MEANING, SOCIALITY AND DIALOG IN BONOBO (*PAN PANISCUS*) GESTURAL COMMUNICATION: AN OBSERVATIONAL STUDY AT THE MILWAUKEE COUNTY ZOO

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Meaning, sociality and dialog in bonobo (*Pan paniscus*) gestural communication: an observational study at the Milwaukee County Zoo

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Abstract

Apes use gestures in an intentional and highly flexible manner. It has been proposed that human language originated in gestural communication and therefore ape gestures have been of great interest to primatologists and psychologists alike. The extensive, flexible and intentional nature of ape gestural communication may also provide new insights to the study of social regulation as large communicative systems are thought to be useful in navigating complex social landscapes. To date studies of bonobos and their use of gestures has occurred in limited contexts and therefore the known repertoire of bonobos is relatively small. It is also unknown as to what bonobos use gestures for and whether they use those gestures flexibly in order to regulate their social relationships.

To investigate these questions I studied a captive population of bonobos for 12 months at the Milwaukee County Zoo, Wisconsin, USA. Milwaukee bonobos used 55 gesture types over the course of the study period. I found that bonobos have particular goals behind their signalling and that bonobos used gestures consistently for specific goals and that the same gestures were used for the same goals across signallers. It was therefore possible to identify to meanings behind over half of the gestures within the bonobo repertoire. Even though the meanings of gestures were consistent across signallers, the age and sex of a signaller influenced what context and for what purpose he or she used gestural communication. Particular types of signallers used gestures for particular goals and directed those gestures towards particular recipients. Bonobos also used gestures within dialog during special circumstances in order to coordinate asymmetrical interactions. These results indicate that gestural communication is an excellent medium for investigating the influence a large, intentional and flexible communication system has on managing a complex social network.

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Chapter 1: Introduction

1.1 Origins of language

Mapping the evolution of language is of long-standing interest to the biological and psychological sciences. One theory states that language evolved from gestural communication (Arbib et al., 2008; Corballis, 2009). Although seemingly a counter-intuitive approach as human language is centred around speech, the gesture-origin hypothesis is supported by several lines of evidence from human research: infants begin gesturing before speaking (Petito and Marentette, 1991), humans employ manual gestures alongside speech (as evidenced even in blind speakers, expressing the fundamental ties of gesture to language: Iverson and Goldin-Meadow, 1998), and through the continued use of "extended" gestures such as written language and the more recent phenomena of cellphone texting (Corballis, 2009). Other researchers posit that language originated from the vocal tract (e.g. MacNeilage, 1998, Ghazanfar and Hauser, 1999), however any theory of language origin must compensate for how integral gestures are in our everyday use of spoken language and from evidence presented in primate communication. From our closest living relatives, the great apes, the gesture-origin hypothesis is supported by the highly flexible use of gestures as compared to their relatively inflexible use of vocalizations and facial expressions (Call and Tomasello, 2007; Pollick and de Waal, 2007). Flexibility, as I am using the term here, refers to the ability of a signaller to moderate her use of communicative signals in response to varying social, contextual and environmental circumstances. Apes use gestures intentionally and flexibly in that they direct gestures towards the audience, they adjust their use of gestures based on the audience's state of attention and they use multiple gestures within a single context and single gestures between multiple contexts (Tomasello et al., 1994; Genty et al., 2009;

Call and Tomasello, 2007). Flexibility is also a fundamental feature of language in that words are used freely between multiple contexts (Corballis, 2009) and can be combined to express an essentially endless range of concepts (Hauser et al., 2002). Therefore understanding how and why apes use gestures can potentially contribute to a better understanding of the roots of language evolution.

1.2 Gestural communication of apes

1.2.1 Intentionality in gestural communication

Gestural communication has been catalogued across ape species (including orangutans: Cartmill and Byrne, 2010; Liebal et al., 2006; chimpanzees: Hobaiter and Byrne, 2011; Tomasello et al., 1985; Tomasello et al., 1989; Tomasello et al., 1994; bonobos: Pollick and de Waal, 2007; and gorillas: Genty et al., 2009; Pika et al., 2003; Pika, 2007; and a comparative study of all great ape species: Call and Tomasello 2007). For the purpose of this study I define a gesture as "discrete mechanically ineffective physical movements of the body observed during periods of intentional communication" (Hobaiter and Byrne, 2011).

Apes use gestures intentionally: an ape will use a gesture with the express purpose of promoting a behavioural reaction in her target recipient. In studying the gestures of apes, researchers have set out strict guidelines for determining whether an ape is using a gesture intentionally (Tomasello and Call, 2007; Tomasello et al., 1994). First, the gesture must be directed towards another individual. As a third party observer a researcher is able to determine whether an ape is directing a gesture towards another individual by the orientation of her head (front of the face is oriented towards the recipient). Second, the signaller should appear to be seeking a specific goal: when signalling to another individual, the ape should appear to be waiting for a response and should the desired response not come, the ape should persist in signalling. Pika and Zuberbühler (2008) showed that juvenile bonobos have intention behind their use of gestures in a study of social games involving gestural communication. In this study, a subject bonobo engages with a familiar human caretaker in a social game of "throw the object": the human and the bonobo take turns in throwing a small object back and forth to each other. When the human participant stops playing the game unexpectedly, the bonobo responds with a variety of gestures until the human continues the play activity with her. The bonobo therefore appears to be using gestures with the explicit intention of influencing the behaviour of her target recipient, the human playmate.

In observational studies, a gesture is considered intentional if at least one of the following three conditions is met: (1) the gesture is directed towards a specific recipient, (2) the signaller waits for a behavioural response from the recipient (i.e. pauses his or her activity for at least 1 second while directing her gaze towards the recipient) and/or (3) the signaller persists in signalling should the recipient fail to respond (Hobaiter and Byrne, 2011).

1.2.2 Flexibility in the use of gestures

Apes use gestures in a highly flexible manner. Flexibility is observed in how apes vary their use of gestures between different contexts. Specifically a single gesture is used for multiple contexts and many gestures are used within the same context. This pattern of flexibility among gestures and associated contexts has been found in all of the great apes (Call and Tomasello, 2007; Liebal, 2007; Pika, 2007a; Pika 2007b).

Flexibility is also observed in how signallers adjust their use of gestures depending on both the attentional state of the recipient and the perceived understanding of the recipient. Gestures come in three basic modalities: gestures that can only be perceived visually, gestures that can be perceived both visually and audibly and gestures that can be perceived both visually and tactually. As gestures are used in a directed manner then it is appropriate to label the modality of a gesture from the perspective of the recipient. I therefore follow Hobaiter and Byrne (2011) and Genty et al. (2009) in categorizing gestures as the following: visual-silent, audible or contact. In terms of attentional state, a signaller will take into consideration what the recipient is best able to perceive when she is planning her use of gestures. For instance, when the signaller happens to be outside of the recipient's field of vision, then the signaller is more likely to use an audible gesture, rather than a visual-silent gesture (for bonobos: Pika et al., 2005; for gorillas: Genty et al., 2009, for orangutans: Liebal et al., 2006; and for chimpanzees: Liebal et al., 2004).

But it is not only the attentional state that an ape takes into consideration when moderating her use of gestures. In a recent experiment with orangutans, signallers adjusted their use of gestures when faced with a non-compliant recipient. In this experiment, a human caretaker presented two types of food treats, a preferred treat and a non-preferred treat. During the experiment the orangutan was able to communicate to a human caretaker (via gesturing) his desire for a preferred food treat via the use of gestures. When the orangutan perceived that the caretaker has not responded correctly to his communicative efforts (i.e. if the human did not respond or gave the orangutan the non-preferred food treat), the orangutan varied her gestures in an apparent attempt to establish comprehension in the human recipient (Cartmill and Byrne, 2007). Persistence in signalling indicates that the signaller has a particular goal behind her use of gestures and it is through elaboration the signaller may achieve her desired goal.

1.2.3 The meaning of a gesture

Only recently has the meaning of a gesture been described from observations of gestural communication (chimpanzees: Hobaiter and Byrne, 2014, Roberts et al. 2012; orangutans: Cartmill and Byrne, 2010; gorillas: Genty et al., 2009). Before, researchers described gestures by the contexts in which they were observed. As the context in which an ape finds herself occurs alongside and independent to her use of gestural communication, then context works as an environmental descriptor of a gesturing event. Therefore, gestures have been described and categorized by the context in which they were used.

Context works as an independent descriptor of gestures but gives only a general idea of what gestures mean. The meaning of a gesture, as I am describing here, is the goal behind the gesture: what the ape is intending for her recipient to do in response to her gesture. In determining that a gesture had been used intentionally then we have also determined that the ape using the gesture had a particular goal behind her signalling. As an ape is using a gesture to elicit a particular response from her intended recipient then a third party observer should sometimes be witness to that preferred behavioural response. Determining what the preferred response was, depends on the corresponding behaviour of the signaller to the recipient's behavioural response. Effectively, the third-party observer considers whether the signaller appears to be satisfied with the behavioural response of the recipient. It is through coding this dance of actions and reactions that researchers have been able to determine what the intended meaning behind a gesture is. For example, when a chimpanzee uses the gesture *arm swing* and the recipient responds by beginning to play with the signaller and the signaller appears to be satisfied with this reaction, then the intended meaning of this gesture would then be labelled as "play start" for this particular communication event (Hobaiter, 2010). Since the intended meaning of a gesture is determined through observing the reaction of the recipient during the communicative event then it is the speaker's meaning that researchers are extracting rather than the semantic meaning of the gesture used (Kripke, 1977).

The approach to studying the intended meanings behind gestures was pioneered by Genty et al. (2009) in observing captive and wild gorillas and was applied to captive orangutans (Cartmill and Byrne, 2010) and wild chimpanzees (Hobaiter and Byrne, 2014; Roberts et al. 2012) in successive years. Prior work focussed exclusively on the context in which gestures occur (e.g. what situational context the gesture occurs within, for example the context of play or the context of grooming, Tomasello and Call, 2007). However, describing a gesture solely by the context in which it occurs can be misleading. For example, within a given context, gestures can be used for multiple meanings (e.g. the meaning 'move away' and 'give affiliation' might both occur in the context of play) and in the reverse, a single meaning can be used between multiple contexts (e.g. the meaning 'move away' can be used in the context of play as well as the context of grooming; chimpanzee gestures, Hobaiter, 2010). Apes use gestures flexibly between different intended meanings where one gesture may be used for multiple intended meanings and multiple gestures may be used for the same intended meaning (Genty et al., 2009; Hobiater and Byrne, 2014). How tight or loose a gesture is associated with a particular meaning has been analysed by Cartmill and Byrne (2010) in orangutan gestures and by Hobaiter and Byrne (2014) for chimpanzee gestures. In these studies a gesture was described as having a “tight” association with a particular meaning if it was used at least 70% of the time for that particular meaning. A “loose” association between a gesture and a particular meaning was specified as when a gesture was used for a particular meaning less that 70% of the time but more than 50% of the time. Anything less than a 50% use of a gesture for a particular meaning was considered an “ambiguous” association. Describing a gesture by both the goal behind it and the context in which it was used gives a deeper look into how apes are using gestural communication.

1.2.4 The acquisition of gestures

Having reviewed why and how apes use gestures I next focus on the acquisition of gestures. From observing young chimpanzees in the wild, early researchers proposed that gestures were being formed through a process of ritualization (Van Lawick-Goodall, 1972; Plooij, 1978). In this scenario a young ape repeatedly interacts with his mother and begins to understand the signal-value of his actions. He then begins to use these actions as signals in order to gain a specific response from his mother. This theory inspired the now dominant theory of gesture acquisition, that of ontogenetic ritualization (Tomasello et al., 1985). In this theory apes develop a repertoire of gestures through ritualizing actions amongst one another. More specifically ontogenetic ritualization would proceed as thus:

- Individual A performs behaviour X (not a communicative signal);
- Individual B consistently reacts by doing Y;
- Subsequently B anticipates A's performance of X, on the basis of its initial step, by performing Y; and
- Subsequently, A anticipates B's anticipation and produces the initial step in a ritualized form (waiting for a response) in order to elicit Y.

(Tomasello and Call, 2007)

Another theory proposes that gestures are developed through a process of co-regulation (King, 2004). In this process gestures are dynamically created through mutual construction as opposed to ontogenetic ritualization where gestures are ritualized in a specific direction.

Although ontogenetic ritualization is the dominant theory concerning gesture acquisition in apes more recent studies on gorillas (both wild and captive, Genty et al., 2009) and chimpanzees (wild, Hobaiter and Byrne, 2011) have suggested that apes are instead using a set of species-typical gestures in a highly flexible manner rather than gaining new gestures through a process of ritualization or co-regulation.

1.3 The role of flexible communication in the evolution of intelligence

Beyond the evolution of language, studies on flexible communication have implications towards the origins of human intelligence. According to the social intelligence hypothesis (Humphrey, 1976; Brothers, 1990), ever-increasing complexities of social group life drive the evolution of greater intelligence and therefore larger brain size. Extended pair-bonding (i.e. non-mating pairs), as observed within the great apes, has been proposed as the underlying selective impetus for complex cognition (Dunbar and Shultz, 2007). There is also a fitness advantage to maintaining many and various relationships. Silk et al. (2010) found that baboons with stronger dyadic relationship ties had greater reproductive success. In humans, French workers with strong inter-personal ties were healthier and ultimately lived longer than their less connected counterparts (Berkman et al., 2004). Sustaining social bonds within large social groups requires tracking the locations and behaviours of social partners while discriminating between dyadic relationships in terms of age, sex, and kinship. Effective management of social relationships not only depends on correctly identifying and categorizing individuals, but also on moderating one's behaviour in light of this information (Pellis and Iwaniuk, 2000).

For animals living in large social groups, using a set of communicative signals can help in both coordinating behaviours and in minimizing conflict between group members (Seyfarth et al., 2010; Call and Tomasello, 2007). The flexible and intentional nature of ape gestural communication may provide new insights to the study of social regulation. As reviewed in the previous section, apes display flexibility in their use of gestures in the following ways: apes modify their use of gestures in light of the recipient's willingness to respond appropriately (Cartmill and Byrne, 2007), apes adjust their use of gestures to accommodate the attentional state of their target audience (Pika et al., 2005; Genty et al., 2009; Liebal et al., 2006; Liebal et al., 2004), and there is a means-ends dissociation between gestures and the contexts in which they are used (Call and Tomasello, 2007) and the meanings they are used for (Genty et al., 2009; Hobaiter and Byrne, 2014). Are apes also capable of adjusting their use of gestures depending upon the social context surrounding a communication event? One of the goals of this study is to examine the influence social variables have on the use of gestural communication and what the effect flexible signalling may have on the maintenance of social relationships.

