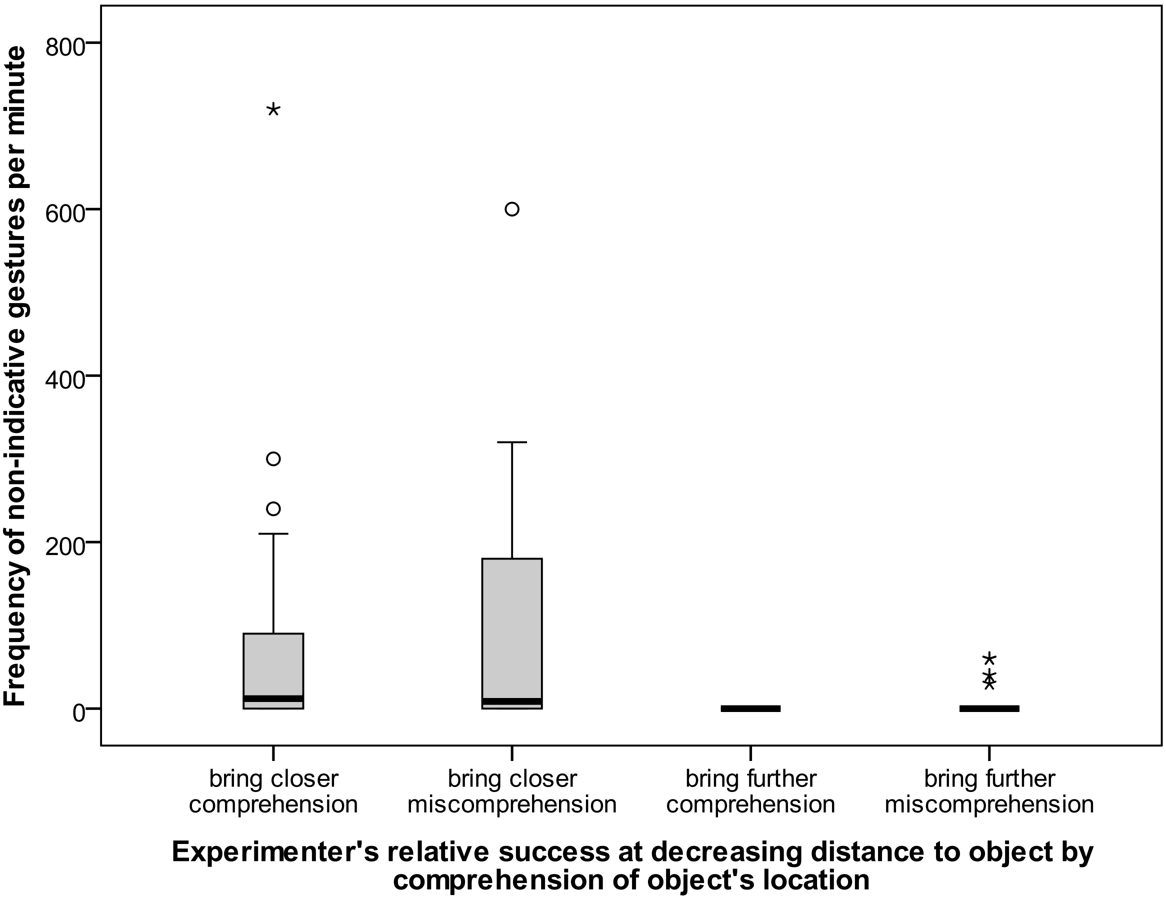
Instead, chimpanzee non-indicative gestures appeared to indicate the right steps that the experimenter needed to take in order to achieve the goal of the interaction. Panzee displayed a significantly higher rate of non-indicative gestures when the experimenter pointed towards a location bringing him closer to the goal (*Mdn* = 8.5) relative to pointing towards a location that would lead him further away (*Mdn* = 0, Mann-Whitney U test: U=507, z = -4.043, p < 0.001, r = -0.43, see Figure 5.11). For Sherman however, the difference in the rate of non-indicative gestures between bringing closer (*Mdn* = 46.6) and further away (*Mdn* = 50) actions was not significant (Mann-Whitney U test: U=250, z = -0.310, p = 0.763, r = -0.04).

Figure 5.11: Median rates of non-indicative gestures per experimenter's relative success at decreasing distance to object on Panzee trial



Moreover, Panzee's differential use of non-indicative gestures in relation to the experimenter's success in getting closer to the goal occurred regardless of whether the experimenter's pointing gesture indicated his comprehension or miscomprehension of the object's location (Kruskal-Wallis test, H(3) = 16.6, *p* = 0.01, see Figure 5.12). Mann-Whitney post-hoc tests (set at 0.025 significance level with Bonferroni correction) revealed no differences in the rate of non-indicative gestures during bringing closer and bringing further conditions in relation to experimenter's state of comprehension about the object's location. There was no significant difference in rate of non-indicative gestures during bringing closer condition whether the experimenter comprehended (*Mdn* = 12) or miscomprehended the object's location (*Mdn* = 8.5, Mann-Whitney U test: U=260, z = -0.216, p = 0.835, r = -0.03). Similarly, there was no significant difference in rate of non-indicative gestures during bringing further condition whether the experimenter comprehended (*Mdn* = 0) or miscomprehended the object's location (*Mdn* = 0, Mann-Whitney U test: U=81, z = -0.917, p = 0.592, r = -0.15).

Figure 5.12: Median rates of non-indicative gestures according to the experimenter's success at decreasing distance to and comprehension of the object's location on Panzee trial



Whilst Panzee used non-indicative manual gestures to signal the experimenter's success at getting closer to the goal, there was no such signalling apparent in manual indicative gestures when the experimenter pointed towards a location bringing him closer to the goal (*Mean* = 26.4) compared to bringing him further away (*Mean* = 26.6, Mann-Whitney U test: U=796, z = -0.942, p = 0.349, r = -0.10). Similarly, Sherman did not show a difference in indicative manual gestures usage between bringing closer (*Mean* = 4.24) and taking further away phases (*Mean* = 6.31, Mann-Whitney U test: U=246, z = -0.583, p = 0.626, r = -0.08).

DISCUSSION

The results of this research suggest that language trained chimpanzees have the ability to communicate referentially and intentionally using gestures to indicate the location of a hidden object in relation to an experimenter's actions. They displayed sensitivity to the visual attention of the experimenter and persisted and elaborated in their communication to specifically inform the experimenter.

The results of this study indicate individual variation between the two chimpanzees in hand positions used when pointing. Sherman displayed higher rates of open hand with all fingers extended and together whereas Panzee displayed more index finger pointing. Leavens and Hopkins (1998) found that whole hand extension was more common in captive chimpanzees than index finger pointing, and suggested that training in linguistic communication with lexigrams (geometric symbols arranged on a panel) may specifically shape pointing behaviour to involve the index or other single finger. However, despite an extensive history of language training, Sherman did not display any index finger pointing towards the object hidden in the surrounding parkland, suggesting that language training does not necessarily result in pointing with the index finger. This is in contrast to the claim that language-trained chimpanzees 'point overwhelmingly with their index fingers' (Leavens et al., 2005a p. 187). One potential reason for these divergent findings may be that the hand gestures of the chimpanzees in this study relate more closely to other species typical gestures, such as food begging gestures, rather than gestures shaped by lexigram training.

There was individual variation between the two chimpanzees in terms of accuracy of direction of pointing. Panzee pointed significantly more to the hidden object than to the experimenter or objects in their environment. This suggests that these pointing gestures are specific and indicate the location of distal entities relative to the recipient. Previous studies have examined pointing in relation to an object only in very close proximity to the chimpanzee (Leavens et al., 2004). In the current study, the objects were hidden some distance away from the chimpanzee, so the pointing had to be very specific to enable the uninformed person to find them. The results show that as well using pointing to indicate desire to obtain a food item, chimpanzees use pointing to specifically direct an uninformed person to a hidden object some distance away. On the other hand, Sherman pointed consistently in a direction other than object's location. This suggests that Sherman may not understand pointing gestures as a means of directing the attention of the experimenter. More trials are required to test this, including successful trials in which the food item is found.

Furthermore, there appear to be differences between the two chimpanzees' pointing, namely in arm position aiming upwards or horizontally or down. This variation may be related to the distance between the chimpanzee and hidden object. For Sherman's trial, the hidden object was closer, whereas on Panzee's trials the objects were hidden further away. Sherman used horizontal points exclusively whereas Panzee showed a higher rate of vertical up points in both trials. In previous research on pointing (e.g. Leavens et al., 2005a, Russell et al., 2005, Call and Tomasello, 1994) the object was hidden at a consistent distance and in close proximity to the chimpanzee. To our knowledge, none of the previous studies reported variation in arm position of pointing gestures displayed. In our study distance to the hidden object varied, and so did the types of pointing gestures displayed. Additionally, Panzee used different types of pointing gestures depending on distance of the experimenter to the hidden object. When the experimenter was far from the object, Panzee used upward gestures significantly more often. In contrast, when the experimenter was close to the object, Panzee used downward gestures more frequently. These results suggest that pointing gestures made by Panzee were able to make distinctions such as ‘near’ and ‘far’ and therefore possessed the capacity to make referential distinctions that deictic words can make.

Furthermore, there was a significant difference in the rate of indicative manual, non-indicative manual and bobbing gestures displayed when the experimenter was looking at the chimpanzee, compared to when the experimenter was not looking. This suggests that the chimpanzees were using manual and some bodily gestures with the intention to communicate about the location of the hidden object. This is further supported by the higher rate of manual and bobbing gestures in object hidden compared to object found trial phases. This is in accordance with previous work on gestures such as pointing in chimpanzees (see e.g. Leavens et al., 2004; Leavens and Hopkins, 1998) and supports the prediction that these gestures are intentional attempts to communicate the location of a hidden object to the experimenter.