1.4 Bonobo gestural communication

My observational studies of gestural communication will be done exclusively with bonobos. The first observations of bonobo gestures occurred in the wild when researchers had set out to observe the natural behaviours and ecology of bonobos (e.g. Badrian and Badrian, 1984; Ingmanson, 1996; Kano, 1980; Kuroda, 1980). Studies focussed exclusively on the use of gestures by bonobos, and employing strict definitions of what a gesture is, have occurred more recently (Pika et al., 2005; Pollick and de Waal, 2007; Savage-Rumbaugh et al., 1977; Halina et al., 2013). The largest gestural repertoire reported by any one research group was 28 distinct gestures (Pollick and de Waal, 2007). However, studies on other ape species such as gorillas (Genty et al., 2009) and chimpanzees (Hobaiter and Byrne, 2011) have shown species repertoires containing at least twice as many gestures. The relatively small number of gestures reported for bonobos is most likely due to the limitations of study group diversity in terms of age range (Pika et al., 2005, Schneider et al., 2011; Halina et al., 2013) social group size (Pollick and de Waal 2007; de Waal, 1988) or context of communication (Savage-Rumbaugh et al., 1977; Halina, et al. 2013). When studies of gestural communication are limited by group size, age range of subjects or by the context in which communication is observed (e.g. focussing on episodes of communication as they occur in play bouts) then the researchers will by default only observe a subset of that communities' repertoire of gestures. To expand upon what is known of bonobo gestures researchers should observe bonobos as they interact with a range of conspecific in as many behavioural contexts as possible.

1.5 Bonobo sociality

Bonobos are of particular interest to the study of gestural communication for their unique behaviours and ecology. Bonobos live in fission-fusion communities where the mixture of individual members within any given group changes over time. A community of bonobos can be as large as 50 individuals including both males and females and their dependent offspring (Kano, 1992). As bonobos approach sexual maturity, males tend to stay in the community in which they were born and females tend to emigrate to other communities (Furuichi et al., 1998; Gerloff et al., 1999; Kano, 1992). When a female leaves her natal community she will temporarily join different communities before settling down into one final community in which she will rear offspring (Gerloff et al., 1999; Hashimoto et al., 1996; Hohmann et al., 1999).

Because males and females have different residence patterns, the difference in relationships they form with other community members is of interest. Males, having stayed with their original community, tend to stay near and form strong bonds with their mothers (Furuichi, 1989). Females, who emigrate to new communities, tend to form strong bonds among many group members within the new community, including both males and females, despite being only distantly related to any one of them. Because of this female-female ties are strong whereas male-male ties are weak (Hohmann et al., 1999; Kano, 1992; Palagi et al., 2004).

In terms of dominance, bonobo social structure has been described as female-biased and egalitarian (de Waal, 1995). There tends to be a single alpha female within a community of bonobos although females are not absolutely dominant over males (Paoli and Palagi, 2008; Stevens et al., 2008). Rather, female dominance depends more on context and the formation of allies. In times when females aggregate, for example during feeding bouts, females support each other in accessing food in defence against males and therefore monopolize the food resource (Hohmann and Fruth, 1993; Hohmann et al., 1999). In general, the fact that females having relatively higher rank within bonobo society is attributed to the following: females grouping together in defence of one another (Furuichi, 2009), overall low aggression rates in bonobos (de Waal, 1987; de Waal, 1995), and relatively weaker ties between male bonobos (de Waal, 1997; Paoli et al., 2006; Parish, 1994; White, 1996).

1.6 Bonobo sexuality

Among the friends and family I've chatted to about my research, it appears to me that bonobos are best known for their remarkable and frequent sexual behaviours. Much of bonobo sexual behaviour is de-coupled from reproduction and is done habitually at a rate that surpasses other primates (de Waal, 1987; Kano, 1992; Kuroda, 1980). The lower aggression rates of bonobos compared to other species of ape has been linked to the prevalence of socio-sexual behaviours found in the species. In times of social tension, such as feeding or inter-group conflict, bonobos are more likely to use socio-sexual behaviour to alleviate tension among group members than other social behaviours such as grooming (de Waal, 1987; Furuichi, 1989; Hohmann and Fruth, 2000; Kano, 1989)

One of the most prevalent socio-sexual behaviours observed in bonobos is between two females. When two females engage in sexual contact it is known as "GG rubbing": two females rub their genitals together side to side while embracing each other vertro-ventrally (Kuroda, 1980). GG rubbing tends to be a social lubricant in bonobo society especially between females of differing rank (de Waal, 1995; Hohmann and Fruth, 2000; Wrangham, 1993). A young female bonobo emigrating into a new community will necessarily start out as a lower-ranking individual. To increase her status she will associate with higher-ranking females and in particular will initiate GG-rubbing with them. In fact, GG rubbing occurs most frequently between bonobos of unequal rank with the lower-ranking bonobo being more inclined to initiate the interaction (Hohmann and Fruth, 2000; Parish, 1994; Parish, 1996). In asymmetrical rank pairings, the higher-ranking bonobo is more likely to take the mounting position where she will position herself above the lower-ranking bonobo (de Waal, 1987; Hohmann and Fruth, 2000).

1.7 Aims of this study

1.7.1 Bonobo gestures and their meanings

Bonobo gestures have been observed in both the wild (Badrian and Badrian, 1984; Ingmanson, 1996) and in captivity (Pollick and de Waal, 2007; Pika, 2007, Pollick et al., 2008; Schneider et al., 2011, Halina et al., 2013) and yet no single study has described more than 28 gestures within the repertoire of bonobos. There are a few reasons why there have been only few gestures observed in bonobos at any one time. In wild studies, gestures were recorded but were never the focus of research (Badrian and Badrian, 1984; Ingmanson, 1996; Hohmann and Fruth, 2003; Kano, 1992) and in captive studies, gestures were the focus of study but those studies were limited by their focus on particular subsets of bonobo communities (Pika et al., 2005; Schneider et al., 2011; Halina et al., 2013; Pollick and de Waal, 2007; De Waal, 1988; Savage-Rumbaugh et al., 1977). The first aim of this study was to describe the gestures that bonobos use, what contexts they use them in, and what the intended meaning of those gestures were. To accomplish this I focussed my studies of gestural communication on a relatively large captive group of bonobos and observed their natural use of gestures for an entire year.

1.7.2 Comparing bonobo gestural communication and with other apes

When I began my study I expected that bonobos and chimpanzees would differ in their use of gestural communication as they have different behavioural patterns. As chimpanzees and bonobos diverged from a common ancestor approximately 0.9 million years ago (Won and Hey, 2005) any differences observed in their species repertoire of gestures should reflect the differences in their ecology and behavioural patterns. Because bonobos have unique behaviour, namely GG rubbing, I predicted that any new gestures found to be uniquely bonobo should revolve around uniquely bonobo behaviours.

1.7.3 Social influence of gestural communication

As apes are able to adjust their use of gestures depending on the attentional state of the recipient and the perceived understanding of the recipient (at least in the orang-utan, Cartmill and Byrne, 2007), do they also adjust their use of gestural communication depending on social circumstances? I argue that since apes have a large repertoire of gestures to their disposal, have a particular goal when gesturing, and are attempting to influence the behaviour of one target conspecific at any one time; then who that recipient is, and indeed who the signaller is, should influence the progression of events. Ultimately, are apes using gestural communication to regulate their social relationships? I attempt to answer these questions by considering the age and sex of the signaller and recipient and how these variables influence patterns of gestural communication.

1.7.4 Dialog

Up to now, gestural communication has been described as being used to manipulate the behaviour of a conspecific. This is what I was expecting of the bonobos I studied: one signaller, one recipient, one goal being expressed from the signaller towards the recipient. However, during my studies of bonobos I became increasingly frustrated with the coding process. When coding gestures, the coding paradigm I was using (developed in turn by Genty et al., 2009, Cartmill and Byrne, 2010, and Hobaiter and Byrne, 2011) directed me to label a gesture and ultimately the goal behind the gesture by the behavioural response given by the recipient that was satisfactory to the signaller. In this coding paradigm, the only possible goal behind signalling is a behavioural response of the recipient. Yet I was observing instances of communication where the goal behind the gesture was to elicit return gestural communication from the recipient bonobo. I was finding scenarios where both bonobos were using gestures towards one another and doing so in a way that suggested a dialog was occurring between them. In the last chapter of this thesis I explore contexts of communication that may result in dialog where both apes must use gestures in order to coordinate their pending interaction.

Chapter 2: General methodology

2.1 Introduction

All four data chapters in this thesis are concerned with the gestural communication of Milwaukee County Zoo bonobos. In this chapter I describe the methodology behind recording and analysing gestures as they are performed naturally among captive bonobos.

2.2 The Milwaukee County Zoo Bonobos

2.2.1 Subjects

I observed 17 bonobos during the course of this study. Age categories were defined as follows: infants as under the age of 2, juveniles as between the ages of 2 and 6, adolescents as between the ages of 7 and 14, and adults as over 15 years of age (Kano, 1992). In the case where an adolescent female gave birth and was rearing offspring she was classified as an adult. Two females were reclassified as adults due to having offspring and being under the age of 15, Claudine and Zomi. The group was composed of 2 infants, (1 male, 1 female) 1 juvenile (female), 4 adolescents (1 male, 3 females) and 10 adults (6 males, 4 females). Two adult males died during the course of my observations (Lody in January and Viaje in March of 2012) while another adolescent female, Elikia, joined the group from Ft. Worth Zoo in the spring of 2012. For an overview of ages and relationships see Table 1.1.

Table 1.1 Age sex and relationships of the Milwaukee bonobos observed in this study.

Ages of the 17 apes at Milwaukee are determined by the age they were at the midpoint of the study period. Observational time span varied between individuals since two males died mid-study (Lody and Viaje) and one female joined the group midway through observations (Elikia).

Name	**Date of birth**	**Age class**	**Birth place**	**Sex**	**Transfer date**	**Offspring in Milwaukee**
Tamia	5/7/1996	Adult	Columbus Zoo	F	2004	Hannah
Hannah	15/12/2007	Juvenile	Milwaukee County Zoo	F	-	-
Brian	1/1/1989	Adult	Yerkes Primate Research Centre	M	1997	-
Murph	15/4/1990	Adult	Yerkes Primate Research Centre	M	1993	-
Lody	-/-/1973	Adult	Wild Born	M	1986	Deidre, Zomi, Hannah, Claudine
Zuri	10/6/1998	Adolescent	San Diego Zoo	M	2000	-
Elikia	25/2/2000	Adolescent	Columbus Zoo	F	2011	-
Claudine	23/8/2002	Adult	Columbus Zoo	F	-	K2
Ricky	19/3/1995	Adult	Columbus Zoo	M	2010	-
K2	19/11/2010	Infant	Milwaukee County Zoo	M	-	-

Name	Date of birth	Age class	Birth place	Sex	Transfer date	Offspring in Milwaukee
Faith	19/2/2005	Adolescent	Milwaukee County Zoo	F	-	-
Makanza	11/8/1994	Adult	Yerkes Primate Research Centre	M	1995	Kitoko
Kitoko	19/2/2010	Infant	Milwaukee County Zoo	F	-	-
Laura	27/8/1967	Adult	San Diego Zoo	F	1993	Murph, Claudine
Viaje	-/-/1980	Adult	Wild born	M	2001	Faith, K2
Zomi	17/6/1999	Adult	Milwaukee County Zoo	F	-	Kitoko
Deidre	4/3/2003	Adolescent	Milwaukee County Zoo	F	-	-

2.2.2 Environment

Bonobos were observable by the public from both indoor and outdoor enclosures. The indoor enclosure was a large open interior space that measured approximately 3 stories high. It was composed of moulded cement flooring and walls. The north wall was composed of metal mesh. There were 2 large glass windows for viewing on the west wall, and several smaller windows along the south wall. The enclosure had logs, fireman ropes, and rubber ropes running along the interior of the enclosure as well as cement towers climbing 2 stories high. The keepers provided wood-based fibrous material as nesting material. The keepers provided t-shirts (torn into pieces during the day by the bonobos), boxes and large hard-plastic hollow balls for the bonobos to play with. Playful activity involving keeper-provided objects was on display to the public.

The outdoor enclosure was composed of a series of metal cages stacked up to 2 stories high. It was located outside of the primate building and was built within the forest surrounding the building. The metal cages were locked together to create tunnels running up to 200 feet long and were also stacked vertically to create multiple levels (see image 1.1). Ladders were provided between levels so that bonobos could easily climb up and down. The cage system had multiple sliding and locking doors with which the keepers used to create up to 4 separated chambers viewable to the public. During the summer the forested area created enough of a canopy so that bonobos had access to both sunny and shady patches in the enclosure. Bonobos were only let into the outdoor enclosure if the weather conditions were suitable. Since food tends to drop through the cages and onto the forest floor, keepers came out to feed the bonobos approximately every hour. Water was freely available throughout the day in both the outdoor and indoor enclosure.

Images 1.1 Photos of the outdoor enclosure from the public viewing area. These images are screen-captures from video recorded during the months of May, June and July of 2012.

Public observation was allowed at the zoo between the hours of 9 am and 5 pm with reduced hours during the winter. Bonobos were sent up to the indoor and outdoor enclosures between the hours of 8 and 10 am. Food was scattered around the floor of the enclosure before bonobos first entered in the morning. Their diet consisted mostly of fresh fruits and vegetables (stocks are kept frozen throughout the winter) along with monkey cakes. Bonobos were taken downstairs to the off-exhibit holding area between 2 pm and 4 pm each day. The keepers trained bonobos to cooperate with medical procedures and health check-ups. Training occurred both within the exhibits for short intervals during the day and downstairs in the holding area (off-view from the public). Sometimes certain bonobos were kept off display for medical, training or research purposes.

Each morning the keepers decided on who was to be sent up to each enclosure. There were some animals that were never put together in the same enclosure, for reasons of inbreeding or aggression; mothers and their immature offspring were always kept together.

2.3 Data Collection

I observed the bonobos between 1 and 3 hours per day, 4 to 6 times per week. Observations were made during the following months: January 2011 (10 days), July 2011 (8 days), September-December 2011 (32 days), February-July 2012 (97 days). Bonobos were observed for a total of 187 hours over the course of 147 days. Since the bonobos were kept in a fission-fusion arrangement and the sub-groupings were mixed regularly, it was necessary to spend a full year recording their gestures in order to record as many different communicating dyads as possible. Although there are a large number of possible combinations between 17 individuals (136 potential dyads), some dyads were never observed since some animals were never put on display together (e.g. aggression, inbreeding).

As an individual within the group was not necessarily on display everyday that I observed them, I used a focal behaviour sampling method (Altmann, 1973) focussing on ‘potentially communicative’ behaviour between two individuals rather than the individuals themselves for my video recordings. A social interaction was said to be potentially communicative when one or both bonobos initiated the interaction. If more than one interaction was taking place at the same time preference was put on filming the interaction most likely to contain gestural communication. For example, if there were simultaneously a pair of bonobos grooming each other and a pair of bonobos playing, preference was given to filming the play bout as apes tend to gesture more frequently during play (Genty et al., 2009). All social interactions judged to be potentially communicative were recorded with a Panasonic HDC-SD60 Full HD Camcorder.

2.4 Analysis

2.4.1 Defining intentional communication and gestures

For this study I define gestures as “discrete mechanically ineffective physical movements of the body observed during periods of intentional communication” (Hobaiter and Byrne, 2011). For example, shoving another individual so that they are forced to move away from one’s person would not count as a gesture as the act was “mechanically effective”. Instead, the signaller might lightly nudge her recipient on the shoulder after which the recipient would respond by moving away from the signaller. In this scenario the nudge would be considered as a potential act of intentional communication. Movements of the arms, legs, head or whole body were considered as potential gestures, pending analysis of intentionality; vocalizations and facial expressions were not included in this analysis. To locate gestures within the footage I first looked for mechanically ineffective behaviours that appeared to be directed from one individual, the potential signaller, to another individual, the potential recipient. I define an intentionally communicative act as follows: communication directed toward a particular recipient with the apparent goal of influencing their behaviour in a particular way. To be directed, the signaller must have angled his head towards the recipient before or during the act of gesturing. Whether a gesture had been used with an apparent goal of influencing another's behaviour (i.e. intentional use) the following criteria were considered for each communicative event (Bates et al., 1975; Tomasello et al., 1994):

1. Audience checking: Does the signaller look towards the target recipient before gesturing?

2. Response waiting: Does the signaller continue observing the recipient after the gesture is completed, effectively monitoring the recipient for their response?

3. Persistence: When a gesture fails to elicit the desired response from the recipient, does the signaller persist in gesturing towards the recipient?

Not all criteria of intentionality would necessarily be present for a communicative event to be labelled as intentional. For instance, if the recipient responded to the signaller's first gesture immediately then I did not expect to observe either response waiting or persistence; as long as audience checking occurred I still labelled the gesture as intentionally performed. Similarly, if the recipient responded to the signaller's first instance of gesturing after a short delay, I expected to observe response waiting from the signaller but not necessarily persistence in signalling. Observing one or more of the above criteria was sufficient for labelling a communicative event as intentional. Each instance of a gesture, having been qualified as intentionally performed, is considered a gesture token. A communication event may include several gesture tokens of different of the same gesture types.

If the signaller used more than one gesture during a communicative event one of two things would happen: either the signaller would perform gestures in rapid succession or would perform a series of gestures, each after distinct periods of response waiting. When two gestures were performed with less than 1 second of separation between them, I coded both gestures as part of the same 'sequence' (Genty et al., 2009, Hobaiter and Byrne, 2011). When two gestures (or sequences) were separated by a period of response waiting of 1 second or more, and the recipient had not responded "successfully" in the interim, I coded both gestures as part of the same communicative bout. Coding of gestures occurred during the re-watching of filmed behaviours.

2.4.2 Training for gesture coding

In preparation for my own analysis of gestures in bonobos, I have consulted with the three field scientists, Drs. Erica Cartmill (orangutans, Cartmill and Byrne, 2010), Emilie Genty (gorillas, Genty et al., 2009) and Catherine Hobaiter (chimpanzees, Hobaiter and Byrne, 2011) whom have all coded gestures as performed by apes. I spent 9 days at the Milwaukee County Zoo in January 2011, to familiarize myself with the population and to begin recording of gesture events between bonobos. I have received ethical clearance to perform this observation study from the University of St Andrews' Animal Welfare and Ethics Committee in December of 2010.

2.4.3 Coding of gestural communication

I coded each instance of gesture into the following categories: 1. Mode of gesture, as contact, visible-silent or audible. 2. The situational context in which the gesture was observed, as affiliation, agonism, feeding, GG rubbing, grooming, resting, sexual, social play, or traveling (see table 1.2 for definitions of situational contexts). 3. The attentional state of the recipient, as "attending" where the recipient maintains eye contact with the signaller and appears to be tracking the signaller's behaviour, "in full view" where the signaller presented her gesture within 25 degrees left and right of the recipient's frontal gaze, "partial view" where the signaller presented her gesture between 25 and 90 degrees left or right of the recipient's frontal gaze, or "out-of-sight" when the signaller presented her gesture beyond 90 degrees left or right of the recipient's frontal gaze. The type of gesture used by the signaller was defined and categorized by the physical form the gesture took. When possible, gesture forms were matched with definitions presented in previous gesture studies of African great apes (Genty et al., 2009, Hobaiter and Byrne, 2011) and named accordingly.

Table 1.2 Definitions of situational contexts in which gestural communication was observed

Context	**Definition**
Affiliation	An individual seeks to move closer to or make physical contact with another
Agonism	An individual directs aggressive behaviour towards another including display and displacement
Feeding	An individual engages in feeding activity including drinking, foraging, masticating and nursing
GG rubbing	An individual seeks to engage in non-penetrative genital contact with another
Grooming	An individual participates in grooming or seeks to initiate grooming with another

Context	Definition
Resting	An individual remains stationary not participating in any obvious physical movement
Sexual	An individual engages or initiates penetrative sexual contact with another
Social Play	Two or more individuals engaged in playful activity including contact play and chasing play
Traveling	Locomotion from one area to another not including short distances travelled between individuals within a group

2.4.4 Coding of Apparently Satisfactory Outcomes

After the signaller had performed a gesture I observed the recipient for their reaction, whether it be gestural or non-gestural behaviour. In the case of a behavioural response I considered whether the behaviour produced by the recipient was a "satisfactory" response for the signaller. A signaller was said to be satisfied if she ceased communicative effort immediately following the recipient's response (Genty et al., 2009). The action performed by the recipient that occurred just before the signaller ended communicative effort was coded as the "apparently satisfactory outcome" or ASO (Hobaiter and Byrne, 2014). For example, if the recipient responded to a signaller's gesture by climbing onto the signaller's back, and the signaller then ceased signalling and moved off, the ASO of the gesture was coded as "climb on me". I classified the ASO as "unknown" in the following situations: the recipient physically prevented the signaller from persisting in communication; the signaller changed his attentional state but made no further response; the recipient left the area (if this had no plausible advantage towards the signaller); or the recipient aggressively chased away the signaller. If the signaller was able to procure an apparently satisfactory response from the recipient through sequential gesturing, then all gesture tokens within the bout were considered as having the same ASO. If the communicative bout included more than one sequence of gestures (separated by periods of response waiting) then only the last sequence of gestures preceding the "right" behavioural response was coded as successful, all other sequences within the same communicative bout were labelled as failures. If the recipient did not produce a satisfactory response then the ASO was coded as "unknown".

2.5 Reliability of coding gestures

All gestures present in the video footage were coded by me . For the purpose of inter-observer reliability testing, 50 gestures were also viewed independently by another experienced gesture researcher, Dr. Catherine Hobaiter (see Genty et al., 2009; Hobaiter and Byrne, 2011). The second observer was asked to code this sample for the following categories: directedness of the gesture, attentional state of the recipient, gesture type and ASO. Directedness of communication events matched completely between coders. Attentional state of the recipient had an inter-observer reliability of kappa = 0.89, which is considered a "very good" level of agreement according to Altman (1990). Gesture type and ASO also had "very good" levels of agreement between coders at kappa = 0.86 and kappa = 0.93 respectively.

As a person new to gestural communication research it was necessary for me to consider how much better at coding I had become by the time I had finished coding all of the video footage. As such, I re-coded the first third of the video footage so as to ensure that my coding was consistent throughout the catalogue of film.

Chapter 3: Repertoire of gestures for Milwaukee bonobos

3.1 Introduction

Great apes engage in intentional and flexible communication through the medium of gesturing. Specifically, apes direct their use of gestures towards a particular recipient with a discernable goal behind their signalling (Tomasello and Call, 2007; Genty et al., 2009; Hobaiter and Byrne, 2011; Cartmill and Byrne, 2010). They use gestures to initiate grooming, play or sex, or to end contact with a conspecific. Apes use gestures flexibly in that the same gesture may be used in different contexts while many different gestures can be used within the same context (Tomasello and Call, 2007). The similarities between ape gestures and human language have led researchers to consider gestural communication a likely origin to human language (Tomasello, 2008; Arbib et al., 2008).

The focus of my study is bonobo gestural communication. The most extensive study of intentional communication in bonobos described 28 distinct gestures (Pollick and de Waal, 2007). Studies on other ape species such as gorillas (Genty et al., 2009) and chimpanzees (Hobaiter and Byrne, 2011) have shown species repertoires containing at least twice as many gestures. The relatively small number of gestures reported for bonobos is most likely due to the limitations of study group diversity in terms of age range (Pika et al., 2005; Schneider et al., 2011; Halina et al., 2013) social group size (Pollick and de Waal, 2007; de Waal, 1988) or context of communication (Savage-Rumbaugh et al., 1977; Halina et al., 2013).

Because gestures occur socially then the social organization of bonobos is of particular interest. Wild bonobos live in fission-fusion societies. At Wamba, one of several wild bonobo research sites, bonobos are found to live in communities of up to 50 individuals that consist of males, females and immature individuals. From these larger units, smaller subgroups will form and break off for short periods of time. Subgroups can consist of different assortments of bonobos: mothers and their offspring, unrelated adult males or young nulliparous females. Males and young females are found to enter and leave subgroups at will. Mother-infant family parties make up the most consistent subgrouping, which can also include adult sons (Kano, 1992).

The aim of this chapter is to document the types of gestures used by a captive population bonobos. To accomplish this I focussed my observations at the Milwaukee County Zoo. Milwaukee has hosted bonobos for over 30 years and maintains one of the largest collections in the world. Milwaukee bonobos are maintained in a fission-fusion sub-grouping system mimicking what wild bonobos tend to do in their natural habitat. Fission-fusion management is beneficial for my study as it means that subject bonobos will be seen with a range of social partners potentially increasing the number of situational contexts a bonobo communicates within. I therefore spent a full year observing a relatively small number of individuals, which in turn provided a relatively large number of observations per individual. For this chapter my goal was to determine what types of gestures bonobos use and how the species repertoire of bonobos compares to that of other species.

3.2 Specific method

3.2.1 Individual Repertoire

Gesture types that were observed as being used intentionally are counted into the group repertoire. For an individual's repertoire, the individual must have used each gesture type at least once and the use of the gesture must have met the criteria for intentionality (see section 2.4.1).

3.2.2 Adjustment of gesture mode to recipient's attentional state

To determine whether signallers adjusted their use of gestures based on the attentional state of the recipient, I looked at how often a signaller used either a visible-silent, contact or audible gesture depending on whether the recipient was attending or out of sight. I considered only gestures occurring at the beginning of a communication bout and only signallers who used at least 5 gesture tokens (i.e. an instance of gesture) for each category (e.g. 5 tokens each for visible-silent, contact and audible). First I calculated how often the signaller used each gesture mode for when the recipient was attending and when the recipient was out of sight. I then compared these two frequencies to determine whether signallers tend to shift their use of gestures depending on their recipient's state of attention. I labelled the proportion of the overall use of each mode as α and the proportion of the use of each mode for a particular attentional state as β. I then then calculated the percentage deviation between the use of gesture modes across attentional states with the follow fomula: $(\alpha/\beta - 1) * 100$ (Hobaiter and Byrne, 2011). If there was a deviation between the use of a particular mode for a particular attenational state and the use of a particular mode across all attentional states then I would conclude that bonobos are adjusting their use of gestures depending upon the attentional state of their recipient.

3.2.3 Statistical Analysis

Data were analysed through the open access statistical programming language R. Data visualizations were created in R as well as the javascript library D3. Data was first tested for skewness and equivalence of variance before running parametric statistical analysis. Data was considered normally distributed if skewness was less than 1.96 times the value of the standard error of skewness. Levene's test was used to determine whether data had equal variances. If both normality and equal variances were demonstrated I continued with parametric statistical analysis. When the data was non-normal and with un-equal variances I continued with non-parametric analysis. Statistical significance was set at $\alpha = 0.05$.

3.3 Results

Milwaukee bonobos were observed for a total of 187 hours over the course of 147 days. Each individual was on display on average 62.29 hours (range = 9-101, sd = 35.33) during periods of observation. As the group was kept in a changing, fission-fusion pattern, groupings varied: I observed 68 unique sub-groupings of individual bonobos. I observed 86 dyads using gestural communication towards one another. A typical sub-group contained many adult females, their dependent offspring along with one or two adult males. Although bonobos put on display were rotated frequently, some animals tended to be on display more often than others. As a result females were observed for a greater total number of hours than were males (n=17, t= -2.90, df= 10.45, p= 0.02). In total, 1181 gesture tokens were coded from the video footage that also fit the criteria of intentionality. On average, an individual performed 71.44 gesture tokens (range= 2-201, sd= 62.16).

3.3.1 Gestures observed in Milwaukee

Milwaukee bonobos used 55 gesture types for intentional communication. Table 3.1 presents the names and definitions of gestures. Table 3.1 also presents a comparison between the gestures reported from previous bonobo research, as well as with gesture studies of other ape species. Previous reports of bonobo gestures come from both studies of intentional communication and studies of general bonobo behaviour that happen to also report observations of bonobos gesturing. From table 3.1, there are two gestures new to ape gesture research based on my observations at Milwaukee Zoo: *rack pose* and *body swing.* Four other gestures have been recorded only in bonobos and not in other apes: *body shake*, *crab pose*, *knock other*, and *starfish pose*. Nine gestures were seen both in Milwaukee bonobos and in other ape species, but had not been observed in previous bonobo studies. Fifteen gestures have been observed in previous bonobo studies but not in the current study, giving a total known gestural repertoire for the bonobo of 70 gestures.

Table 3.1 The gestures of Milwaukee bonobos.

The table includes gestures reported in previous studies of all great apes. Gestures not seen in Milwaukee bonobos but seen in other bonobo populations are presented in italics under the column "Gesture Type".

Captive bonobos: (1) Pika et al., 2005, (2) de Waal, 1988, (3) Pika and Zuberbhuler, 2008, (4) Pollick and de Waal, 2007, (5) Schneider et al., 2011, (6) Halina et al., 2013, (13) Savage and Bakeman 1978, (14) Savage-Rumbaugh et al., 1977; **Wild Bonobos**: (7) Nishida et al., 2000, (8) Hohmann and Fruth, 2003, (15) Kano, 1992, (16) Kuroda, 1980, (17) Kuroda, 1984; **Chimpanzees**: (10) Hobaiter and Byrne, 2011; **Gorillas**: (11) Genty et al., 2009; **Orangutans**: (12) Cartmill and Byrne, 2010

Gesture Type	**Definition (Milwaukee unless otherwise specified)**	**Other captive bonobos**	**Wild bonobos**	**Chimpanzee, wild (10)**	**Gorilla, wild and captive (11)**	**Orangutan, captive (12)**
Arm raise (visual-silent)	Arm or arms are raised above the head	Arm raise (4), Arm raise (5), Raise up (13), Raise arm with palm down (14), Move hand toward another portion of the cage (14), Arm waving (2)	Raise (7)	Arm raise	Arm raise	Raise arm, arms up

Gesture Type	**Definition (Milwaukee unless otherwise specified)**	**Other captive bonobos**	**Wild bonobos**	**Chimpanzee, wild (10)**	**Gorilla, wild and captive (11)**	**Orangutan, captive (12)**
Arm swing (visual-silent)	Arm is extended and moved in large arcing movements below the shoulder	Swing, Flap (4), Move toward particular location (13), Stand bipedally and wave arms out from body (14)	-	Arm swing	Arm swing, Arm swing under	-
Beckon (visual-silent)	"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" Pollick and de Waal, 2007	Beckon (4)	Beckoning (15)	Beckon	-	Beckon

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Bite (contact)	The open mouth is placed onto the body of the signaller	-	-	Bite	Bite	Bite, mouthing
Bite object (visual-silent)	Mouth is closed around an object, such as a rope	-	-	Object in mouth approach	-	-
Body swing (visual-silent)	While holding onto a stationary object above her head, signaller swings both legs toward recipient	-	-	-	-	-
Body shake (visual-silent)	Torso is wiggled back and forth while standing quadrupedally	Shake (5), Swagger quadrupedal (1)	-	-	-	-