Manual indicative gestures increased in relation to the experimenter’s distance to the hidden object, the number of manual non-indicative gestures and bobbing gestures declined. It is possible that there was element of arousal in non-indicative gestures and bobbing gestures, in anticipation of discovery of the hidden object. However, it seems more likely that as the experimenter’s distance to the object declined, his pointing gestures became more specific and accurate about the location of the hidden object. Other data show that manual non-indicative and bobbing gestures were used by the chimpanzees to indicate the experimenter’s success at decreasing distance to the object (see section on experimenter’s comprehension further in the text).

The rates of auditory and dynamic behaviours such as scratch, vocalisations and rocking appeared inconsistent; these did not increase when the experimenter was not visually attending. This pattern of results suggests that the chimpanzees were not using these auditory and dynamic behaviours in order to attract the experimenter’s attention. These results contrast with earlier studies which examined frequency of auditory behaviour in relation to the attention status of the chimpanzees (Leavens et al., 2004; Hostetter et al. 2001). One potential reason for the divergent findings is that in the present study the uninformed experimenter’s attention alternated between looking towards and away from the chimpanzee; attention getters may not have been necessary for the chimpanzees in this study. In contrast, in previous studies, the experimenter simply faced away from the subject for the whole condition, and thus the use of attention getters in this context is more warranted. This may indicate that the chimpanzees in the present study distinguished between when the experimenter’s attention is temporarily elsewhere and when the use of attention getters is required. This could be tested in future studies by using the same methodology as in Hostetter et al. (2001) in the present context, to examine whether chimpanzees are able to distinguish between when the experimenter’s attention is alternating between themselves and elsewhere (present study) and when it is oriented elsewhere throughout the condition.

A second explanation for the lack of attention getting behaviour could be that there was no need to alert the experimenter to a change in gestural behaviour by the chimpanzee. Chimpanzees in our study pointed relatively consistently in one direction throughout the trial. Alternatively, it may be that scratches, rocking and vocalisations may indicate involuntary expression of excitement rather than an intentional attempt to communicate with the experimenter. This is supported by the significant increase in the rate of scratch, rocking and vocalisations when the object was found in comparison to when it was hidden, and a higher rate of these behaviours when the experimenter was close to the hidden object compared to when he was far. Thus, suggestions that chimpanzees employ auditory and dynamic communication tactically and intentionally should be treated with caution. This has implications for studies of persistence and elaboration, which have often included auditory and bodily gestures such as scratch and rocking (see e.g. Cartmill and Byrne, 2007a, Leavens et al., 2005a). These results suggest that only manual and certain bodily gestures may be intentional behaviours, and future studies should focus on these behaviours when examining evidence for elaboration and persistence in chimpanzee gestures. This could be further explored in similar studies including an experimenter unfamiliar with chimpanzee gestures, vocalisations and behaviour patterns, to examine whether chimpanzees would use these signals interchangeably when their usual communication strategies are less effective.

Panzee and Sherman differed in the strategies employed to direct the experimenter to the hidden object. For Panzee, there was variation between rate of indicative and non-indicative intentional gestures when the experimenter comprehended the object's location, as compared to when indication of the object's location by the experimenter was inaccurate. Panzee had a significantly higher rate of manual indicative gestures when the experimenter miscomprehended the object's location compared to when his pointing indicated comprehension. In contrast, Panzee did not have a significantly higher rate of non-indicative gestures when the experimenter comprehended the object's location as compared to miscomprehension.

Instead, Panzee displayed a significantly higher rate of non-indicative gestures when the experimenter pointed towards a location bringing him closer to the goal relative to pointing towards a location bringing him further away, regardless of his true comprehension of object's location. On the contrary, there was no such difference in manual indicative gestures of Panzee when the experimenter pointed towards a location bringing him closer to the goal as opposed to bringing him further away.

Moreover, there was variation between types of indicative gestures used by Panzee in accordance with experimenter's comprehension of direction and distance to the hidden object. When the experimenter misunderstood the direction in which object was located, Panzee used slow pointing gestures to correct him. In contrast, rapid pointing was more frequently used to correct the experimenter's comprehension of accurate distance to the object.

Finally, types of hand and arm positions used varied when correcting the experimenter's comprehension of distance to the hidden object. When the experimenter's pointing indicated that the location of the object was too close, Panzee directed her indicative gestures vertically up more frequently than downwards. In contrast, when the experimenter's pointing indicated that the experimenter's suggested location of the object was too far, Panzee used pointing gestures which were positioned horizontally or downwards more often than gestures positioned upwards.

Whilst Panzee showed flexible use of gestures to successfully guide the experimenter to the hidden object, Sherman was unsuccessful in his task and did not employ any of the tactics used by Panzee. One possibility may be that Sherman simply did not remember the location of the hidden object. However, research has shown that language trained chimpanzees could reliably remember locations of hidden objects on a spatial memory task (e.g. Menzel, 1999). Alternatively, Sherman did not understand how to use gestures flexibly to guide the experimenter and instead used simple repetition of a small range of gestures, regardless of the experimenter's actions. More trials of Sherman responses to the experimenter are necessary to explore the differences between Sherman and Panzee.

The results for Panzee clearly contrast with the behavioural tactics displayed by captive groups of apes not enculturated by language training. For instance, Leavens et al.

(2004) and Cartmill & Byrne (2007a) presented captive chimpanzees and orang-utans respectively with the problem where subjects had to request an out of reach food item from a human experimenter. They experimentally manipulated whether the requests were understood or misunderstood, and found that subjects modified their communicative tactics flexibly in that they continued to communicate when their intentions were not understood (i.e. there was a delivery of undesirable food item) and ceased any communication when their communicative intentions were understood (i.e. experimenter delivered a full quantity of the desirable food item). They also reported that subjects modified their communicative tactics in relation to the degree of comprehension, i.e. replaced original gestures with new gesture types when there was complete miscomprehension (i.e. there was a delivery of undesirable food item) and repeated gestures more often when there was partial miscomprehension (delivery of the half quantity of desirable food). In contrast, Panzee not only signalled miscomprehension but also comprehension by elaborating and persisting in her gesture use. She responded flexibly and simultaneously to various levels of miscomprehension about the object's direction and distance, at the same time communicating about the experimenter's success at decreasing distance to the object relative to his previous location.

One reason for these differences may be that Panzee's success required more flexibility in the use of intentional gestures and sensitivity to the experimenter's success and failure in locating the object, as the object was hidden some distance away and the experimenter was unaware of the object's location. In contrast, previous experiments have been much less interactive and required only that the subjects react to being presented with a visible food item which was more or less desirable. Panzee thus showed a greater degree of flexibility and specificity in her intentional gestures compared to non-language trained subjects. Whether these results would be replicated with other captive groups not enculturated by language training could only be established by testing such groups in an experimental design similar to that used in the current study.

In summary, the results of our research are clear: chimpanzees can communicate intentionally and referentially about objects in the external world. In agreement with previous studies, our research demonstrates that production of chimpanzee gestures is sensitive to the recipient's visual attention and chimpanzees flexibly persist and elaborate in their communication to achieve their communicative goals.

Furthermore, we demonstrate for the first time the referential function of pointing gestures, given variable distances to the hidden object. Previous studies have examined pointing in relation to an object in close proximity. Our study demonstrates that pointing gestures displayed at greater distance are highly specific about the object's location. Furthermore, our data suggest that chimpanzees can refer to distance of a hidden object such as 'near' or 'far' through position of an arm when pointing, and therefore posses the capacity to make referential distinctions that humans using deictic words can make. Earlier studies that examined pointing by chimpanzees suggested that the prevalent form of pointing in great apes is by the whole hand; other forms of pointing gestures, such as those with index finger extended, resulted from linguistic training and enculturation. Here we describe variable use of hand positions in language-trained chimpanzees and suggest that index finger pointing is not invariably predetermined by language-training.

Our research also examined the use of auditory and dynamic behaviours (other than bobbing); the results suggest that neither are these behaviours produced to attract the experimenter's attention, nor is their production sensitive to the recipient's visual attention. Although this finding is difficult to interpret given our experimental setup, we suggest that these gestures and vocalisations are an expression of emotional arousal rather than voluntary attempts at communication. This has implications for studies of intentional persistence and elaboration in communication, which have often included vocalisations and other gestures in the analyses. Thus, contrary to previous claims, the degree to which chimpanzees are able to intentionally persist in and elaborate their communication remains unresolved.

Finally, our research demonstrates the diversity of communicative tactics employed by language trained chimpanzees in directing an experimenter towards hidden object. Chimpanzees persisted in their use of indicative gestures to correct the experimenter's comprehension of the object's location. In contrast, chimpanzees repeated non-indicative gestures to acknowledge experimenter success at getting closer to the goal relative to his previous location. When correcting the experimenter's comprehension of the object's location, chimpanzees flexibly modified the morphology of their gestures. Chimpanzees used slow indicative gestures to correct direction miscomprehension, and rapid gestures to correct distance miscomprehension. Chimpanzee indication of distance to the object was further specified by modification of the elevation of the indicative gestures. When the experimenter's indication was too close, chimpanzees used upward indicative gestures, but if the experimenter's indication was too far, chimpanzees used downward indicative gestures. Earlier research that examined persistence and elaboration in gesture use suggested that the subjects only persist and elaborate in their communication when there is partial or complete miscomprehension. Here we showed that language trained chimpanzees signal both comprehension and miscomprehension. Additionally, they use more complex and more flexible tactics to guide and correct the experimenter's miscomprehension.

To conclude, the results of this study suggest that the gestural communication of language trained chimpanzees is underpinned by complex cognitive skills. The ways in which they responded to the experimenters' behaviour indicate that they were able to maintain a structured representation of where the food was hidden. Further, they understood what steps the experimenter needed to take in order to find the hidden food, and possibly were able to attribute goals and knowledge states to the experimenter when helping to guide him to the commonly desired goal - the food. A novel experimental approach was used in this study, in which the food was hidden some distance away and the experimenter was unaware of the location of the food. Thus whilst the results are difficult to compare directly with studies of communication in relation to food items in other captive chimpanzees, overall the results do suggest that chimpanzee cognition has been influenced by language training procedures. In particular, these cognitive skills were evident in the signalling of not just miscomprehension by the experimenter but also comprehension, and the use of pointing gestures that were specific with regard to the hidden object's location.