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Bow (visual-silent)	"Animal raises and lowers its torso by stretching and flexing the limbs alternating includes also movements such as nod head, shake head, tip head or turn head" Pika et al., 2007	Bow (1)	-	Bow	Bow	-
Chest beating (visual-silent)	"The own chest is loosely tapped a couple of times with the finger or palm of hand. The rhythm is variable and no audible sound in produced" De Waal, 1988	Chest beating (2)	-	-	Chest beat play	-

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Clapping (audible)	"Two hands, two feet, or a hand and a foot are brought together one or several times, often resulting in audible clapping" De Waal, 1988	Clapping (2), Clap (1)	-	Clap	Clap	Clap
Crab pose (visual-silent)	With the belly facing upwards and all limbs in contact with the floor the swelling and rump are brought upward between the legs	Present venter (6), Present (1)	Raise buttocks, shows sexual organs (15)	-	-	-
Directed push (contact)	A gentle nudge from the hand or arm of the recipient onto the body of the recipient	Push limb across body, Push leg or arm out from body, Position partner's lower body with both hands, Push under chin (14)	-	Directed push	Positioning	Turn head, nudge

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Display back (visual-silent)	Signaller angles her back towards the recipient	Present back (6), Present (1), Rump present (2)	Sit and turn back (7), Direct rear end (15),	Present grooming, Present climb on me	-	Look back
Display chest (visual-silent)	In the sitting position, shoulders are stretched back, knees are spread outward while the chest is angled toward the recipient, the penis may or may not be erect during the gesture	Concave back (2)	Spreads thighs (15)	Present sexual, Present grooming	-	Present genitals
Display face (visual-silent)	The face towards the recipient	-	Lower head, Turn face downward (7)	Present grooming	-	-

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Display limb (visual-silent)	The arm or leg is partially extended and the forearm or elbow (calf or knee) is angled toward the recipient	Foot/leg gesture (4), Move arm and forearm across body (14)	Extend leg (7)	Present climb on me, Present grooming	-	Present body part
Embrace (contact)	Both arms are wrapped around the body of the recipient	Pull toward self by putting arm around partner's back (14), Lateral embrace, ventral embrace (2)	Embrace half (7)	Embrace	Embrace	Embrace
Feet shake (visual-silent)	Both feet are moved back and forth repeatedly from the ankle	Wiggle leg (3)	-	Feet shake	Feet shake	-

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Flail (visual-silent)	"Arms and hands are completely raised above head and are shaken in rapid succession (usually in tantrum or approach). Repetitive." Pollick and de Waal 2007	Flail (4)	-	-	-	-
Gallop (audible)	Signaller runs quadrupedally making noise through hand and foot strikes onto the ground	Gallop (1), Stamp trot (2)	-	Gallop	Gallop, Stiff gallop	-
Grab (contact)	One or both hands are wrapped around a body part of the recipient	Grab (1,3,6)	-	Grab	1-handed grab, 2-handed grab	Grab, grasp, restrain

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Grab-pull (contact)	One or both hands are wrapped around a body part of the recipient and then tugged in one direction	Pull limb toward self (14), Grab-Push-Pull, Pull (1), Hand lead (4)	-	Grab-pull	Grab-pull, 2-handed grab-pull	Pull away, Pull, Pull away appendage, Pull hair
Hand on (contact)	One or both palms are placed onto the body of the recipient, contact is held for at least 2 seconds	Arm on (5)	-	Hand on	Hand on, hands on	Cover
Hand fling (visual-silent)	Signaller moves hand up and down from the wrist in a swift motion	Move closer, Move genitalia around (13), Raise arm and flip hand upward at wrist (14)	-	Hand fling	-	Shoo
Hand shake (visual-silent)	Hand or hands are moved side to side from the wrist in a repetitive motion	Shake wrist (4), Turn around (13), Wrist shaking (2), Finger flexing (2)	-	Hand shake	-	-

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Hang upside down (visual-silent)	Signaller hangs from a fixed substrate with the head pointed downwards at the ground	Shake (1)	-	Dangle	Rope swinging	Dangle
Hang upside up (visual-silent)	Signaller hangs by the arms from a fixed substrate with her head pointing upwards	-	Hanging above (15)	Dangle	Rope swinging	Swing
Head nod (visual-silent)	Head is moved up and down	Head shake (5), Head bob (3)	-	Head nod	Head nod	-
Head shake (visual-silent)	Head is moved from side to side in a fast motion	Head shake (5)	-	Head nod	Head shake	-

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Head stand (visual-silent)	While standing on two feet, the body is bent over so that the head and hands are close to or touching the floor	-	-	Head stand	-	Head Stand
Hit with object (contact)	Signaller takes an object in hand and strikes the recipient with said object	-	-	Hit with object	Hit with object	-
Hunch over (visual-silent)	"One arm is swept over back of another individual but there is no hugging or extended contact (less than two seconds)" Pollick and de Waal, 2007	Hunch over (2,4)	-	Tandem walk	Tandem walk	-

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Jump (audible)	Signaller propels her body into the air with her legs, a noise is made by striking the ground upon landing	Jump (1)	-	Jump	Jump	-
Kick (contact)	Leg is brought into contact with the body of the recipient in a hard short movement	Kick (1)	-	Kick	Kick	-
Knock object (audible)	The knuckles of one or both hands are used to strike an object making a sound	Rap knuckles (4)	-	Knock Object	Knock Object	-
Knock other (contact)	Knuckles of the hand are brought into light contact with the recipient's body	Dab (4)	-	-	-	-
Leg swing (visual-silent)	Leg is moved in a large arc from the hip	-	-	Leg swing	Leg swing	-

Gesture Type	**Definition (Milwaukee unless otherwise specified)**	**Other captive bonobos**	**Wild bonobos**	**Chimpanzee, wild (10)**	**Gorilla, wild and captive (11)**	**Orangutan, captive (12)**
Leaf clip by hand/mouth (audible)	"Immatures of both sexes and mature females clip leaves from herbs or trees and hold them in their lips (and perhaps teeth) while looking at another individual" Hohmman and Fruth, 2003	-	Leaf clip by hand/mouth (8)	Leaf clipping	-	-
Limp hand (visual-silent)	Palm of hand is flexed towards the wrist, fingers are pointing downwards and the back of the hand is angled towards the recipient	Bent wrist (4)	-	Present grooming, Reach	-	-

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Lip-lip touch (contact)	"Touch recipients' mouth with one's own mouth" Schneider et al., 2011	Lip-lip touch (5)	-	-	-	Kiss
Object move (audible)	Signaller grasps an object by hand or foot and then moves it along the floor making a sound	Move object (5), Move (1)	Branch shaking, Branch waving (7)	Object move	Object move	Drag Object
Pat (contact)	"Rapidly repeatedly contacting another individual with flattened palm surface of hand, not in play. Repetitive" Pollick and de Waal, 2007	Body beat (5), Pat (4), Patting (2)	-	-	Drum other	-
Peer (visual-silent)	"Closely approach recipient and stare at its mouth or hands" Schneider et al., 2011	Walk to other end of cage and gaze at partner (14), Peer (1,5), Look (1)	Peer (15)	Look	Look	Peer

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Pirouette (visual-silent)	While standing bipedally the body is rotated around the head-feet axis in full circles	Spin body (6), Ice skate (1)	-	Pirouette	Pirouette	-
Poke (contact)	Extended finger or fingers are brought into contact with the recipient's body	Poke, Hard touch (4)	Poke (7)	Poke	Poke	Poke
Pounce (contact)	Body displaces through the air to land onto the body of the recipient	-	-	Pounce	Pounce	-
Punch other (contact)	Knuckles of hand are brought into hard short contact with the body of the recipient	Hit (5), Punch (1), Punching (2)	-	Punch other	Punch	-

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Push other (contact)	Palm is placed against the recipient's body and a brief but strong force is applied	Push (1)	-	Push	Push 1-handed	Push
Rack pose (visual-silent)	One or both arms are extended above the head where the hands grasp onto the substrate above and/or behind the signaller	-	-	-	-	-
Reach (visual-silent)	Arm is extended towards the recipient with the palm facing up or down	Reach out down, Reach out side, Reach out up, Point (4), Extend arm (5), Raise limb (6), Approach (13), Move hand toward another portion of the cage (14), Reach (1), Stretch over (2), Beg (3), Beg with hand (4), Begging gesture (2)	Extend hand palm downward (7), Extend hand (15), Food begging (15), Begging (16)	Reach	Reach	Reach

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Rocking (visual-silent)	While seated, the body is moved forward and backward repeatedly	-	Rocking (17)	-	Rocking	-
Shake hands (contact)	Signaller grasps the recipient's hand and proceeds to move the recipient's hand back and forth in repeated movements	-	-	Shake hands	-	Hold hands
Shake object (visual-silent)	"Wave object mainly with ones hand" Schneider et al., 2011	Shake object (5)	Branch shake (8), branching (15)	Object shake	Shake object	Shake object
Side roulade (visual-silent)	While lying on the ground the signaller rolls along the floor, side over side	-	Rolls over (15)	Side roulade	Side roulade	-

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Slap object (audible)	Palm of hand is brought down onto an object in a hard short movement resulting in a sound	Hit object (5), Rhythmic movements (2), Slap ground (1, 4)	Branch slap (8)	Slap object	Slap object 1-handed, Slap object 2-handed	Hit ground/object
Slap other (contact)	Palm or palms are brought down onto the body of the recipient in a hard short movement	Hit (5), Slap (1)	-	Slap other	Slap other, Slap other 2-handed	Hit, simultaneous hit
Slap stomp (audible)	"Simultaneous slap ground and stomp" Pollick and de Waal, 2007	Slap stomp (4)	-	-	-	-
Somersault (visual-silent)	"Animal makes a flip" Pika et al., 2005	Somersault (1)	-	Somersault	Somersault	-

Gesture Type	**Definition (Milwaukee unless otherwise specified)**	**Other captive bonobos**	**Wild bonobos**	**Chimpanzee, wild (10)**	**Gorilla, wild and captive (11)**	**Orangutan, captive (12)**
Stand with one foot slightly lifted (visual-silent)	"Stand with one foot slightly lifted, the sole facing toward the rear, in a stationary walking position" Kano, 1992	-	Stand with one foot slightly lifted (15)	Foot present	-	-
Starfish pose (visual-silent)	The signaller lies back onto the ground and spreads out both arms and legs, the genital region remains oriented towards the recipient	Spread legs (6), Present (1), Ventral present (2)	Rolls over on back and spreads thighs (15)	-	-	-
Stomp (audible)	One of both feet are used to strike the ground in a loud and repetitive manner	Stomp (1, 4), Foot stomp (5), Step foot (6), Rhythmic movements (2), Stomp with foot (3)	Stamp bipedal (7)	Stomp, Stomp 2-feet	Multiple stamp, 2 feet on object; Stamp 2-feet, on object, Stamp object, Stamp, 2-feet, Stamp	-

Gesture Type	**Definition (Milwaukee unless otherwise specified)**	**Other captive bonobos**	**Wild bonobos**	**Chimpanzee, wild (10)**	**Gorilla, wild and captive (11)**	**Orangutan, captive (12)**
Stomp other (contact)	One or both feet are used to strike the body of the recipient	-	Stamp other (7)	Stomp other, Stomp 2-feet other	-	-
Stroking (contact)	The fingers of the hand are moved lightly across the body of the recipient in a sweeping motion	-	-	Touch Other	Stroking	Brush
Suspended hand (visual-silent)	One or both hands are held in the air at eye level, palms are angled toward the recipient	Hold hand toward partner (14), Arm up (2)	Raise arm with elbow bent (7)	Present grooming	-	-
Swagger (visual-silent)	Signaller shifts weight from one leg to the other while standing bipedally, arms are raised slightly from below the shoulder	Arm wave (4), Bipedal swagger (2)	Bipedal swagger (15)	-	Bipedal run/walk	-

Gesture Type	**Definition (Milwaukee unless otherwise specified)**	**Other captive bonobos**	**Wild bonobos**	**Chimpanzee, wild (10)**	**Gorilla, wild and captive (11)**	**Orangutan, captive (12)**
Tandem shake object (contact)	One or both hands are used to grasp and shake an object in which the recipient is currently in bodily contact with	Shake object (5)	Branch shake (8), branching (15)	Object shake	Hand shake with object, Hands shake with object	-
Tandem slap object (contact)	One or both palms are used to strike an object in which the recipient is currently in bodily contact with	Hit object (5), Rhythmic movements (2), Slap ground (1, 4)	Branch slap (8)	Slap object	Slap object 1-handed, Slap object 2-handed	-
Tap other (contact)	A finger or fingers are brought into short light contact with the recipient's body in a repetitive motion	-	-	Tap other	Tapping	Tap

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Throw aimed (visual-silent)	"Over or underarm throw of object, including loose dirt, in forward direction while looking at target, not in play" Pollick and de Waal, 2007	Throw aimed (4)	-	Throw object	Throw object	-

Gesture Type	Definition (Milwaukee unless otherwise specified)	Other captive bonobos	Wild bonobos	Chimpanzee, wild (10)	Gorilla, wild and captive (11)	Orangutan, captive (12)
Touch other (contact)	One or both hands are brought into brief light contact with the body of the recipient	Gentle touch (4), Touch (1, 3, 6), Touch outside of partner's shoulder, hip or thigh, and motion across body with hand and forearm movement, Touch hand or arm and motion outward from partner's body, Rest knuckles on arm or back and move arm toward self, Touch shoulder or back and move hand toward self, Touch head, chin or inside of shoulder and lift hand upward, Touch partner and walk to other end of the cage (14), Finger/hand in mouth (4)	Touch (15), Gentle touch (7)	Touch other	Touch	Touch

3.3.2 Individual Repertoire

Repertoire size for each bonobo ranged from 2 to 36 gesture types (n= 17, mean= 18 ± 10.53). The effect of age class on repertoire size was not tested as there were too few individuals in each category. Does sex affect how many types of gestures a bonobo performed throughout the study period? Considering the full repertoires of each bonobo, there was a significant effect of sex with females using more gesture types than males (Mann Whitney U test two-tailed, $U = 68.5$, $P = 0.001$, $r = 16.61$). Does sex affect how often a bonobo uses gestures (i.e. how many gesture tokens per unit time)? Controlling for the amount of time each animal was present during hours of observation I found that females gestured more frequently than males (Mann Whitney U test two-tailed, $U = 62$, $P = 0.007$). Overall, the size of an individual's repertoire increased along with the amount of time he or she was present during observation. As seen in figure 3.1, the group as a whole were approaching asymptote in their use of new gesture types. When plotting the individual repertoire size for each bonobo a similar curve to the overall group repertoire is observed. However no individual appears to have reached asymptote for individual repertoire size.

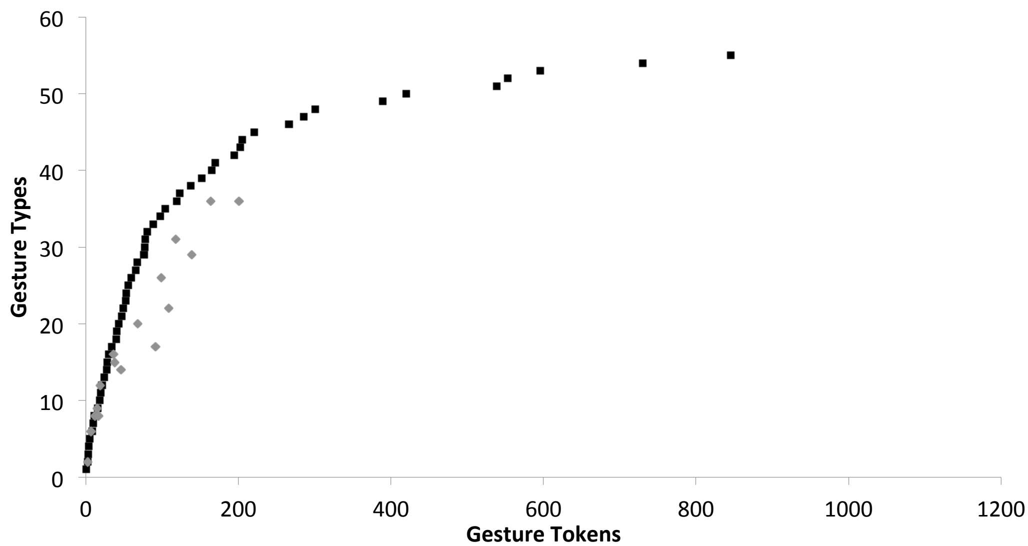


Figure 3.1. The cumulative record of gesture types used by Milwaukee bonobos. The cumulative number of gesture types is plotted against the y-axis and the cumulative number of gesture tokens is plotted against the x-axis. Black squares represent new gesture types seen across all signallers. Grey diamonds represent each individual studied for a total of 17 data points. Each grey dot represents the total number of gesture types seen by an individual plotted against the total number of gesture tokens performed by the signaller throughout the study.

3.3.3 Adjustment to Recipient's Attentional State

Do bonobos adjust their use of gestures depending on the attentional state of their intended audience? For this analysis I only considered gestures that were used in the beginning of a communication bout, leaving 1080 gesture tokens for analysis. Only two attentional states were considered: attending and out-of-site (see section 2.4.3 for definitions). Using a one-way anova, comparing the proportional use of gesture mode for each attentional state, I found a significant effect of gesture mode in terms of the recipient's attentional state ($f_{5,24} = 9.46$, $P < 0.001$) Specifically, contact gestures were more likely to be used by a signaller towards a recipient who was outside of her view (i.e. out-of-site, see definition in section 2.4.3) than towards a recipient who was attending (attending: n = 5, mean = 69.05 ± 45.00; out-of-sight: n = 4, mean = -10.17 ± 5.90; planned t-test $t = -3.90$, $df = 4.14$, $p = 0.016$) and visible-silent gestures were more likely to be used for a recipient who was attending than for one who was out-of-sight (attending: n = 5, mean = 13.23 ± 6.88; out-of-sight: n = 5, mean = -76.64 ± 29.32; planned t-test $t = 6.67$, $df = 4.44$, $P = 0.002$). The use of audible gestures did not differ between attentional states (attending: n = 5, mean = 1.62 ± 15.79; out-of-sight: n = 5, mean = -13.29 ± 61.63; planned t-test $t = 0.52$, $df = 4.52$, $P = 0.625$, see figure 3.2).

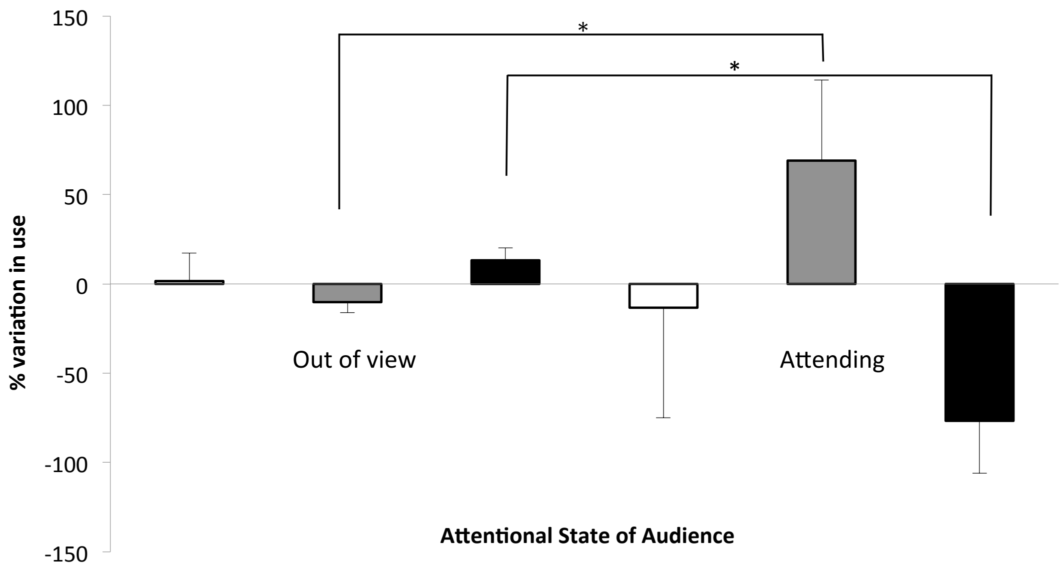


Figure 3.2. Variation in the use of gesture modes based on the recipient's state of attention.

Black bars represent contact gestures, grey bars represent visible-silent gestures and white bars represent audible gestures. The percentage variation of each gesture mode is presented on the y-axis and the types of mode are presented on the x-axes, divided by attentional state. Changes from the zero point indicate that the use of a particular gesture mode (contact, visible-silent or audible) for the particular attentional state (attending or out-of-sight) increased or decreased from the overall use of that particular gesture mode. Planned t-tests were used to explore whether the type of gesture mode used changed based on the attentional state of the audience. Both contact and visible-silent gestures differ significantly in their relative usage between attentional states.

3.3.4 Flexibility

In line with previous studies of ape gestural communication (Genty et al., 2009; Hobaiter and Byrne, 2011; Call and Tomasello, 2007) I analysed the flexibility of gestures in terms of how many situational contexts each gesture type was used for. I calculated the number of associated situational contexts for each gesture type (see figure 3.3). Gestures used at least 3 times by each signaller were included in analysis (Genty et al., 2009). Signallers who used a gesture type at least 3 times were included in analysis. Most gesture types were used for 3 contexts or less across signallers (3 contexts or less: n = 14, mean = 7.71 ± 4.75; 4 contexts or more: n = 14, mean = 1.79 ± 1.81; Wilcoxon signed rank test $Z = 104$, $P < 0.001$).

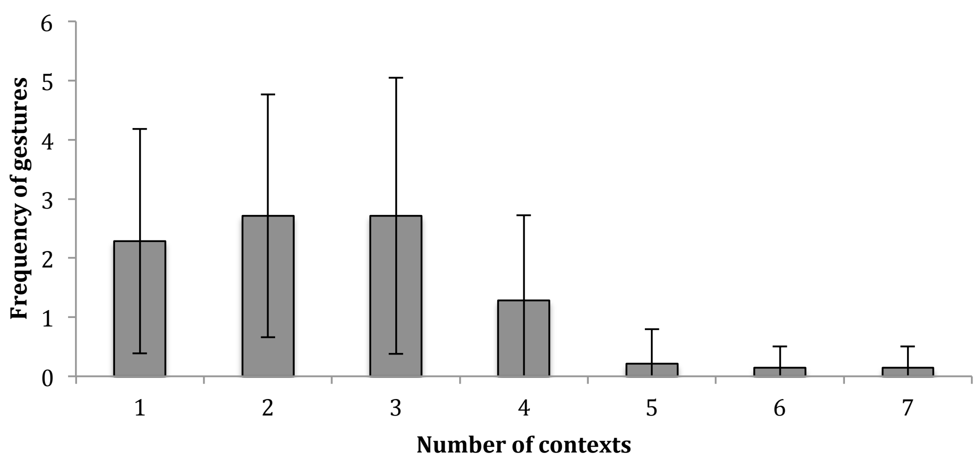


Figure 3.3. Number of behavioural contexts in which a gesture type was used. Error bars represent standard deviations across signallers.

3.4 Discussion

This study demonstrated that bonobos use a range of gestures with intention and that they use those gestures within a range of situational contexts. Milwaukee bonobos were observed using 55 distinct gesture types, almost twice as many as have been reported in any single previous study of bonobo gestural communication (Pika et al., 2005; Schneider et al., 2011; Halina et al., 2013; Pollick and de Waal, 2007; de Waal, 1988; Savage-Rumbaugh et al., 1977). When including gestures observed in previous bonobo studies, the count of gestures within the bonobo repertoire rises to 70 putting bonobos in the same range as the number of gestures reported for chimpanzees (66 gestures, Hobaiter and Byrne, 2011). Two gestures described in this study were new to the study of ape gestures: *body swing* and *rack pose*. Although it is possible that these gestures are novel to Milwaukee bonobos, a new female, Elikia, who entered the group mid-way through the study period, was also observed using the gesture *rack pose.* It is unknown whether she used this gesture at her previous zoo. Although this study has added a large number of gestures to the bonobo repertoire, most of the gestures reported here for the first time in bonobos have actually been described already in other ape species.

Bonobos use gestures within 9 contexts: affiliation, agonism, feeding, GG rubbing, grooming, resting, sexual, social play, or traveling. These contexts are similar to the ones used by previous gesture researchers for other ape species (Hobaiter and Byrne, 2011, Genty et al., 2009) and were maintained for this study for the benefit of comparative analysis. Most gesture types were used for 3 contexts or less across signallers showing that bonobos are using gestures flexibly across contexts confirming what has been found in previous studies of ape gestural communication (Call and Tomasello, 2007; Liebal, 2007; Pika, 2007a; Pika 2007b).

I found that bonobos adjust their use of gestures depending on whether their target recipient is attending to them. When the recipient is looking away from the signaller then the signaller is more likely to direct a contact gesture towards the recipient. When the recipient is attending to the signaller then the signaller is more likely to direct a visible-silent gesture towards the recipient. The result indicates that bonobos are flexible in their use of gestures dependent upon their recipient's current state of attention which confirms what has been found in previous studies of ape gestural communication (for bonobos: Pika et al., 2005; for gorillas: Genty et al., 2009, for orangutans: Liebal et al., 2006; and for chimpanzees: Liebal et al., 2004)

Considering the entire known repertoire of bonobos (including both gestures observed in this study and gestures observed in previous studies of bonobo gestures), 70 gestures, how many overlap with other species of ape? From a study of wild chimpanzees there are 57 gestures that are shared between chimpanzees and bonobos (Hobaiter and Byrne, 2011). From a study of wild and captive gorillas there are 46 gestures that are shared between gorillas and bonobos (Genty et al., 2009). From a study of captive orangutans there are 28 gestures that are shared between orangutans and bonobos (Cartmill and Byrne, 2010). The pattern of decreasing overlap in number of gesture types between bonobos and other ape species follows that of decreasing relatedness between bonobos and other ape species. Chimpanzees are the most closely related great ape to bonobos and they share the largest number of gestures types (last common ancestor 0.9 million years ago, Won and Hey, 2005). Gorillas are more distantly related and share fewer gestures (diverged 6.4 million years ago from the great ape line, Stauffer et al., 2001). Orangutans are the most distantly related great ape to bonobos and in turn orangutans and bonobos share the least gesture types (diverged from the great ape line between 11.3 million years ago, Stauffer et al., 2001). Overall, there were 21 gesture types shared by all four species of great ape.

This study has presented an analysis of captive bonobo gestures. I have compared the repertoire of Milwaukee bonobos, as observed during my time at the Milwaukee County Zoo, to that of previous work from other researchers of bonobo gestures both of wild and captive animals. By compiling these studies I have shown that bonobos have a known repertoire of 70 gestures and that those gestures overlap with other ape species more or less depending on the relatedness between the two ape species. To further my study of bonobo gestural communication I next evaluate the meanings of gestures.

Chapter 4: Meanings of Gestures

4.1 Introduction

Only recently have researchers analysed ape gestures for the *effect* they have on the target audience: i.e. what the goal behind gestural communication is (Genty et al., 2009; Cartmill and Byrne, 2010; Hobaiter and Byrne, 2014, Roberts et al. 2012). Prior work focused exclusively on the associated contexts of gestures (e.g. what situational context the gesture occurs within, for example the context of play or the context of grooming, Tomasello and Call, 2007). However, describing a gesture by context alone can be misleading. For example, gestures may occur during a bout of grooming, but those gestures could be used for several different goals within the context of grooming. A gesture may elicit grooming from the recipient, may initiate grooming towards the recipient, or may stop the grooming session all together. Should the signaller be satisfied with the behavioural reaction of the recipient, however, then those behaviours can be inferred to be the intended meaning of the gesture. If it happens that gestures are used consistently for the same intended meanings across signallers then it is possible to build a 'dictionary' of gestures and their associated intended meanings. Building a gesture dictionary for apes could resemble a word dictionary, as both are supposed to extract the core meaning of the gestures or words present within a population's repertoire. I also expect that if individual bonobos are found to use gestures consistently for the same meaning then the same gestures should be used for the same meanings across bonobos in Milwaukee.

Bonobos are of particular interest for studies of gestural communication due to their novel social structure and behaviours. Bonobos have been described as having an egalitarian and female-biased society (de Waal, 1995). Female bonobos maintain close relationships with one another (Wrangham, 1993), a quality which is assumed to raise their dominance status, as compared to female chimpanzees (Furuichi, 2009). Bonobos also exhibit heightened levels of socio-sexuality, with sex frequently divorced from reproduction and used socially (de Waal, 1989; Furuichi, 1989; Hohmann and Fruth, 2000; Idani, 1991; Kano, 1989). Indeed, one particular sexual behaviour unique to bonobos is GG rubbing, where two participating bonobos rub their genitalia together in a vigorous fashion (Hohmann and Fruth, 2000; Kuroda, 1980). Since bonobos seek novel interactions with their conspecifics they may also use novel gestures to initiate those interactions. In chapter 3, I identified 6 gestures unique to bonobos: *rack pose*, *body swing, body shake*, *crab pose*, *knock other*, and *starfish pose.* In this chapter I explore the uses of these gestures by Milwaukee bonobos and whether or not they were used to initiate bonobo specific behaviour such as GG rubbing.

4.2 Specific method

Only successful communication bouts contributed to analysis of Apparently Satisfactory Outcomes (i.e. the action performed by the recipient that occurred just before the signaller ended communicative effort, ASO, see section 2.4.4). The ASO that was used more frequently than all other ASOs was labelled the primary ASO for the particular gesture type. The second most frequently used ASO was labelled as the secondary ASO. To determine whether specific gestures were used for specific ASOs I compared the frequency with which each gesture type was used for each ASO with the overall frequency all ASOs were used across all gestures types and signallers.

I then compared primary ASOs across signallers for each gesture type. In previous studies of ape gestures play was found to be the most common use of gestural communication (Cartmill and Byrne, 2010, Genty et al., 2009). The broad use of gestures for play-related ASOs poses a problem for gesture meaning. Play itself is a special circumstance where signals and behaviours are used in a playful way and gestures used within play may not represent the general meaning of a gesture.

For example, a play bout may include behaviours that outside of play would be considered aggressive. For instance, a slap used outside of play may lead to an aggressive encounter between two individuals. Within the context of play, however, a slap may lead to more playing. Since the context of play may modify how a behaviour is perceived then it is imperative that the context of play receive special attention in the analysis of gesture meanings.