These data are the first to give systematic insight into intentionality underlying use of species specific gestures in language trained chimpanzees. Whilst our data set represents relatively small sample size, significant findings presented here indicate that language trained chimpanzees may be doing something really rather complex. Future studies may address communicative intentions underlying gesture use in larger sample of subjects to substantiate findings of this pilot research. In particular, examining how the process of flexible modification in the use of gestures, in light of a recipient's comprehension states, varies according to the life stage of the chimpanzee (infant, juvenile, sub-adult, adult) in subjects unexposed to language training may provide vital insight into complexity of cognitive skills underpinning these processes in relation to language training.

The results of this chapter are in preparation for publication:

Roberts, A.I.; Vick, S-J. & Menzel, C. Referential and intentional use of gestural communication in language trained chimpanzees

Chapter 6: General discussion

Overview

This thesis presents a systematic insight into the repertoire and the underlying role of intentionality in gesture use in wild and language trained chimpanzees. I aimed to explore homologous traits in the cognition underlying chimpanzee gestural communication and human language. Specifically, I aimed to examine complexity in the structure of chimpanzee manual gestures and provide evidence for intentionality in both the production and comprehension of gestural communication. The research presented here strongly suggests that chimpanzee gestural episodes are cognitively complex, in that they illustrate a priori awareness in the chimpanzees that others have goals and intentions different from one's own, a realisation that also marks the onset of verbal symbolic capacities in human development (Bates et al., 1979). Prior research on the repertoire of manual gestures has provided a descriptive repertoire of gestures in chimpanzees primarily reared in captivity - this current research advances the field further by undertaking a structural analysis of repertoire of manual gestures in chimpanzees in the wild. Additionally, prior research on the intentions underlying gestural communication in captive chimpanzees has suggested that they display sensitivity to the visual awareness of the recipient; the data within this thesis also support this interpretation for gestural behaviour in wild chimpanzees. This study of wild chimpanzees has shown that they flexibly use a multifaceted repertoire of manual gestures to influence the goals and comprehension states of their interactants. They displayed complex cognition as evidenced in their ability to interpret the meanings of gestures in a flexible way in light of the interactant's ultimate goals and intentions. The episodes of gestural communication in both wild and language trained chimpanzees support this interpretation of cognitive abilities and complexity in chimpanzee gestural communication.

Summary of findings

In Chapter Two, the focus was on identifying the repertoire and structure of wild chimpanzee manual gestures. The primary aim of previous studies was to provide a descriptive gesture ethogram, usually within the broader framework of all bodily movements in captive chimpanzee populations (see e.g. van Hooff, 1971, Tomasello and Frost, 1989, Tomasello et al., 1984, Liebal et al., 2004a, Pollick and de Waal, 2007). Whilst this approach is a useful basis for many behavioural studies, it is valuable to use a quantitative approach; there are potential biases inherent in the qualitative method, such as difficulty in deciding how to lump and how to split units of behaviour (van Hooff, 1971). Additionally, whilst descriptive ethograms of gestures can provide information about repertoire size and types of units of gestures present within a population, it is difficult to obtain any information about repertoire structure using a descriptive methodology (Bortz, 1993). However, it is important to understand the structure of the gestural repertoire because the level of gradation within the repertoire structure can provide an indication of the flexibility and cognitive abilities inherent in the production of gestures.

Here, I addressed this empirical gap by using a systematic quantitative assessment based upon the statistical determination of the units of gestures; at least 20 manual gesture types were identified in wild chimpanzees, including new gesture types not previously reported in the wild or in captivity. The repertoire of chimpanzee manual gestures was more graded than discrete, with morphology of the gesture types more clumped and overlapping than distanced greatly from each other. This indicates that while gestures have many morphological attributes, they display a lot of similarity in their morphological components, with just a few salient unique features and a low degree of distinctiveness. This is in contrast to the morphology of vocalisations which display a more distinct structure and which frequently co-occur with gestural communication. These findings suggest that the production of gestures is cognitively more complex than vocalisations because the high degree of grading is suggestive of flexibility and voluntary control over gesture production and perception. Thus, chimpanzees do not simply produce a relatively fixed number of discrete gestural signals, as with vocalisations, but instead make a flexible behavioural decision about the type and structure of the gesture to achieve their communicative goals. One possible alternative explanation to this pattern of flexible structure production could be that gestures are socially acquired and hence grading in gesture production would be observed to coincide with the gradient of relatedness and association (Tomasello et al., 1997). Future studies may address this question through exploration of intra and inter-individual differences in gesture morphology, within and across chimpanzee populations (see e.g. McGrew et al., 2001).

Chapter Three examined the intentional use of gestures from the signaller's perspective, i.e. whether signallers modify their use of gestures flexibly in light of the recipient's comprehension states. Whilst previous research in captivity examined intentionality in the use of gestures using experimental approaches and human interactants (see e.g. Leavens et al., 2005b, Cartmill and Byrne, 2007b); nothing is known about intentionality underlying use of gestures in wild chimpanzees, or how the communicative tactics of wild apes compare with captive populations in interactions between conspecifics. Here I examined how wild chimpanzees overcome misunderstandings and adjust their usage of manual gestures to ensure effective communication. Sequences of gestural communication were examined to address how the type, meaning and frequency of gestures within sequences varied in relation to the recipient's state of comprehension. Wild chimpanzees displayed complex communicative tactics when attempting to achieve their goals by use of different communicative means with homogenous meanings. They ceased communicative attempts when immediately successful in achieving their goal but persevered at gestural communication when misunderstood, by both substituting and repeating their original signals.

When the behaviour of the recipient was indicative of an only partially met goal, the chimpanzees repeated their original gestures more often, focusing on the original signals which had proven to work partially. On the other hand, when the recipient's behaviour was indicative of complete comprehension failure, chimpanzees avoided repetition. These results suggest that wild chimpanzees possess complex cognitive skills illustrated by their ability to recognise their desired goal state and to understand which necessary steps need to be taken to achieve these goals. Chimpanzee production of gestures is cognitively demanding because it requires possession of a priori awareness of the effects that the gesture will have on the recipients and possibly the attribution of mental states to the recipients when attempting to achieve the desired goals. Whilst these findings illustrate that chimpanzees view their recipients as autonomous agents who can be influenced by informative signals, it is difficult to confidently ascertain whether signallers' actions are based upon an understanding that the recipients possess specific states of comprehension, or whether they rely on a more simple understanding of their recipients' behaviours (Tomasello and Call, 1997).

Examining how the process of flexible modification in the use of gestures, in light of a recipient's comprehension states, varies according to the life stage of the chimpanzee (infant, juvenile, sub-adult, adult) may provide some further insights into the cognitive mechanisms underpinning these processes. If chimpanzees are able from a very early age to flexibly modify their use of gestures in this way, this may suggest a lower cognitive complexity than if the skill is only slowly developed through the life span. For example, infants' alarm vocalisations indicate that they initially over-generalise with respect to eliciting stimuli and only gradually learn to give appropriate responses to particular predators, indicating some fine-tuning of the alarm response (Fischer et al., 2002, Fischer et al., 2000). Similarly, the ineffective modification of gestural sequences in response to a recipient's miscomprehension by infant or juvenile chimpanzees may yield important insights into the complexity of these processes.

The aim of Chapter Four was to examine the intentional use of gestures from the recipient's perspective, namely the comprehension of gestural signals, where recipients not only understand the semantic content of a gesture, but also take into account the perceived goals of the signaller in deciding how to respond, i.e., the ability to infer the common cooperative goal of the signaller from the combination of gestural events and context (Grice, 1975, Levinson, 1983). Whilst previous research in captivity has explored the association between gesture and context (see e.g. Pika and Tomasello, 2002, Pika et al., 2005b, Pika et al., 2005a, Liebal et al., 2004b, Liebal et al., 2006), the current research has gone further in addressing fundamental questions about the recipient's comprehension. The data in Chapter Four indicate that while chimpanzees understood gestures specifically and inflexibly, they were also able to respond flexibly, by inferring the goal of the signaller from the combination of gesture and context. Whilst chimpanzees understood the signaller's ultimate goals, they also took their own interests into account when making decisions about cooperating and sharing this goal with the signaller. These findings suggest that gesture comprehension in wild chimpanzees is cognitively complex; recipients show a capacity to recognise the desired goal state of the signaller, by drawing and connecting information from relevant sources (i.e. both the gesture and the context) to model hypothetical situations. Thus, whilst gesture meanings themselves are fixed and formed by a simple association between a signal and preceding behaviour, the overall interpretation of the communicative event appears cognitively sophisticated and may require a complex understanding of the signaller's intentions.

Although the recipient's understanding indicates a capacity to entertain multiple states when inferring the signaller's goals and intentions, it is difficult to know whether wild chimpanzees act through simple association between the signaller's gesture and immediate and preceding behaviours, or whether they project goals and intentions onto the signaller. This is because when the immediate and preceding behaviours are identical to the signaller's intention, it is difficult to determine from the recipient's response whether they are responding to the behaviour or to the intention. If, however, the signaller's intention is different from that which may be inferred from their immediate behaviour, then this may allow an examination of whether the recipient responds to the signaller's behaviour, or their true intention. For example, an analysis of instances of deception in communication may reveal whether the recipients are responding to the behaviour (i.e. the gesture and its context), or the actual intention of the signaller. For example, Tanner and Byrne (1993) described an incident of deception in gorillas in which an individual's play face was concealed by covering the mouth with a hand – if the recipient acts on the intentions rather than the actions of the signaller, they might be expected to respond to the attempted concealment of the play-face with play behaviours. However, detecting deception in communication is difficult and such convincing descriptions are rare in the literature, making a more systematic study of this issue very challenging.

Chapter Five examined evidence for referential and intentional use of gestural behaviour in language trained chimpanzees. While previous research has examined the cognitive skills accompanying lexigram and sign language use in language trained apes (Patterson, 1978, Gardner and Gardner, 1969, Miles, 1990), very little is known how such instruction impacts on cognitive skills of chimpanzees in general, as displayed in their species typical communicative repertoire. This chapter examined whether language trained chimpanzees use gestures referentially and intentionally to guide a naïve experimenter to the location of an object, hidden in surrounding parkland. Language trained chimpanzees displayed complex communicative tactics not displayed by other chimpanzees when referring to location of the hidden object. Specifically, they displayed the ability to make referential distinctions that have not previously been reported in the use of gestures in any other captive chimpanzees. They also displayed specificity in their pointing gestures about the hidden object's location and were able to refer to a distance of a hidden object by indicating 'near' or 'far' through the position of their arm when pointing. These data suggest that language trained chimpanzees possess the capacity to make referential distinctions that humans are able to make using deictic words.

Additionally, language trained chimpanzees employed complex intentionality as evidenced in their communicative tactics when guiding the experimenter to the hidden object. They signalled both comprehension and miscomprehension to guide the recipient's efforts at attaining the commonly understood goal. The chimpanzees persisted in their use of indicative gestures to correct the experimenter's comprehension of the object's location and repeated non-indicative gestures to acknowledge the experimenter's success at getting closer to the goal relative to his previous location. When correcting the experimenter's comprehension of the object's location, chimpanzees flexibly elaborated the morphology of their indicative gestures; using slow indicative gestures to correct an inaccurate indication of direction and rapid indicative gestures to correct an inaccurate indication of distance. The chimpanzee's indication of the distance to the object was further augmented by modification of the elevation of the indicative gestures. When the experimenter's indication of distance was too close, chimpanzees used upward indicative gestures, however when experimenter's indication was too far, they used downward indicative gestures.

These findings suggest that language trained chimpanzees possess complex cognitive skills underpinning their gestural communication. They responded to the experimenter's behaviour in ways that suggest a structured representation of the object's hidden location. They understood the necessary steps to be taken by the experimenter, and were able to attribute goals and knowledge states to the experimenter when guiding him to achieve the commonly desired goal. Although the presence of these complex communicative abilities in language trained chimpanzees could be explained by use of a particular methodological approach, they nevertheless suggest that general cognitive abilities have been influenced by their experiences with language training procedures. Future research using comparable and suitably complex tasks with captive chimpanzees (reared under more standard conditions) would further clarify role of language training in shaping cognitive skills of chimpanzees.

Exploring homologies with human language

In summary, the findings of our research demonstrate that there is considerable cognitive complexity in chimpanzee gestural communication. Chimpanzees have a multifaceted and complex repertoire of manual gestures, which appears to be reproduced flexibly. There are somewhat prototypical gestures, within which there is variation, and between which the boundaries are not clear-cut but there is gradation apparent along several morphological components. Chimpanzee gestures do not appear to simply express emotions, but rather communicate intentionally about desires and actions that they want recipients to undertake. They persist and elaborate in communicative attempts when met with miscomprehension and adjust their communicative tactics to the comprehension states of their interlocutors. Chimpanzees comprehend gestures intentionally and do not just respond reflexively to the communicative attempts of the signaller. Specifically, they understand specific gesture meanings but accept and reject gesture requests flexibly in light of the signaller’s ultimate goals and intentions.

The fact that chimpanzees communicate flexibly and intentionally informs us about the complexity of cognitive abilities underlying gesture use in chimpanzees. It also enhances our understanding about which cognitive abilities underlying communication use are characteristic of Hominoidea more generally and which cognitive skills present during the evolutionary transition from pre-linguistic to linguistic communication were likely to have been exclusive to humans. The study of cognitive skills underlying the production of the repertoire and role of intentionality informs us about cognitive processes underlying language evolution; these skills are cognitively demanding features of human language which are prerequisite for infants' ability to acquire words (Bates et al., 1979).

The study of repertoire complexity informs us about the cognitive processes underlying language evolution because an ability to generate and flexibly reproduce a large and open ended vocabulary of signals is cognitively complex. The emergence of flexible signal production is necessary for human linguistic communication (Fitch, 2005). The cognitive skills underlying flexible signal production are crucial to language development in human infants because infants need to possess voluntary control over their signal production and a capacity to link visual and auditory output to corresponding motor outputs in order to be able to acquire spoken language (Jurgens, 1998). While the processes shaping the structure of chimpanzee manual gestures require further explanation, it nevertheless seems reasonable to assume that flexibility in the repertoire of manual gestures is an inherent feature of wild chimpanzee manual gestures, reminiscent of pre-linguistic human infants and as shown by the results reported within this thesis.

Moreover, the study of intentionality underlying communication use is important in illuminating the likely cognitive processes underlying language evolution. Intentionality is one of the most cognitively demanding features of human language and the emergence of communicative intentions is a foundational capacity required for the human ability to acquire words (Baldwin, 1995, Olson, 1993). The cognitive skills underlying intentionality are crucial to language development in human infants because infants need to understand one's own and other's goals and intentions before they can gain ability to acquire words (Baldwin, 1995, Olson, 1993). It is currently contentious whether human infants possess the cognitive skills required to understand self and others' minds, or whether they simply understand others' behaviour prior to acquisition of language (see e.g. Adamson, 1996, Adamson and Bakeman, 1985, Dunham and Dunham, 1995, Leavens et al., 2005b). Nevertheless, it seems reasonable to argue that the current research suggests that wild chimpanzee communication indicates a certain underlying capacity for secondary representation, similar to pre-linguistic children (see e.g. Golinkoff, 1993, Golinkoff, 1986, Bretherton and Beeghly, 1982, Shwe and Markman, 1997). For instance, the chimpanzees studied here displayed a high degree of awareness about how their signals function, evident in the understanding that as they emitted signals, these would have an effect on the recipient. The chimpanzees seemed to know what effect the signals should have on the recipient, as evidenced in monitoring and the employment of necessary steps to achieve the desired goal state when their efforts were met with misunderstanding. They perceived others as autonomous agents that could be influenced by one's informative signals, as shown by use of informative signals rather than physical force. They understood that others had comprehension states which could be moulded by one's communicative tactics, as shown by the use of specific communicative tactics in response to the perception of different states of comprehension in recipients.

Thus, these findings suggest that chimpanzees possess some cognitive skills considered to be necessary for language development, in terms of repertoire flexibility and intentionality. However, they lack some linguistic means, such as an ability to control vocal tract to produce vocal sounds. This is particularly evident with language trained apes, who despite being able to produce symbolic labels and syntactic forms with gestures (Patterson, 1978, Gardner and Gardner, 1969, Miles, 1990) are unable to produce words (see e.g. bonobo Kanzi, Savage-Rumbaugh, 1986). This suggests that the common ancestor of humans and chimpanzees would have possessed the cognitive skills necessary for language acquisition, and thus that the underlying cognitive capacity required for language acquisition is shared within Hominoidea. The presence of similar cognitive skills in both wild and language trained chimpanzees further supports the notion that the cognitive skills underlying communication in chimpanzees are not simply an acquired trait, resulting from language training or extensive contact with humans, but rather a shared capacity between humans, other apes and a common ancestor.

Explaining language evolution

The present data support the theory that gesture has played a key role in human language evolution (Corballis, 2003). Human language is unique in the animal kingdom because it depends crucially on linguistic symbols, which are produced and understood flexibly and intentionally by humans interacting with each other. Spoken language is not used by any other species in the natural environment (Burling, 1993, Hewes, 1973). When looking for the possible evolutionary roots of language, researchers first considered primate vocalisations. However, from a behavioural point of view there are more similarities between human and apes in terms of gestural communication (Burling, 1993, Hauser et al., 2002a, Fitch et al., 2005a, Hewes, 1973, Corballis, 2003). Data from this thesis shows that the capacity for flexible, intentional communication is not uniquely human and instead it is a synapomorphic trait within Hominoidea; chimpanzee gestural communication is produced flexibly and intentionally and they have some capacity to use language-like gestural expressions. These data on chimpanzee gesturing suggests that the evolution of human linguistic symbols may have been preceded by an ability to represent objects manually (Arbib et al., 2008) and also to manipulate the visual attention and comprehension states of recipients in order to ensure effective communication.

Whilst the present data render theories of the gestural origins of language more plausible (Corballis, 2003), it is also important to consider role of vocalisations. Chimpanzee vocalisations frequently co-occur with gestural communication (de Waal, 2003, Pollick and de Waal, 2007) and these display a more distinct structure as compared with more graded structure of manual gestures. The chimpanzee call-gesture system displays features that are homologous with our human speech-gesture communicative system. Although human gestures are more graded, human spoken language is more discrete and together gesture and speech convey the same idea unit at the same time (Kendon, 2004, Burling, 1993). Like human language, the chimpanzee call-gesture system is an inherently combined construct, whereby the message is conveyed through both auditory and visual means in a complementary way. It may therefore be reasonable to suggest that while gesture played a key role in language evolution, vocalisation evolved into language with support from gestural communication. For example, the more specific structure of vocalisations may have provided recipients with information about the specific emotional states of the signaller, while gestures indicated to the recipient precisely what the signaller wanted of them in light of this emotional state. This scaffolding of vocalisations by gestures might have provided recipients with an arena in which to interpret the meanings of vocalisations more broadly and a gradual attribution of specific meanings to vocalisations in light of the interpretation of the meanings of gestures. As humans gained neural control over vocal output, this scaffolding of vocalisations by gestures may have provided a starting point for a gradual move towards intentional communication in the vocal domain, as illustrated by today’s pivotal role of gesture in supporting human language.