Therefore, I first excluded play-related ASOs from the initial analysis of gestures and their associated primary and secondary ASOs. I next included play-related ASOs and analysed gestures that were not analysed in the previous analysis (i.e. did not have enough successful communication events to qualify for the initial analysis when play-related ASOs were removed).

4.3 Results

4.3.1 Apparently Satisfactory Outcomes of Milwaukee bonobos

Within the data set, there were 562 communication events for which I was able to code an ASO. Table 4.1 provides definitions for the 16 ASOs in this study along with a comparison with other ape species and their reported communicative ASOs (There was a 17th ASO categorized as "unknown" indicating an unknown outcome of an act of gestural communication. Such events are excluded from further analysis). Of the 16 ASOs 14 were used to increase association between the signaller and the recipient: "climb on me", "follow ahead", "follow behind", "GG rub start", "give affiliation", "grab on", "groom me", "move closer", "move into position", "play start chase", "play start contact", "start sex", "straddle me" and "travel together". Two ASOs were used to decrease association between signaller and recipient: "move away" and "stop behaviour".

Table 4.1 Cross-species comparison of ASOs observed during intentional communication.

ASOs reported for other ape species from the following studies: (1) Hobaiter and Byrne, 2013, (2) Genty et al., 2009, (3) Cartmill and Byrne, 2010

Function	**Definition**	**Chimpanzee equivalent (1)**	**Gorilla equivalent (2)**	**Orangutan equivalent (3)**
Climb on me	Recipient climbs up onto the body of the signaller and rests on top of the signaller's back	Climb on me	Travel invitation	-
Follow behind	Recipient follows behind the signaller while both are travelling in the same direction	Follow me	-	-
Follow ahead	Recipient walks ahead of the signaller while both are travelling in the same direction	-	-	-
GG rub start	Recipient presses his or her genitals onto the genitals of the signaller and initiates GG rubbing	-	-	-
Give affiliation	Recipient associates with the signaller through bodily contact	Contact	Cuddle invitation	-
Grab on	The hands of both signaller and recipient are used to grab hold of each other, usually in the context of travel	-	-	-
Groom me	Recipient begins grooming the signaller	Initiate grooming, Attend to specific location	-	-
Move away	Recipient moves away for the signaller	Move away	Displace	Move away
Move closer	Recipient moves closer to the signaller	Move closer	Approach invitation	-
Move into position	Recipient moves and holds the indicated body part towards the recipient.	Reposition body, Climb on you, Groom you	-	-

Function	Definition	Chimpanzee equivalent (1)	Gorilla equivalent (2)	Orangutan equivalent (3)
Play start contact	Recipient and signaller engage in a play bout where bodily contact is maintained	Play start, play change: increase intensity, Play resume	Contact play invitation	Affiliate/Play
Play start chase	Recipient either runs ahead or runs behind the signaller during a bout of chasing play	Play start, Play change: decrease intensity, Play resume	Chase invitation	Affiliate/Play
Start sex	Recipient presses his or her genitals onto the genitals of the signaller and initiates sexual intercourse	Give sexual attention to female, Give sexual attention to male	-	Sexual Contact
Stop behaviour	Recipient stops performing the behaviour that was previously being directed towards the signaller	Stop that	Calm down request, stop approach, stop	Stop action
Straddle me	Recipient climbs onto the signaller's body and wraps her legs around the signaller's torso while facing the signaller	-	-	-
Travel together	Recipient puts one or both arms onto the back of the recipient while both travel together in tandem.	-	Travel invitation	Co-locomote
Unknown	No observable response or an unsatisfactory response is give to the signaller	Unknown	No outcome	No outcome

4.3.2 Specificity of meaning

Is a given gesture associated with a specific ASO? In other words, do gestures have specific meanings? For the analysis of gesture meanings I only considered gestures that were used singly (e.g. not within a sequence of gestures). Although a conservative analysis, removing communication events that included multiple uses of gestures was necessary as the analysis of gesture meanings assigns cause and effect between gestures and changes in recipient behaviour. To include communication events where gestures are used in a rapid sequence assumes that these communication events initiated the same outcome as when gestures were used individually. Such a comparison, between communication events involving a single gesture token and communication events involving multiple gesture tokens and whether those communication events effect the same change in recipient behaviour, is beyond the scope of this study as I only recorded 23 communication events where a signaller used gestures in a rapid sequence and that also ended with an identifiable ASO. Thus this study focuses on the 459 communication events where a signaller used gestures singly and that ended with an identifiable ASO. In order to preserve comparability between studies of chimpanzees and bonobos I followed Hobaiter and Byrne (2014) in their analysis of meaning. There were 32 gesture types that were used at least 3 times across signallers. On average a gesture type was associated with 3.75 ASOs (n = 32, range 1-12, sd= 2.38). Because most gestures were not associated with a single ASO I identified the primary and secondary ASO for each gesture type. Excluding play-related ASOs from analysis, there were 22 gesture types that were used at least 3 times across the remaining ASOs. After identifying the primary and secondary ASOs for each gesture type I then compared the distribution of ASOs for each gesture type against the overall distribution of ASOs for all gesture types. If there were at least 3 signallers using a particular gesture type at least 3 times each I employed a 2-way ANOVA. Because different signallers contribute different amounts to each analysis individual identity was set as a random variable. ASO type was set as the dependent variable. I compared the percentage use of a gesture towards each ASO with the percentage use of all gesture types towards each ASO. When insufficient data was available for a parametric ANOVA, I used a chi-square test comparing the distribution of ASOs for a single gesture type with the distribution of ASOs for all gesture types. Results of statistical analysis are presented in table 4.2. Individual identity did not significantly influence the outcome of any of the 2-way ANOVAs. Fifteen of the 22 gestures analysed had a significantly different distribution of ASOs as compared to the distribution of ASOs for all gesture types.

Table 4.2 Gesture meanings (excluding play-related ASOs)

Gesture tokens that have been used outside of a sequence and have been assigned an Apparently Satisfactory Outcome (ASO) are included in the analysis of gesture meanings. Primary and secondary meanings are presented under the column 'ASO (%)'. If more than one ASO qualified as a primary meaning then the primary meanings were listed side by side with forward slashes separating them. Secondary meanings are presented in parenthesis. The distribution of each gesture towards different ASOs is compared to the overall distribution of gestures towards different ASOs. Bold p-values represent significant statistical tests.

Gesture type	**ASO (%)**	**Evidence**
Arm swing	Climb on me/Move away/Travel together 33%	X^2=28.32, df=13, N=3, **p=0.008**
Body swing	GG rub start 67% (Straddle me 33%)	X^2=21.90, df=13, N=3, p=0.057
Directed push	Follow ahead/Move into position 37% (Move away 16%)	f=1.86, df=13, 26 p=0.086
Display back	Climb on me 76% (Groom me 15%)	f=11.88, df=13, 65 **p<0.001**
Display chest	Start sex 78% (Groom me 22%)	X^2=168.51, df=13, N=9, **p<0.001**
Display face	Groom me 100%	X^2=17.43, df=13, N=4, p=0.180
Display limb	Groom me 93% (Give affiliation/Move away 3%)	f=393.1, df=13, 39 **p<0.001**
Grab	Grab on 63% (Move into position 25%)	X^2=22.06, df=13, N=8, p=0.054
Grab pull	Climb on me/Follow behind/Move into position 22% (Follow ahead/GG rub start/Groom me 11%)	X^2=18.95, df=13, N=9, p=0.125
Hand on	Grab on 43% (Straddle me 29%)	X^2=22.15, df=13, N=7, p=0.053

Gesture type	ASO (%)	Evidence
Hand shake	Give affiliation 50% (GG rub start/Move into position/Start sex 17%)	X^2=40.21, df=13, N=6, **p=0.001**
Head shake	Move closer 50% (Give affiliation/Move away 25%)	X^2=50.41, df=13, N=4, **p<0.001**
Head stand	Move into position 100%	X^2=35.63, df=13, N=5 **p<0.001**
Limp hand	Groom me 77% (Grab on/Move away/Stop behaviour 8%)	f=20.71, df=13, 26 **p<0.001**
Rack pose	GG rub start 55% (Groom me/Start sex 15%)	f=3.26, df=13, 26 **p=0.005**
Reach	Grab on 62% (Climb on me/Groom me 15%)	X^2=29.01, df=13, N=13, **p=0.007**
Slap other	Move away 33% (Follow behind/Give affiliation/Move closer 117%)	X^2=32.57, df=13, N=6, **p=0.002**
Starfish pose	GG rub start 75% (Straddle me 25%)	X^2=60.20, df=13, N=8, **p<0.001**
Stomp	Follow behind 75% (Straddle me 25%)	X^2=89.93, df=13, N=4, **p<0.001**
Stroking	Follow ahead 74% (Move into position 25%)	X^2=44.18, df=13, N=4, **p<0.001**
Suspended hand	Grab on 56% (Move into position 27%)	f=5.03, df=13, 52 **p<0.001**
Touch other	Follow ahead/Grab on 12% (Groom me/Move away/Move closer 10%)	f=1.41, df=13, 65 p=0.18

When play-related ASOs were included in the analysis of gesture meanings there were a 10 further gesture types that had been used at least 3 times across signallers. As with the analysis of gestures without play-related ASOs, I used either parametric 2-way ANOVAs or chi-square tests comparing the distribution of ASOs for a specific gesture type with the distribution of ASOs for all gestures. All 10 gesture types in this analysis have either "play start contact" or "play start chase" as the primary ASO (see table 4.3). In 5 of the 10 gesture types was there a significant difference between the gesture specific distribution and the null distribution of ASOs. The relatively low number of significant results is unsurprising since the most frequently used ASOs across all gesture types are play-related ASOs.

Table 4.3 Gesture meanings (including play-related ASOs)

Gesture tokens that have been used outside of a sequence and have been assigned an Apparently Satisfactory Outcome (ASO) are included in the analysis of gesture meanings. Primary and secondary meanings are presented under the column 'ASO (%)'. If more than one ASO qualified as a primary meaning then the primary meanings were listed side by side with forward slashes separating them. Secondary meanings are presented in parenthesis. The distributions of each gesture towards different ASOs compared to the overall distribution of gestures towards different ASOs. Bold p-values represent significant statistical tests.

Gesture type	**ASO (%)**	**Evidence**
Arm raise	Play start contact 75% (Groom me/Straddle me 13%)	X^2=20.10, df=15, N=8, p=0.168
Bite	Play start contact 67% (Move away 33%)	X^2=11.73, df=15, N=3, p=0.700
Hang upside down	Play start contact 100%	X^2=45.09, df=15, N=11, **p<0.001**
Hang upside up	Play start contact 91% (GG rub start 9%)	X^2=36.77, df=15, N=11, **p=0.001**
Jump	Play start contact 100%	X^2=12.08, df=15, N=3, p=0.673
Kick	Play start chase 60% (Play start contact 40%)	X^2=42.57, df=15, N=5, **p<0.001**
Object move	Play start chase 74% (Follow behind 25%)	X^2=63.08, df=15, N=4, **p<0.001**
Punch other	Play start contact/GG rub start/Follow ahead 33%	X^2=12.90, df=15, N=3, p=0.610
Push other	Play start chase/Move away 50%	X^2=44.28 df=15, N=4, **p<0.001**
Stomp other	Play start contact 50% (Play start chase 33%)	X^2=21.74, df=15, N=6, p=0.115

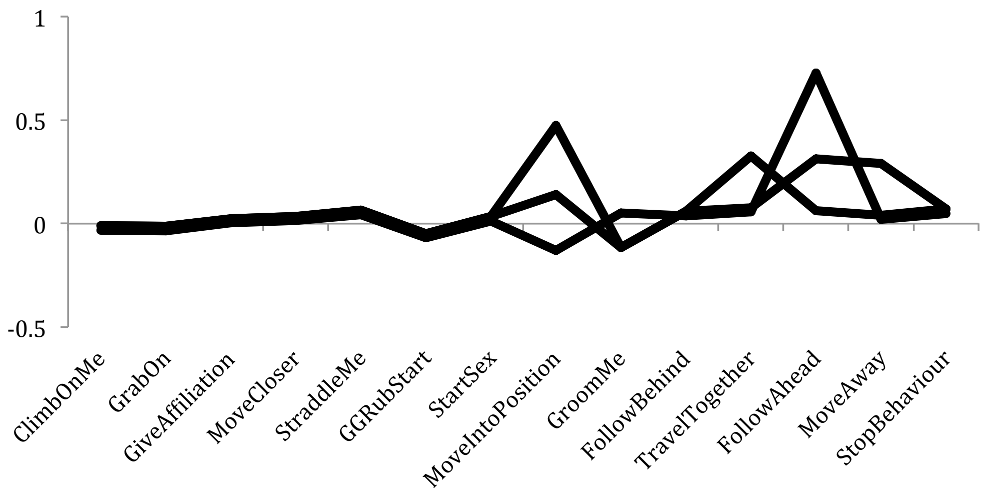
4.3.3 Comparing the primary use of gestures between signallers

In section 4.3.2 I presented the population wide uses of gestures. Combining the numbers for all signallers who used a particular gesture type at least 3 times successfully, I extracted the primary and secondary ASOs for the gesture in question. In this section I explore the individual uses of gestures. Do different signallers use the same gesture to achieve a given ASO? To be included in the analysis a gesture type must have been used by at least 3 signallers at least 3 times each (and used successfully). As in section 4.3.2 I've removed instances where gestures were used for play-related ASOs. The gestures that qualified for this analysis are the same that qualified for the non-play-related ANOVA analyses in section 4.3.2 (see table 4.2). Seven gestures qualified for analysis and are presented in figure 4.1. Whether individual signallers use gestures for the same ASOs is visually presented in figure 4.1. For each gesture, the signallers that qualified for analysis are represented individually. I plotted each signaller's use of each ASO as the deviation from the null distribution for the general use of the gesture for each ASO.

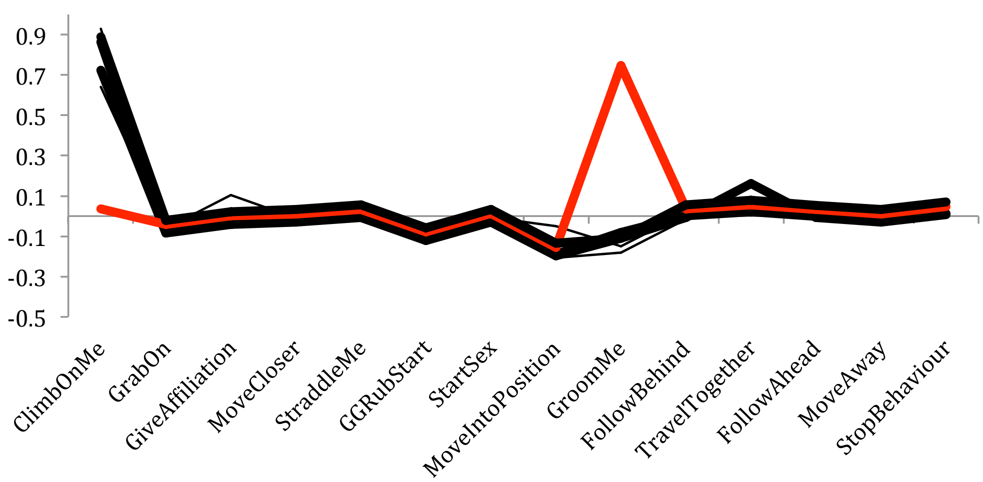
According to figure 4.1, 5 of the 7 gestures have clear associations with ASOs across signallers (where a majority of signallers use a gesture type for the same primary ASO), namely *display back* with "climb on me", *display limb* with "groom me", *limp hand* with "groom me", *rack pose* with "GG rub start", and *suspended hand* with "grab on". For 2 gestures there was not a clear association between gestures and ASOs across signallers: *directed push* and *touch other*.