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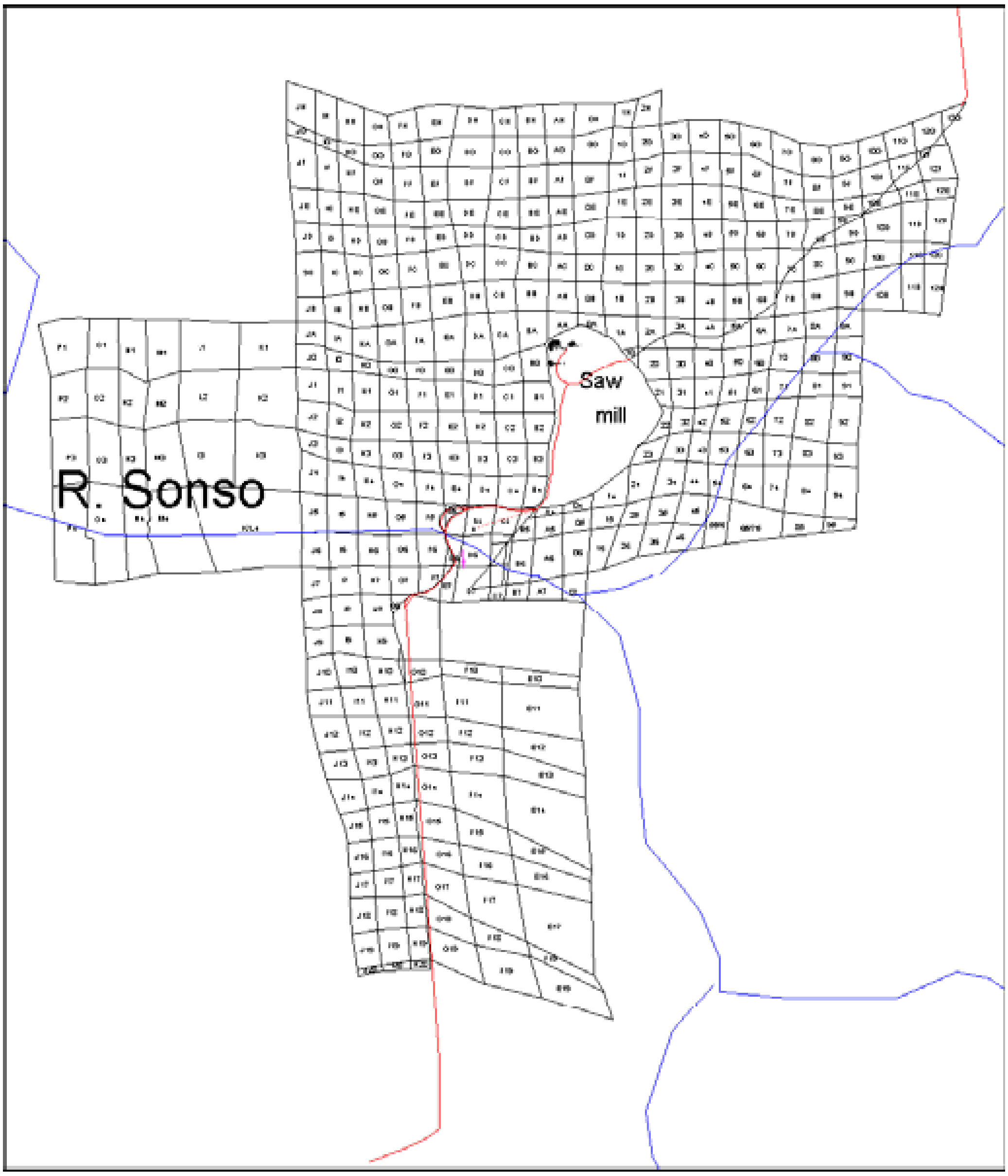
Appendix 1

Map of Uganda with indication of Budongo Forest reserve (from Slocombe, 2005).

Appendix 2

Map of the grid system at Budongo Conservation Field Station used to navigate the Sonso Community home range (from Townsend, 2009). Each block covers an area of approximately 100 m2, named by a letter and a number to assist navigation through the forest.



Roads and tracks

River Sonso

Budongo Conservation Field Station grid

Appendix 3

Details of Sonso Community Chimpanzees

Sonso Community Chimpanzees

(N.E Newton-Fisher & C.L. Davis June 2004; last update in December 2009 by Muhumuza Geresomu & Roman Wittig)

FEMALES & THEIR OFFSPRING

- *AN* **Anna** (90 ± 1 yr): crooked swelling, thin-bodied, paler face than Lola (~16 yrs) (first seen early 2003, named March 2006, formerly Stranger F)
- *BH* **Bahati** (Dec 94 ± 1 wk): *last seen in August 2009 (most likely emigrated to the East/South East)* upturned nose, pointy head like mother, puckered lips, small swelling when in estrous (= 11 yrs)
- *BN* *Banura (in or before 68): Last seen in June 07* .club right foot, balding, pointed ears (~ 38 yrs or older) (first identified Oct 20th 1993)
  - *ZF* **Zefa** ♂ (82 ± 6 mo)
  - *SH* *Shida ♀ (90 ± 1 yr): disappeared Sep 04*
  - *BT* **Beti** ♀ (1 Oct 96 ± 3 days): juvenile (= 10 yrs)
  - *BE* *Ben ♂ (13 Sep 01 ± 3 days – 01)*
  - *BD* *Banda ♀ (23 Oct 04 – 7 Nov 05)*
- *BC* **Beatrice** (76 ± 5 yrs): right hand missing, broad ears, short fingers (3rd and 4th on left hand) (first seen May 21st 2004, named April 2006, formerly Stranger H)
  - SQ **Squibs** ♂ (91 ± 1 yr) possibly son of Beatrice
  - BG **Birungi** ♀(March 04 ± 4 months)
- *BW* *Bwera (in or before 75)* (first identified April 28th 1992) (last seen with infant Biso August 9th 1994)
  - *BI* *Biso ♂ (90 ± 1 yr – 94)*
- *CL* **Clea** (86 ± 2 yrs): dark brown face w/ black circles under the eyes, slim, small head (~ 20 yrs) (first identified March 21st 1997 and named August 28th 1997)
  - *CT* **Clint** ♂(27 Apr 02 ± 2 days); (= 3 yrs)
- *EM* *Emma (Sep 91 ± 2 yrs):* light spotty face, immigrated in 97, disappeared Jan 03 (~15 yrs)
- *FL* **Flora** (in or before 79): missing RH from wrist, slit in right ear, splayed toes on right foot (~ 27 yrs or older) (first seen Jan 03 with FD and FK, formerly Stranger C))
  - *FD* **Fred** ♂ (94 ± 1 yr) (~12 yrs)
  - *FK* **Frank** ♂ (99 ± 1 yr): pale face and large ears (~ 7 yrs)
  - ?? *Unnamed/unsexed infant (04 Jun 05 ± 2 weeks – 25 July 05)*
  - *FA* **Faida** ♀ (Oct 06 ± 1 month)
- *GL* **Gladys** (76 ± 5 yrs): long body, size of Janie, wide vagina when swollen (~35 yrs) (first seen in Easter 2004 with juvenile GN, named in June 2006, formerly Stranger G)
  - *GN* **Gina** ♀ (96 ± 2 yrs)
  - GR **Goria** *unsexed* (06 ± *1 yr*)
- *HT* **Harriet** (in or before 78): black face, left ear slit, wrinkled cheeks, small bald patch, nervous, (~28 yrs or older) (first seen with infant HW Sept. 11th 1996)
  - *HW* **Hawa** ♂ (93 ± 1 yr) (~ 13 yrs)
  - *HL* **Helen** ♀ (Feb 01 ± 3 wks): (= 5 yrs,)
  - HY **Honey** ♀ (4 Oct 05 ± 3 days)
  - ?? ?? unknown sex (7 Nov 09 ± ? wks)
- *JN* **Janie** (84 ± 1 yr): black face, cresent-cut in right ear, long tufts of hair on lower jaw, droopy eyes (~22 yrs) (emigrated Sept. 28th 1995)
  - *JT* **Janet** ♀ (1 Oct 99 ± 3 days): juvenile, bold (= 6 yrs)
  - *??* *Unnamed ♂ infant (12 Jan 05 ± 1 week – 24 Jan 05)*
  - JS **James** ♂ (4 May 06 ± 1 month)
- *JL* **Juliet** (90 ± 1 yr)**:** left hand in permanent fist (snare injury) brown face, very large swelling when in full estrous (~16) (first seen Jan 02, named Jan 03, formerly Stranger D2)
  - *??* *Unnamed ♂ infant (13 Aug 09 ± 2 weeks – 13 Aug 09) Infanticide by NK, NB and NR*
- *KL* **Kalema** (79 ± 1 yr): hooked right hand w/o hair, pointy head, brow hairs below bald patch, grey beard (~28 yrs) (first identified April 28th 1992)
  - *BH* **Bahati** ♀ (Dec 94 ± 1 wk): uptumed nose, pointy heads like mother (= 11 yrs)
  - *KM* **Kumi** ♀ (17 Sep 00 ± 2 days): pointy head, small for age (= 5 yrs,)
  - ?? *Unnamed/unsexed infant (22 Sept 05 ± 7 days – 30 Sept 05)*
  - *KC* **Klauce** ♂ (5 Sept 06 ± 2 days)
- *KY* **Kewaya** (83 ± 1 yr): deformed/wasted RH, close set eyes, heavy brow ridge (~23 yrs) (first identified April 28th, 1992)
  - *KA* **Katia** ♀ (30 Dec 98, exact): big ears, confident (= 8 yrs)

Sonso Community Chimpanzees

(N.E Newton-Fisher & C.L. Davis June 2004; last update in December 2009 by Muhumuza Geresomu & Roman Wittig)

	??	*Unnamed/unsexed (July 05 ± 2 weeks – 25 Nov ± 3 weeks)*
	KX	**Kox** ♀ (7 April 07, +/- 2 months)
KG		**Kigere** (in or before 1976): missing right foot (~ 30 yrs or older) (first identified March 11th, 1992)
	KD	*Kadogo ♂ (90 ± 6mo – 99)*
	??	*Un-named (97, born prematurely, and dead)*
	KE	**Keti** ♀ (1 Sep 98 ± 1 wk)
	KI	**Kuki** ♀(16 Sep 03 ± 3 days)
	KP	**Kaspa** ♀(28 Oct 08 ± 1 wk)
KU		**Kutu** (in or before 79): left ear slit horizontally, high up. (~ 27 yrs or older) (first identified August 8th, 1992)
	KT	**Kato** ♂ (Sep 93 ± 1 mo): close-set eyes, large brow ridge, subadult (~ 13 yrs) [Non-Sonso father]
	KN	**Kana** ♀ (29 Oct 98 ± 1 day): oval-shaped eyes, black marking under left eye, juvenile
	KS	**Kasigwa** ♂(15 Aug 03 ± 2 wks): prominent bald patch
	KH	**Kathy** ♀ (28 Jul 08 ± 3 days)
KW		**Kwera** (in or before 81): long, brown, spotted face, "crew cut" hair style, slim, large ears (~ 25 yrs or older) (first identified August 5th, 1992)
	KZ	**Kwezi** ♂ (14 Jan 95 ± 2 wks): subadult, sharp eyes, long face, long hair on sides of face (~ 11 yrs)
	KR	**Karo** ♀ (1 Nov 01 ± 1 day) (= 4 yrs)
	KB	**Karibu** ♀ (9-10 Jan 07)
LL		*Lola (88 ± 1 yr – 15 Jan 08 ± 1 week): dark face, face is squeezed like Mukwano, skinny (~18 yrs) (first seen 2003, named on 9 May 2005)*
MM		*Mamma (in or before 1970 – 99): large body size, hairy* (first seen June 1995 with MH, last seen August 13th, 1998)
	MH	*Muhara ♀ (85 ± 1 yr – 01)* (last seen Aug 01)
MT		*Matoke (62 ± 5 yrs – 93)*
	TT	*Toto ♂ (88 ± 1 yr)*
ML		**Melissa** (1975±*5 years*): wrinkled face w/ white scars, brown back/legs, ear tufts (~ 24 yrs or older) (first seen Sept. 26th 2001 with MR)
	MR	*Mark ♂ (97 ± 1 yr – 2007): white beard, juvenile (~9 yrs) [Non-Sonso father]*
	??	*Un-named (02, still-born)*
	MN	**Monika** ♀ (13 July 03 ± 2 wks)
	MB	**Mbotella** ♂ (14 Jan 09 ± 3 wks)
MK		**Mukwano** (80 ± 3 yrs): small brown face w/ black spots, tufted hair on back of neck, balding head (~ 26 yrs) (first identified April 28th, 1992)
	MD	*Monday ♂ (Nov 02 ± 1 mo – 03)* (last seen May 2nd 2003)
	??	*Unnamed/unsexed infant* (2 July 06 ± *1 day: killed on 2 July 06 infanticide*)
	MI	**Marion** ♀ (11 Nov 07 ± 1 month)
NB		**Nambi** (in or before 62): Buddha belly, balding, small slit in left ear (~ 44 or older) (first identified June 21st 1994)
	MU	*Muga ♂ (77 ± 1 yr – 00)*
	AY	*Andy ♂ (82 ± 6 mo – 00)*
	MS	**Musa** ♂ (91 ± 6 mo): (~ 15 yrs)
	NR	**Nora** ♀ (Feb 96 ± 3 wks): juvenile, right hand snare injury (= 10 yrs)
	NT	**Night** ♀ (6 Feb 03, exact): (= 3 yr)
PL		*Polly (in or before 84): white scar on right arm; (~ 22 yrs or older) (first seen Jan 2003 with PS, formerly Stranger A, last seen Aug 2008 in weak conditions)*
	PS	**Pascal** ♂ (98 ± 1 yr): large ears and long hair (~ 8 yrs)
	PN	**Polina** ♀ (22 Oct 04 ± 1 month, most likely the 'lost baby' seen first on 25/10/2008)
RD		*Ruda (in or before 76 – 01)* (first identified Nov 1992, died January 29th 2001)
	BO	*Bob ♂ (90 ± 6 mo- Last seen July 07):* big ears, long face (~ 16 yrs) [Non-Sonso father]
	RE	**Rachel** ♀ (Jun 97 ± 1 mo): white beard, pointy ears (~ 9 yrs)
RE		**Rachel** (Jun 97 ± 1 mo): white beard, pointy ears, ('aged elf') travels with BO since orphaned (~ 9 yrs)
RH		**Ruhara** (1965 ± 5 years): grey hair, a most completely bald, large bodied (~ 38 or older) (first identified April 14th 1992)
	NK	**Nick** ♂ (82 ± 1 yr) (~ 26 yrs)
	GT	*Grinta ♀ (90 ± 1 yr – 99)*
	RS	**Rose** ♀ (15 Nov 97 ± 1 day): tanned face w/ pale lips, juvenile (= 8yrs)
	RM	**Ramula** ♀ (6 Sep 02 ± 1 wk)

Sonso Community Chimpanzees

(N.E Newton-Fisher & C.L. Davis June 2004; last update in December 2009 by Muhumuza Geresomu & Roman Wittig)

- *RF* **Rafia** ♀ (4th July 07 ± 2 wks)

SB **Sabrina** (in or before 81) (first seen with SL 2001 and named in April 2001)

- *SA* **Sally** ♀ (96 ♂1 yr): (~ 10 yrs)
- *SN* *Sean ♂ (Sept 02 ± 1 mo – 2007)*
- ST **Sharlot** ♀ (Jan 6th 07 ± 1 week)

SL *Salama (81 ± 2 yrs – ??, seen briefly 95 & 01)*

SR *Sara (?? – 00)* (first seen November 27th 1995, last seen February 29th 2000)

SE **Sarine** (71 ± 5 yrs): formerly Stranger I, brown legs like RH, hairy black arms like Black, big ears pointing to the side, brown hair in front of ears, looks like TK around the eyes, missing hair on the wrists (35 years) (first seen May 2004 with SM, named April 2006, formerly Stranger I)

- *SM* **Simon** ♂ (93 ♂ 1 yr) (13 yrs)
- *??* *Unnamed/unsexed infant (May 04* ± 1 month – Sept 05 ± 8 months)
- *SK* **Sokomoko** ♀ (Oct 06 ± 2 weeks)

SH *Shida* (90 ± 1 yr): missing left hand, right ankle snared, shy, disappeared Sep 04 (~ 16 yrs)

TJ **Tanja** (84 ± 5 yrs; named 01/03/09): formerly stranger E.

- *TP* **Tapura** ♀ (99 ± 2 yrs)
- *TM* **Tamara** ♀ (04 ± 2 yrs)

VR **Verena** (97 ± 1 yr: named on 30/11/08): formerly juvenile female moving with HT. She has fluffy side cheek beard, very dark face, formerly known as the 'juvenile female that is with Harriet' (she was seen occasionally in the west part of the home range since 2006).

VT *Vita (90 ± 1 yr – 98)*

WL **Wilma** (in or before 81): right hand missing, wart under right eye, (~ 25 yrs or older) (first seen Oct 16th, 2001 with WS, named Nov 2001)

- *WS* *Willis ♂ (96 ± 1 yr – 01)* (last seen Dec. 2001)

ZN *Zana (in or before 81-2007- 03 Aug 07):* both hands deformed, droopy lips (~ 25 yrs or older) (first identified Sept. 1992). Died 03-08-2007

- *ZL* **Zalu** ♂ (29 Jun 95 ± 3 days): sub adult (= 10 yrs, [Non-Sonso father?]
- *ZD* **Zed** ♂ (May 01 ± 1 mo): juvenile (~ 5 yrs)

ZM **Zimba** (in or before 68): broad ears, brown face, scrunched face (~ 38 yrs or older) (first identified August 11th, 1993)

- *KY* **Kewaya** ♀(83 ± 1 yr) [Non-Sonso father]
- *GZ* *Gonza ♀ (90 ± 1 yr – 02)* (last seen 2002, possible emigration)
- *ZP* *Zip ? (15 June 96 ± 2 wks – 96)*
- *ZG* **Zig** ♂ (24 Jun 97 ± 2 wks): large sticking out ears, thin limbs, snare injury on RH (~ 9 yrs)
- *ZK* **Zak** ♂: (21 Nov 02 ± 1 day): (= 3 yr,)
- *??* *Unnamed ♂ infant (08 Mar 09 ± 1 day – 19 Mar 09)*

MALES & THEIR OFFSPRING

AY *Andy (82 ± 6 mo – 00)* (body recovered July 20th 2000)

BK *Black* (74 ± 2 yrs – 20 Jan 05): long black hair covering body, small bald patch, white forehead scar (~ 32 yrs) (died after falling out of tree Jan 20th, 2005).