There were two cases where the who the signaller was influenced how a gesture was used. In the first example, one male differed in his use of the gesture *display back* as compared to the several female signallers who qualified for analysis. The male in question, Lody, used *display back* primarily for the ASO "groom me" while the female signallers used the gesture *display back* primarily for the ASO "climb on me". However, Lody using *display back* for "groom me" is not a novel use of the gesture: 7 other signallers of both sexes also used *display back* for the ASO "groom me". In fact, "groom me” can be considered the secondary ASO for the gesture type *display back* (see table 4.2). In the second example, one male differed in his use of the gesture *rack pose* as compared to the several female signallers who qualified for analysis. The male in question, Zuri, used *rack pose* primarily for the ASO “start sex” while the female signallers used the gesture *rack pose* primarily for the ASO “GG rub start”. However, Zuri using *rack pose* for “start sex” is not a novel use of the gesture: 4 other signallers of both sexes also used *rack pose* for the ASO “start sex”. In fact “start sex” can be considered the secondary ASO for the gesture type *rack pose* (see table 4.2). In these two examples, only one male is included in each of the analyses. The males may have behaved differently from the females but with only a single example male to compare with, the data is too limited to claim actual sex differences in the usage of gestures for particular ASOs.

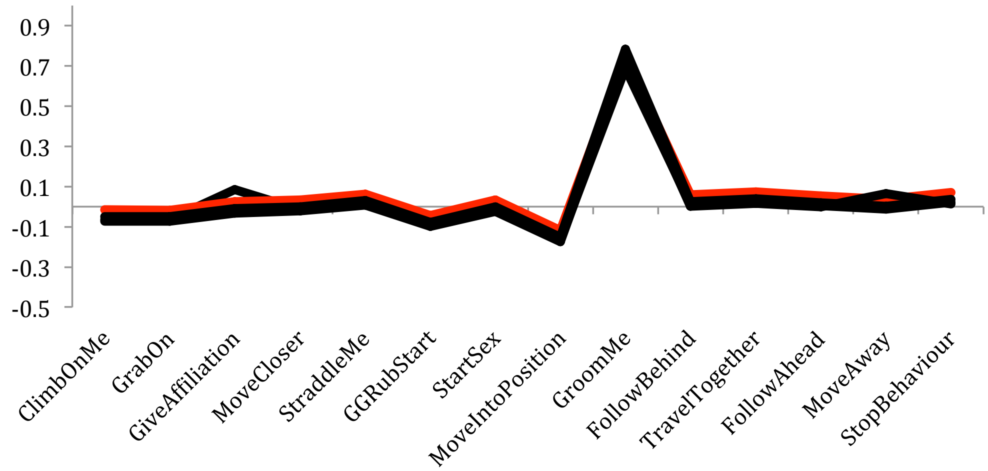
Directed Push



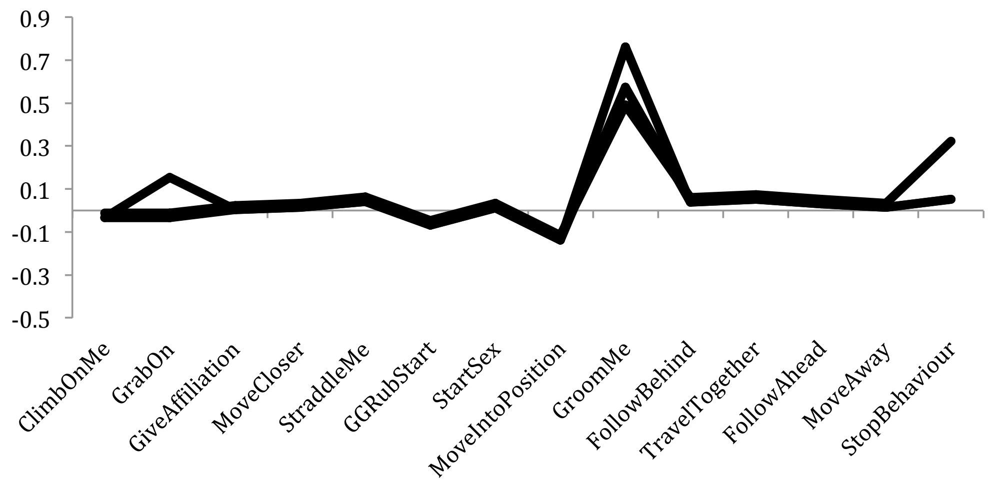
Display Back



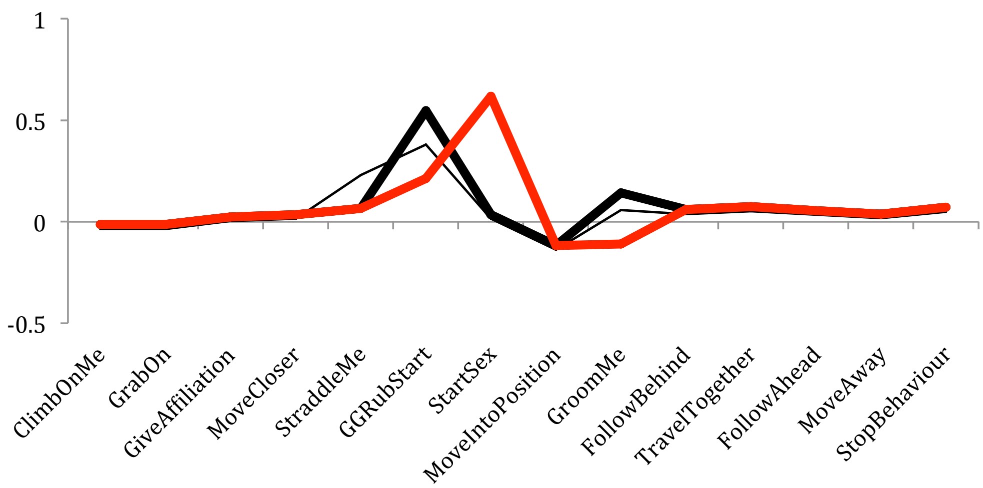
Display Limb



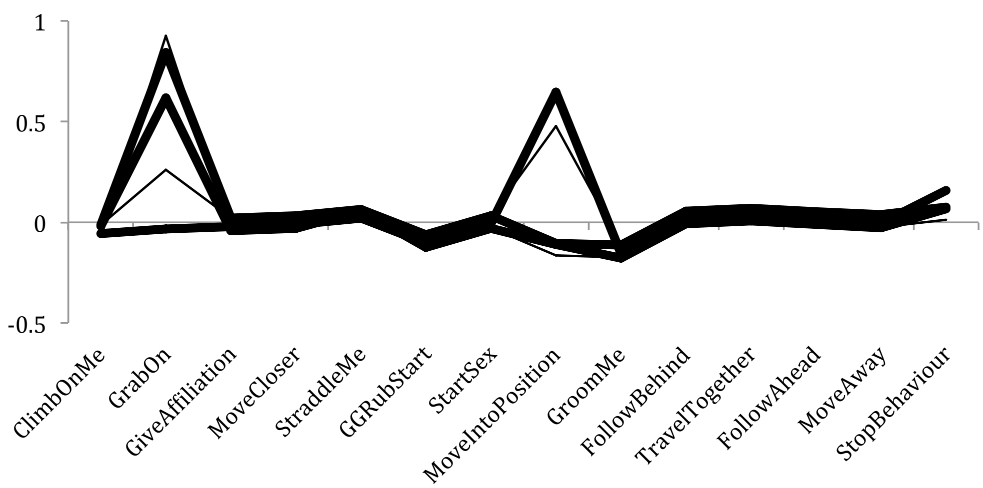
Limp Hand



Rack Pose



Suspended Hand



Touch Other

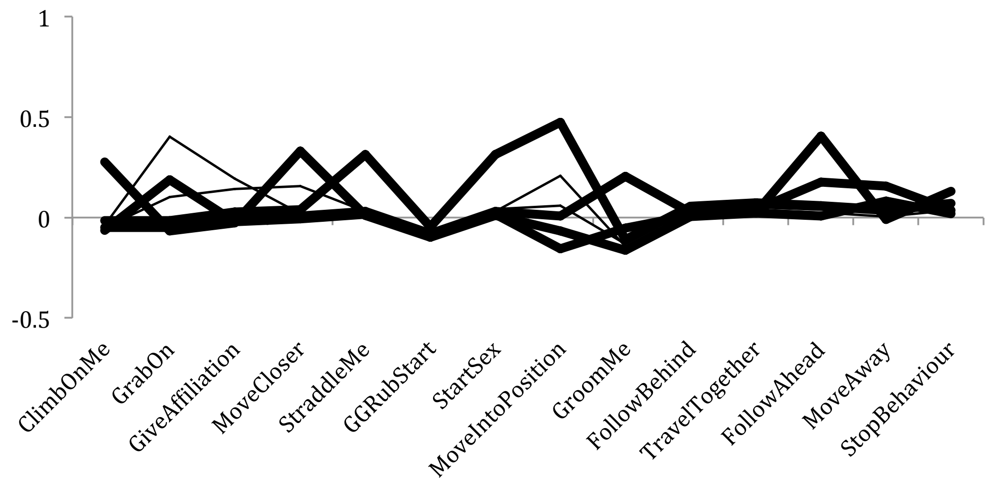


Figure 4.1 Individual uses of gesture types

For each gesture type the signallers who have used the gesture at least 3 times each are plotted. Y-axis represents the percentage deviation from the null distribution of ASOs that each signaller used the gesture type. ASOs are listed along the x-axis and are grouped by similarity in meaning. Bold lines = mature signallers; Thin lines = immature signallers; Black lines = females, Red lines = males.

4.4 Discussion

This study demonstrated that bonobos use gestures for particular meanings. Milwaukee bonobos used gestures for 16 Apparently Satisfactory Outcomes most of which were used to increase contact or to amplify an already occurring interaction between the signaller and the recipient (14 of the 16 ASOs involved positive requests such as “move closer”, 2 involved negative requests such as “move away”).

Bonobos tended to use the same gestures for the same meaning: an individual bonobo is consistent in her use of gestures for particular ASOs, and gestures are used for the same ASOs across signallers. In most cases a gesture was used primarily for one ASO and secondarily (i.e. to a lesser extent) for another ASO. Any signaller can theoretically use either the primary or secondary ASO of a gesture. However, some ASOs are only used by specific types of signallers or directed towards specific types of recipients. For example, *display back* is primarily used to mean “climb on me” and secondarily used to mean “groom me”. “Climb on me” is always directed towards a conspecific smaller than the signaller herself. Therefore a younger bonobo should never be observed using the gesture *display back* to mean “climb on me” if her recipient is larger than herself. In the same vein, if an adult male bonobo is never observed carrying an infant on his back then he should never be found using the gesture *display back* to mean “climb on me”. Instead his use of the gesture will fall towards the secondary meaning of *display back,* that being “groom me”. Who is using the gesture and whom he or she is sending the gesture to is of great interest for studies of gestural communication for though individual use of gestures may not affect the primary meaning of gestures at the population level, individual use of gestures for particular ASOs may deviate based on other variables (i.e. age and sex). As apes use gestures to regulate social interactions through imperative requests, then it follows that the social context surrounding a communication event should influence who is communicating with whom and for what purpose. Further analysis into the association between variables associated with different types of signallers and their different uses of gestures is presented in chapter 5.

By assigning ASOs to communication events, I was able to uncover the uses of gestures unique to bonobos. Three of the six bonobo-specific gestures, *body swing*, *rack pose* and *starfish pose*, are primarily used to mean “GG rub start”. The other 3 gestures were not observed frequently enough to ascribed meaning to; however, both *crab pose* and *body shake* were observed being used for the ASO “GG rub start”. Thus there appears to be an association between a bonobo-specific gestures and bonobo-specific behaviours.

All four species of great ape use gestures to both increase and decrease association between a signaller and her recipient. It is also true for all four species of great ape the meanings that increase affiliation between signaller and recipient out weigh the meanings that decrease affiliation between signaller and recipient. In bonobos, there were 14 ASOs that involved increasing contact or affiliation between the signaller and the recipient while there were only 2 ASOs that involved decreasing contact between the signaller and the recipient. A similar disparity between positive and negative ASOs have been observed in chimpanzees (15 vs. 2, Hobaiter, 2010), gorillas (7 vs. 3, Genty et al., 2009) and orangutans (10 vs. 2, Cartmill and Byrne, 2010). Why this trend persists across the great ape species is unknown. Are there more meanings attributed to positive interactions because there are more positive interactions occurring among apes? Or is it that apes are more likely to use intentional communication surrounding positive interactions as compared to those of negative interactions?

This study has presented an analysis of the meanings of bonobo gestures. I have shown that many gestures used by bonobos are used consistently for the same meanings both by an individual and across individuals. Next I consider the influence sociality as on gestural communication and whether age or sex of the signaller influences what types of meanings are communicated and in what context.

Chapter 5: Sociality and gestural communication

5.1 Introduction

Primates are well known for forming bonded relationships amongst group members that mimic the intense form of pair-bonding found in other animal taxa where two animals spend a significant amount of time together caring for their common offspring. This type of extended pair-bonding in apes take the form of extended time investment where two group members will engage in a variety of affiliative behaviours together. An individual can therefore expect to maintain many different types of relationships across her lifetime (Dunbar and Schultz, 2007). Maintaining social relationships has evolutionary advantages: it has been shown that for female chacma baboons, an individual who is better at maintaining social bonds will tend to live longer (Silk et al., 2010) and in wild savannah baboons, highly social females tend to have more offspring survive to adulthood, thereby increasing their reproductive success (Silk et al., 2003). Sustaining multiple social relationships requires tracking the locations and behaviours of social partners, while discriminating between dyadic relationships in terms of age, sex, kinship and previous interactions (e.g. dominance relationship) of the other. Effective management of social relationships not only depends on correctly identifying and categorizing individuals, but also on moderating one's behaviour in light of this information (Pellis and Iwaniuk, 2000). For animals living in large social groups, using a set of communicative signals can help in both coordinating behaviours and in minimizing conflict between group members (Seyfarth et al., 2010; Call and Tomasello, 2007). Since gestural communication is used to mediate social interactions between a signaller and her intended recipient (see chapter 4), I propose that apes should modify their use of gestures depending on whom their recipient is. More than adjusting one's use of gestures for the type of audience, a signaller will be more or less likely to use gestures in certain contexts or for certain purposes dependent upon who he or she is (i.e. the signaller's age and sex).