- *BH* **Bahati** ♀ (Dec 94 ± 1 wk)
- *NR* **Nora** ♀ (Feb 96 ± 3 wks)
- *KN* **Kana** ♀(29 Oct 98 ± 1 day)
- *CT* *Clint ♂(27 Apr 02 ± 2 days)*

BO *Bob (90 ± 6 mo- 07):* long, light face, big forward facing ears, hunched body (~ 16 yrs). Snare around middle finger right hand. Disappeared May 2007. [Mother = RD | Non-Sonso father]

BB *Bwoba (87 ± 1 yr – Feb 09): brown skin (most noticable on face), large jaw, bald patch, stocky (~ 19 yrs)*

BY *Bwoya (65 ± 5 yrs – 01)* (last seen Dec. 8th 2001)

CH *Chris (67 ± 3 yrs – 97)* (last seen Aug. 9th 1997)

DN *Duane (66 ± 2 yrs – 26/02/08): prominent brow ridge, grey back hair, pronounced dimples, slit in right ear, alpha until 2006. Died a sudden death (within 20 min) on 26/02/2008*

- *RS* **Rose** ♀ (15 Nov 97 ± 1 day)
- *KE* **Keti** ♀(1 Sep 98 ± 1 wk)
- *SH* **Shida** ♀ (90 ± 1 yr)

Sonso Community Chimpanzees

(N.E Newton-Fisher & C.L. Davis June 2004; last update in December 2009 by Muhumuza Geresomu & Roman Wittig)

  - *JT* **Janet** ♀ (1 Oct 99 ± 3 days)
  - *KM* **Kumi** ♀ (30 Dec 98, exact)
- FD **Fred** (94 ± 1 yr): large brown face, hands and feet are brown (~12 years) [Mother = FL]
- *GS* *Gashom (87 ± 1 yr – 26/02/08): brown face, small testicles, missing third finger, hairs on lower jaw (first seen 7/94, last seen 26/02/08 at dead body of Duane).*
- HW **Hawa** (93 ± 1 yr): long haired, very dark face, pale ears, line around nose (~13 yrs) [Mother = HT]
- *JK* *Jake (88 ± 1 yr – 95)* (first seen 9/94, immigrant with no mother, last seen Feb 4th, 1995)
- *JM* *Jambo* (78 ± 2 yr – 03) (found murdered in sugar cane May 6th 2003)
- *JG* *Jogo (88 – 94)* (first seen 11/92, last seen April 23rd 1994)
- *KK* *Kikunku (76 ± 1 yr – 98)* (last seen July 6th 1998)
  - *HW* **Hawa** ♂ (93 ± 1 yr)
  - *KA* **Katia** ♀(30 Dec 98, exact)
- *KT* **Kato** (Sep 93 ± 1 month): close set eyes, large brow ridge, black spots on face, still with tuft (~13 yrs) [Mother = KU]
- *KZ* **Kwezi** (14 Jan 95 ± 2 weeks): sharp eyes, long face, long hairs on sides of face, dark muzzle (~11 yrs) [Mother = KW]
- *MA* *Maani (1965 ± 5 yrs – Aug 08) : long narrow face and body, grey back hair, white around nipples, chest scar (last seen Aug 08 in very weak conditions)*
  - *KR* **Karo** ♀ (1 Nov 01 ± 1 day)
- *MG* *Magosi (alpha until 94; died 99, approx. age: 50s??)* (body found July 4th, 1999)
  - *MU* *Muga ♂(77 ± 1 yr – 00)*
  - *NK* **Nick** ♂ (82 ± 1 yr)
  - *BB* **Bwoba** ♂ (87 ± 1 yr)
  - *GZ* *Gonza ♀(90 ± 1 yr – 02)*
  - *MS* **Musa** ♂ (91 ± 6 mo)
  - *ZG* **Zig** ♂ (24 Jun 97 ± 2 wks)
- *MO* *Mukono (1967 – 94)* (last seen Feb 12th 1994). First seen 1992.
- *MR* *Mark (97 ± 1 yr – 07): white beard, still with tuft, spots on face (~9 yrs) [Mother = ML]*
- *MU* *Muga (77 ± 1 yr – 00)*
  - *KZ* **Kwezi** ♂ (7 Jan 95 ± 3 wks)
- *MS* **Musa** (91 ± 6 mo): face darkening, tufts of hair stick out from face (~ 15 yrs) [Mother = NB]
- *MU* *Muga (77 ± 1 yr – 00)* (disappeared and presumed dead 2000)
  - *KZ* **Kwezi** ♂ (7 Jan 95 ± 3 wks)
- *NJ* *Nkojo (1968 ± 5 yrs)* (last seen Sept 29th, 2001)
  - *ZF* **Zefa** ♂ (82 ± 6 mo)
  - *GS* **Gashom** ♂(87 ± 1 yr)
  - *RE* **Rachel** ♀ (Jun 97 ± 1 mo)
- *NK* **Nick** (82 ± 1 yr): long hairs on lower jaw, pink ears, 'elvis-syle sideburns', current alpha (~ 24 yrs) [Mother = RH]
- *PS* **Pascal** (98 ± 1 yr): large ears and long hair (~ 8 yrs) [Mother = PL]
- SM **Simon** (93 ± 1 yr): folds in both ears, dark face, same size as Hawa, no tuft (~13 yrs) [Mother = SE]
- SQ **Squibs** (91 ± 1 yr): protruding bottom lip, turgid testicles, brownish face (~15 yrs) [Mother = BC]
- *TK* **Tinka** (1960 ± 5 yrs) : hooked/wasted left hand, hooked right hand w/ hair loss, slow moving (~ 46 yrs)
- *VN* *Vernon (1965 ± 2 yrs – 99)* (last seen June 29th 1999)
- *ZT* *Zesta* (1980 ± 3 yrs – 98). (First seen 1993). Killed by BK and DN.
- *ZF* **Zefa** (82 ± 6 mo): stout build, dark brown face, cheek dimples, brown ears, thin hair (~ 25 yrs) [Mother = BN]
- *ZL* **Zalu** (29 Jun 95 ± 3 days): left ear is damaged, face looks like Bahati, long hair by side of face like Nick, 'tattooed' face (11 yrs) [Mother = ZN]

OFFSPRING WITH UNKNOWN PATERNITY

Birungi
Frank
Fred
Helen
Honey
James

Kasigwa
Kuki
Mark
Monika
Night
Pascale
Polina
Ramula
Sally
Sean
Simon
Squibs
Zak
Zalu
Zed

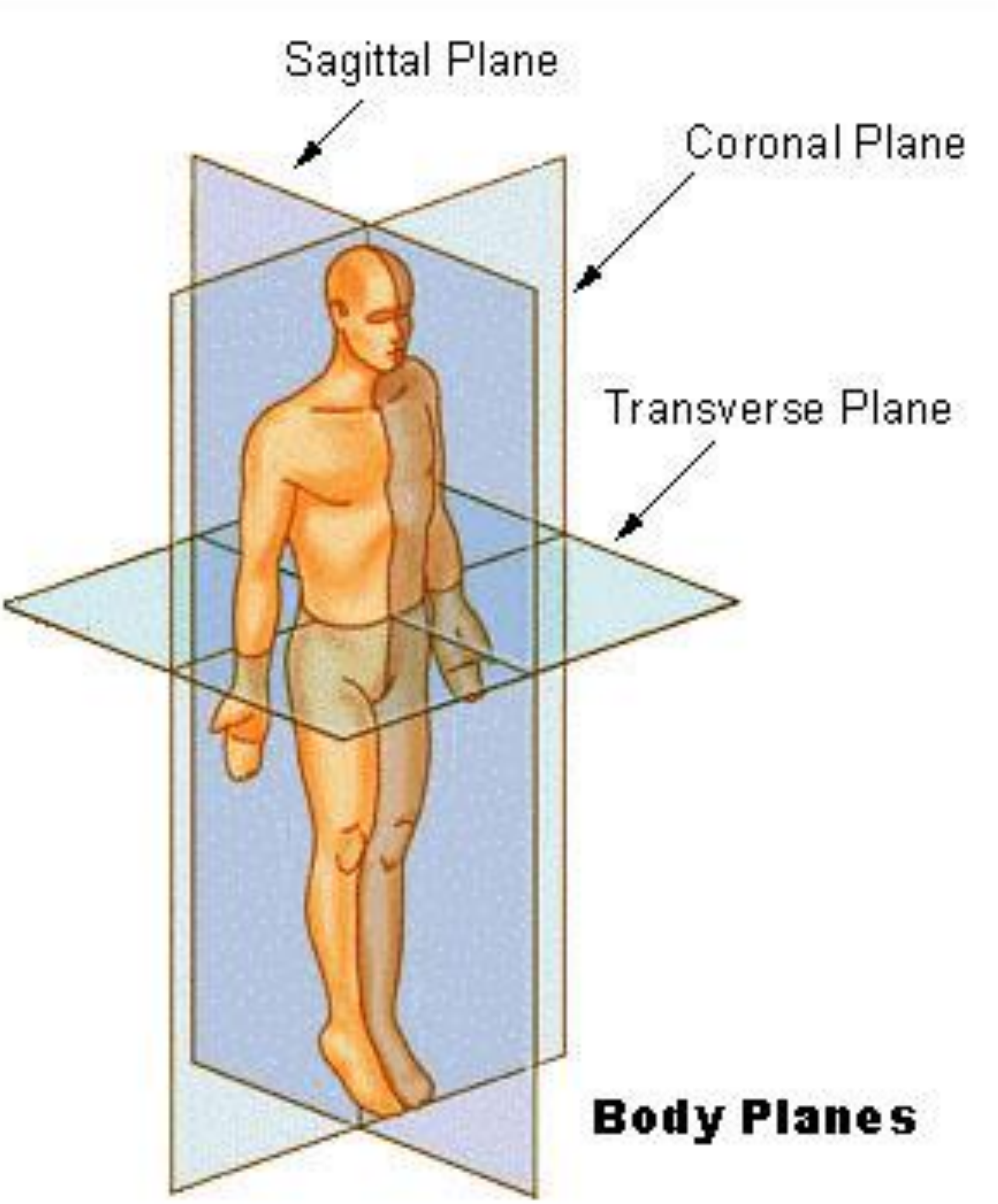
Appendix 4

Focal subjects and their known offspring. Ages for focal subjects and offspring are as of March 2008.

Name	**Abbreviation**	**Sex**	**Age (years)**	**Known offspring, gender and age in years**	**Number of observation hours**
Nick	NK	Male	26		18
Bwoba	BB	Male	21		16.9
Musa	MS	Male	17		15.2
Squibs	SQ	Male	17		16.23
Kato	KT	Male	15		18.1
Hawa	HW	Male	15		18.46
Nambi	NB	Female	~46	Musa, Male, 17 Nora, Female, 12 Night, Female, 5	15.8
Zimba	ZB	Female	~40	Kewaya, Female, 25 Zig, Male, 10 Zak, Male, 5	18
Ruhara	RH	Female	~43	Nick, Male, 26 Rose, Female, 10 Ramula, Female, 5 Rafia, Female, 9 months	18.9
Melissa	ML	Female	~33	Monika, Female, 4	18
Kwera	KW	Female	~27	Kwezi, Male, 13 Karo, Female, 6 Karibu, Female, 1	15.23
Kutu	KU	Female	~29	Kato, Male, 14 Kana, Female, 9 Kasigwa, Male, 4	17.76

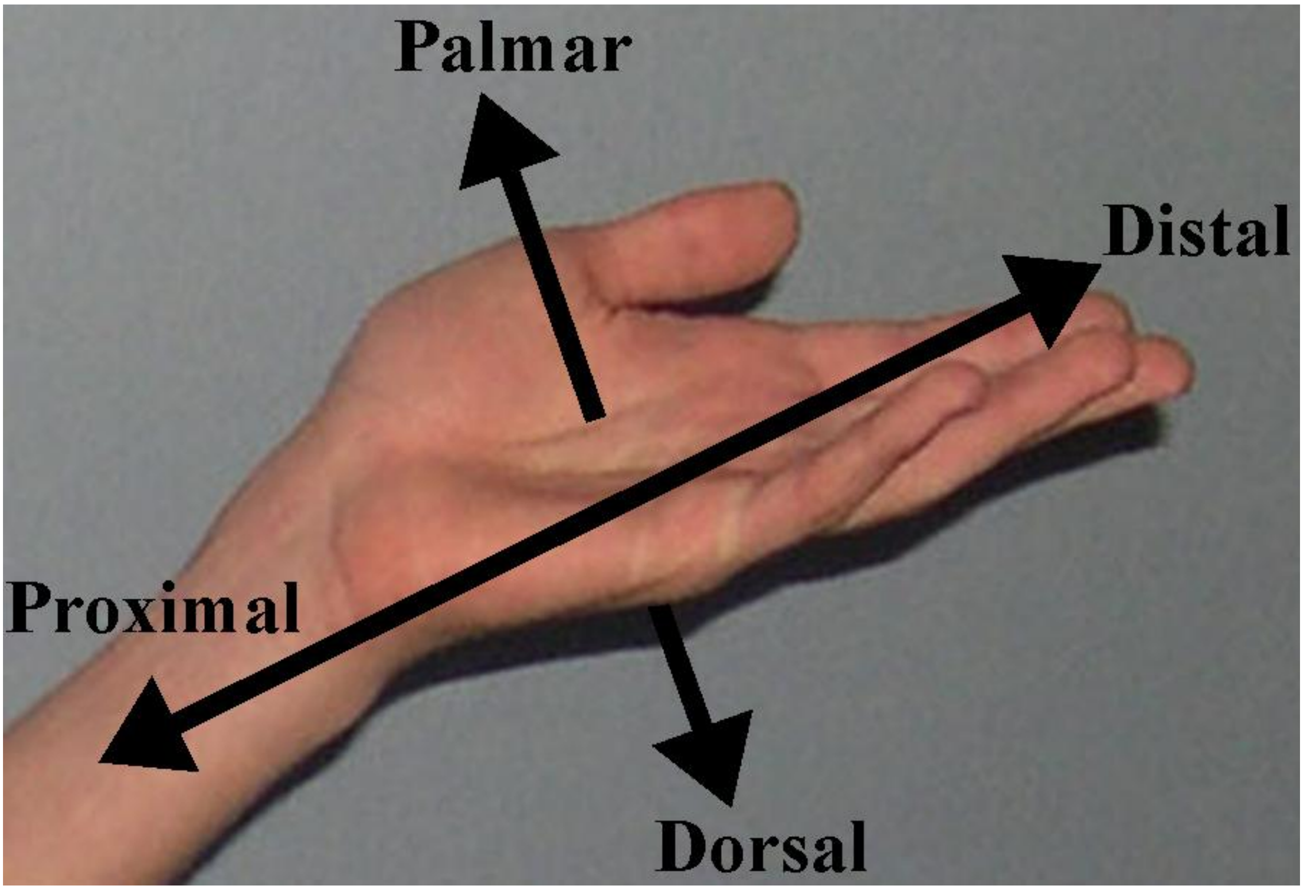
Appendix 5

Planes of the body



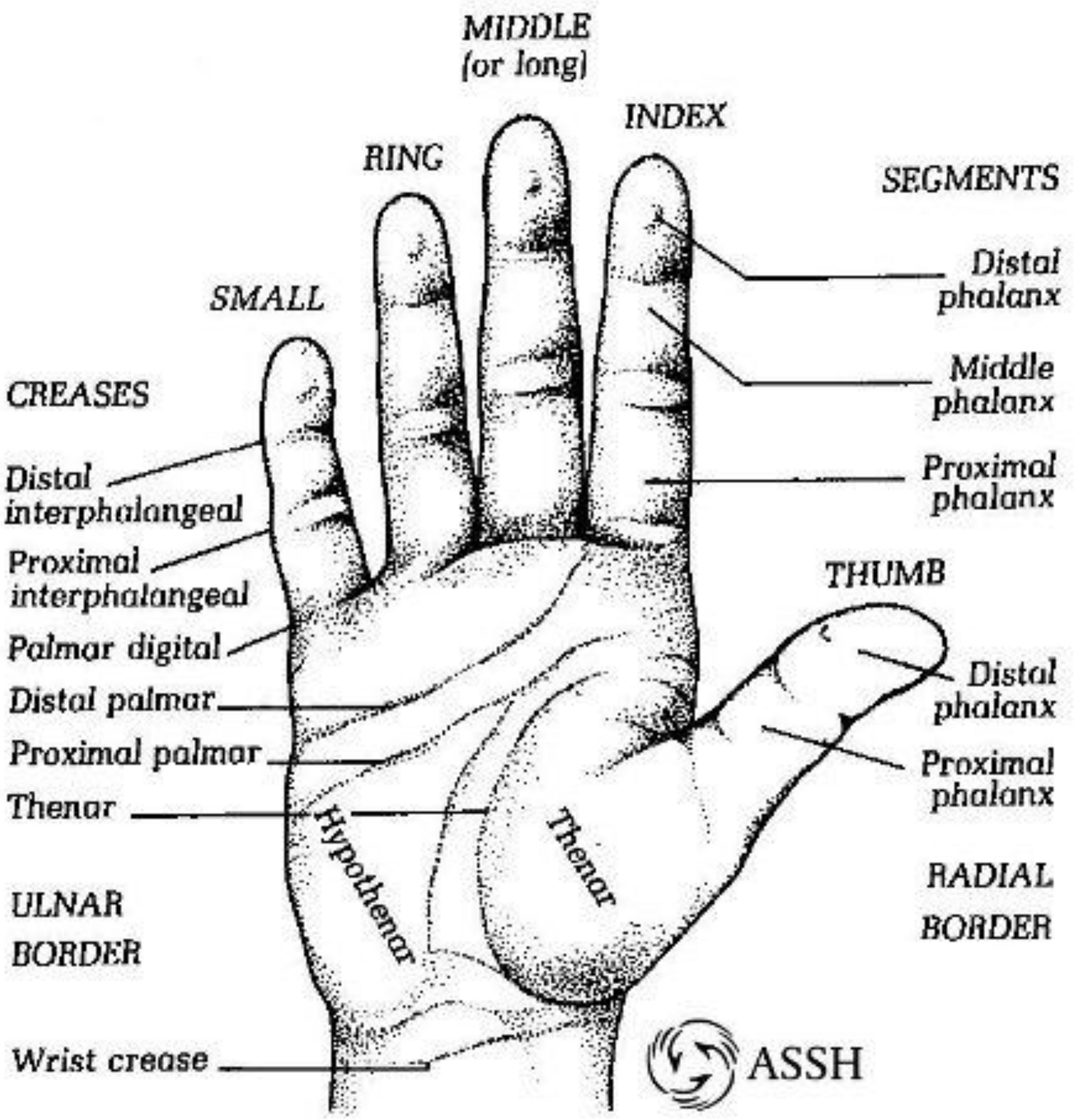
Appendix 6

Axis of arm



Appendix 7

Morphology of hand



Appendix 8

Matrix of observed pant-grunt vocalizations between adult females of Sonso community. Names of females given by initials; for full names see Appendix 3. Table from Newton-Fisher (2006).

	Performer																						
Recipient	NB	ZM	RH	ML	KY	BN	KW	KG	KL	JL	PL	JN	FL	HT	CL	KU	MK	SB	SH	WL	ZN	DV	Status
NB	—	2		3	1		3		4	5					4	3			1		1	0.79	Alpha
ZM		—			1				1	2					3	1	1					0.58	High
RH			—				1		1	2					1							0.46	High
ML				—	2					2					4				1			0.46	High
KY					—					1					2	1				1		0.46	High
BN		1			1	—				1												0.40	Medium
KW							—			2									4			0.32	Medium
KG								—							1	1						0.32	Medium
KL									—					1	2							0.32	Medium
JL										—						1						0.23	Medium
PL											—			2								0.23	Medium
JN												—										0.00	Low
FL													—									0.00	Low
HT														—								0.00	Low
CL															—							0.00	Low
KU																—						0.00	Low
MK																	—					0.00	Low
SB																		—				0.00	Low
SH																			—			0.00	Low
WL																				—		0.00	Low
ZN																					—	0.00	Low

Note. Status is assigned by DV score, the arcsine square-root of the proportion of individuals from which each female received pant grunts.

Appendix 9

Male dominance rank

Dominance value scores for adult males of the Sonso community.

Male	Dominance value score	Rank group
Nick	0.5	High
Duane	0.48	High
Zefa	0.48	High
Bwoba	0.45	High
Maani	0.38	High
Musa	0.2	Low
Bob	0.14	Low
Gashom	0.14	Low

Dominance values scores determined for each male by calculating the proportion of other males in the community from whom that male received a pant grunt vocalisation. Dominance value calculated as the arcsine of the square root of the proportion. Data from Townsend (2009)

Female dominance rank

See Appendix 8.

Appendix 10

Map of enclosure for language-trained chimpanzees. Dark lines indicate enclosures.