For non-human primates, the number of types of vocalizations a species produces correlates with the overall social group size of that species (McComb and Semple, 2005). There is also a positive relationship between facial mobility (an indirect measure of variation in facial expressions) and social group size (Dobson, 2009). The suggested evolutionary function of a larger communicative repertoire has been to enable better management of a complex social network (Freeberg et al., 2012). In a comparative study, Gustison et al. (2012) compared two closely related primates: geladas and chacma baboons. Geladas had an overall larger vocal repertoire as well as greater social bondedness between males and females of the species. Moreover, the derived vocalizations found in geladas were used exclusively by males towards their female associates suggesting that the larger vocal repertoire was directly useful towards maintaining social bonds between male and female geladas. If increasing communicative complexity provides a social group with an increasing ability to regulate social interactions, then it is fundamental to understand how social interactions are being regulated via communication. The study of gestural communication in apes brings a new tool to the field. By observing natural gestural communication in ape species, researchers can describe both the gesture being used as well as what the gesture is being used for (Genty et al., 2009; Hobaiter and Byrne, 2011; Cartmill and Byrne, 2010). As apes use gestures to regulate social interactions then I expect the social context surrounding a communication event to influence what is being communicated.

As a bonobo, age and sex determines whom you will interact with and in what way. A bonobo begins life as an infant being cared for and carried about by his or her mother and other older members of the community. As the bonobo grows older he or she will spend more time playing with peers and engaging socio-sexual behaviours (Kano, 1992). Eventually the bonobo reaches adulthood. At this life stage the largest differences are seen between the sexes in terms of whom one associates with. As adults, female bonobos tend to maintain close bonds with other female bonobos. Adult males do not form close bonds with other male bonobos but they do maintain close relationships with their mothers during adulthood (Furuichi, 1989). As a bonobo's age and sex influences the types of social interactions she will have and whom she will interact with, age and sex should also influence how a bonobo uses gestural communication.

The aim of this study is to uncover the communication patterns of bonobos as it varies with signaller's age and sex. As described in chapters 3 and 4, Milwaukee bonobos use 55 gestures within 9 contexts and for 16 purposes. I studied a population of bonobos that represented a range of age and sexes: was there an influence of signaller age or sex on patterns of gestural communication? First I explore the influence of age and sex on the signaller's use of gestures for different contexts and for different types of ASOs. Next I explore the influence of recipient age or sex as it pertains to a signaller's use of gestures for different ASOs.

5.2 Specific method

To explore communicative similarities among classes of signallers, I employed multivariate analyses. Initially I ran hierarchical clustering analysis to identify groups of signallers with similar communicative profiles. Agglomerative hierarchical clustering analysis was based on distance matrices between signallers and either contexts or ASOs. The agglomerative method of clustering begins with n groups of size 1 and joins groups based on similarity. P-values are calculated by multi-scale bootstrap resampling and indicate how strongly the cluster assignments are supported by the data (Suzuki and Shimodaira, 2006). Only successful communication events were included in the hierarchical clustering analyses.

I next ran correspondence analysis to explore associations between types of signallers, contexts and ASOs. Correspondence analysis (CA) works like principal component analysis, in that it attempts to explain most of the variability within a dataset with as few dimensions as possible, but is optimized for count data. Two similar and common approaches in multivariate analysis are factor analysis and principal component analysis. Factor analysis is optimized for data that has a high number of subjects relative to the number of variables (Mundfrom et al., 2005); this was not true for my data, as there were a relatively equivalent numbers of subjects (i.e. 17 bonobos) to number of variables in each category (i.e. 16 ASOs and 9 contexts). Principal component analysis requires that variables be linearly correlated. From an initial exploration of the data I found that signallers, ASOs and contexts have low levels of linear correlation (Spearman rho correlation estimates: signallers with context, $r = 0.009$; signallers with ASOs, $r = 0.085$; context with ASOs, $r = 0.090$). I therefore used correspondence analyses to investigate the communication behaviour of Milwaukee bonobos. CA assumes that the data being analysed is categorical, non-negative and that there is dependency between the columns and rows in the contingency table. As with principal component analysis, CA is particularly useful for graphically representing the data as points in a 2 or 3-dimensional plot.

For each CA I set up a matrix by entering signallers as the rows and the corresponding communicative element, either context or ASO, as the columns. Minimum frequency for row and column totals was set at 10 (Bendixen, 2003); employing a minimum frequency requirement for rows and columns ensures that the contexts, ASOs and signallers that are included in analysis are well represented within the dataset. Only successful communication events were included in the analyses. Any signaller that did not meet criteria for inclusion in the model was set as a supplementary point; in CA supplementary points have no influence on the approximating space but are still assigned dimensional coordinates.

After running an initial CA I looked for any outliers. An outlier is a row or column that has dimensional coordinates greater than 1 (representing standard deviation from the centre of the mass in the system) and contributes significantly towards the total inertia, the percentage of total variance, of that dimension. Outliers are a problem in CA as they dominate the results and mask other correlations (Bendixen, 2003). Outliers were set as supplementary points and the analysis was re-run. Results of each CA are presented in two or three-dimensional plots.

5.3 Results

5.3.1 Do similar types of signallers communicate within similar types of contexts?

Milwaukee bonobos use gestures in 9 contexts. To identify groups of signallers with similar communication profiles based on their use of gestures within contexts I ran a hierarchical cluster analysis. The dendrogram from the analysis is presented in figure 5.1. Red boxes indicate significance at $\alpha \leq 0.05$ and represent clusters with strong support based on the data. Two main clusters are identified in figure 5.1. The two clusters group signallers by sex, with most females falling into cluster 15 (the right-most cluster, figure 5.1) and all of the males plus two females (Elikia and Laura) falling into cluster 13. This result indicates that males and females tend to communicate within different contexts.

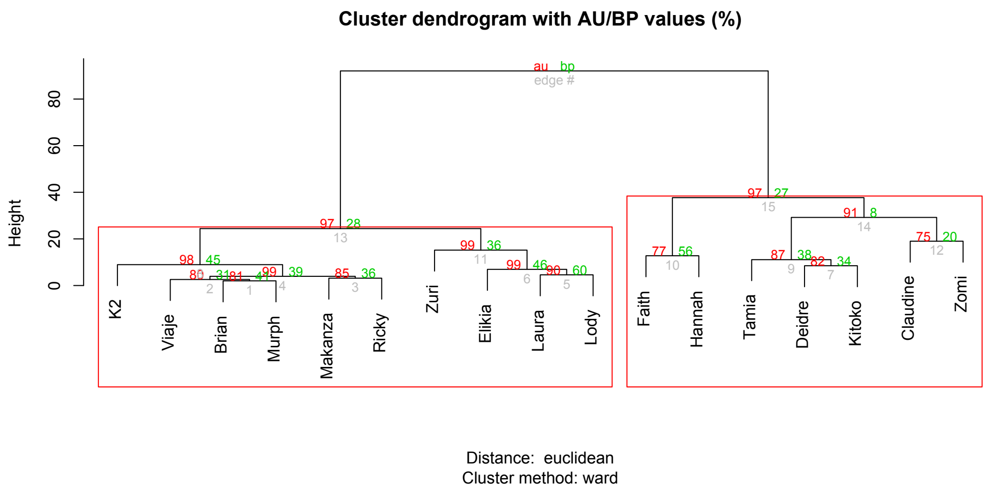


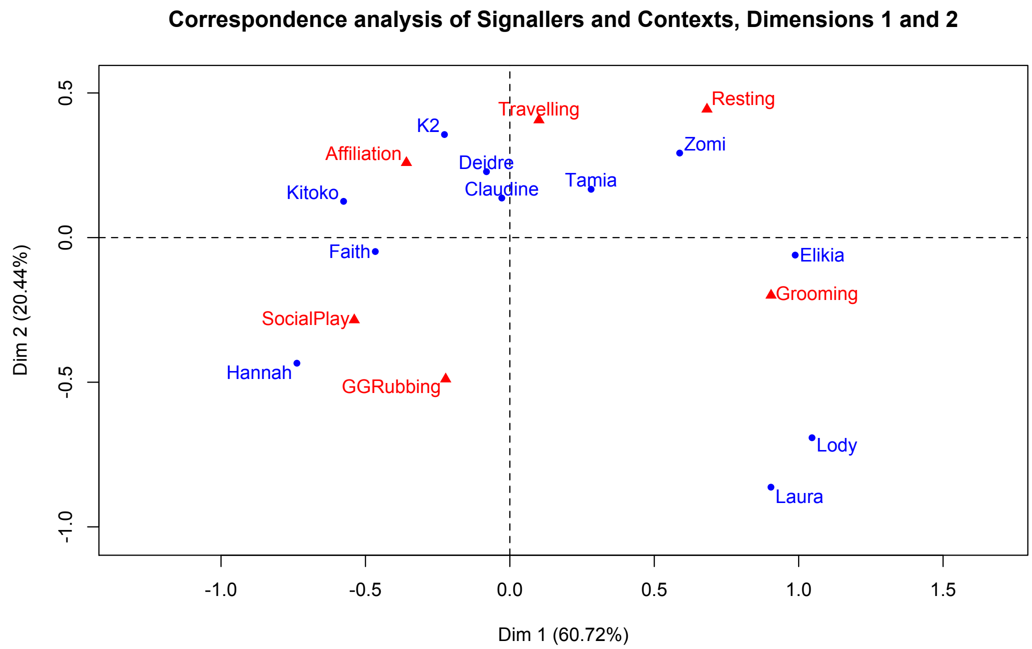
Figure 5.1 Hierarchical clustering of signallers by the contexts of communication in which they gesture.

Values at branches are approximately unbiased p-values (AU, left side, labelled in red) and bootstrap probability (BP, right side, labelled in green). Red boxes indicate clusters with p-values less than 0.05 (i.e. AU > 95). Height on y-axis represents the Euclidian distance between the clusters that each node joins.

To identify associations between signallers and specific contexts I ran a correspondence analysis, with signallers entered as the rows and contexts as the columns. Twelve signallers and 7 contexts qualified for analysis: signallers Claudine, Deidre, Elikia, Faith, Hannah, K2, Kitoko, Laura, Lody, Tamia, Zomi and Zuri; contexts affiliation, GG rubbing, grooming, resting, sexual, social play and travelling. There was a significant dependency between the rows and columns (Chi square = 352.9, df = 78, $P < 0.001$). After running an initial CA I identified two outliers: the signaller Zuri and the context sexual. Entering both outliers as supplementary points I ran the final CA. Out of 5 dimensions, 4 accounted for over 90% of variance within the model. The values for dimensions 1 through 4 are as follows: 60.7, 20.4, 9.4 and 6.3 respectively. The first two dimensions are presented in graph 5.1. Each signaller and each context were assigned coordinates (i.e. the level of association between the signaller or context in question and the particular dimension) for each dimension and those coordinates are used to plot signaller and contexts in graph 5.1. Each context's level of contribution to the total inertia for each dimension is presented in table 5.1. Signallers located near each other have similar patterns of communication in terms of context; signallers located away from each other on the graph have dissimilar patterns of communication in terms of context. Contexts located near each other have similar profiles of signallers; contexts located away from each other on the graph have dissimilar profiles of signallers.

To interpret the meaning of the dimensions extracted, I first identified contexts that contributed most highly towards each dimension. Since 6 contexts were entered for the final analysis, a high-contributing context was one that had a contribution higher than $1/6^{th}$ or 16.67 to the total inertia of the dimension in question (see table 5.1). There were two contexts that contributed more than average to dimension 1: grooming, which has a positive dimension coordinate, and social play, which has a negative dimension coordinate. Older bonobos (adults) tend to be on the positive end of dimension 1, while younger bonobos (infants, juveniles and adolescents) are found further to the negative end. Using a chi square test of independence I found that older bonobos were more likely to communicate in the context of grooming, as compared to younger bonobos who were more likely to communicate in the context of social play (Chi square test, $X2 = 39.78$, $n = 208$, $P < 0.000$).

For dimension 2, there were 3 contexts that contributed more than average towards the dimension (based on inertia, see table 5.1): affiliation and travelling, which have a positive dimension coordinates, and social play, which has a negative dimension coordinate. Infants and females with dependent offspring tend to be located on the positive end of dimension 2, indicating that infants and mothers were more likely to communicate within the contexts of affiliation and travelling as compared to the context of social play. No clear grouping by age or sex appears on the negative end of dimension 2. Using a binomial test I found that infants and mothers were more likely to communicate in the context of affiliation and travelling as compared to the context of social play (Exact binomial test, number of instances where infants and mothers communicate within the contexts of affiliation and travelling = 100, number of trials = 136, $P < 0.001$).



Graph 5.1 Correspondence analysis plot of signallers and context dimensions 1 and 2.

Signallers and contexts are plotted by dimension coordinates. Signallers are coloured blue, contexts are coloured red.

Table 5.1 Contribution of each context towards the first two dimensions (percentage)

Context	Contribution towards dimension 1	Contribution towards dimension 2
Affiliation	11.43	17.69
GG rubbing	1.28	13.01
Grooming	60.64	6.98
Resting	3.90	1.68
Social play	22.21	25.56
Travelling	0.53	35.08

5.3.2 Do similar types of signallers communicate similar types of goals?

Milwaukee bonobos use gestures for 16 ASOs. To identify groups of signallers with similar communication profiles based on ASOs I ran a hierarchical cluster analysis. The dendrogram from the analysis is presented in figure 5.2. Red boxes indicate significance at $\alpha \leq 0.05$ and represent clusters with strong support based on the data. Four main clusters are identified in figure 5.2. The four clusters split the signallers into groups of mixed sex and age. Cluster 6 (the left-most cluster, figure 5.2, clusters are labelled as they are created by the statistical package) contains most of the males. Cluster 11 contains older females along with two males (Lody and Zuri). Cluster 12 contains two younger females; Hannah, a juvenile; and Kitoko, an infant. Cluster 9 contains Claudine and Faith: an adult and an adolescent female. These results indicate that neither age nor sex influences the types of goals a signaller tends to communicate.

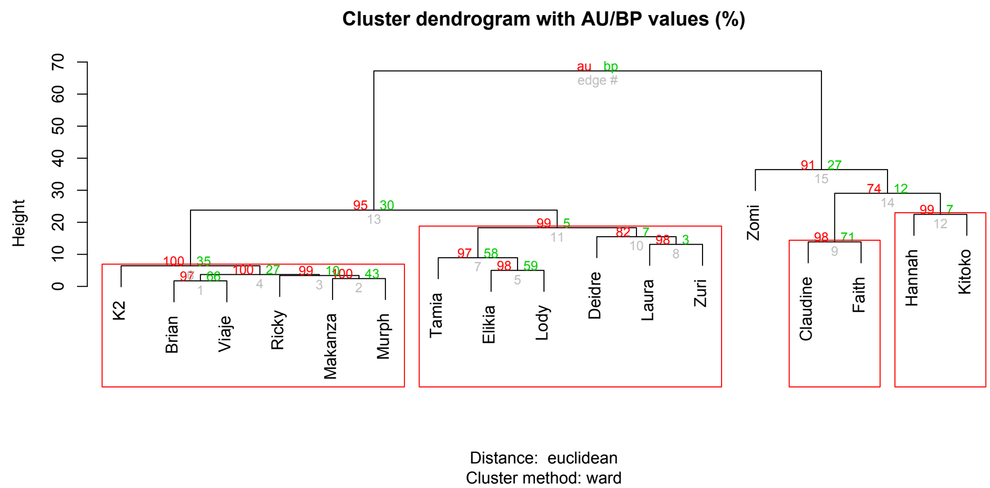


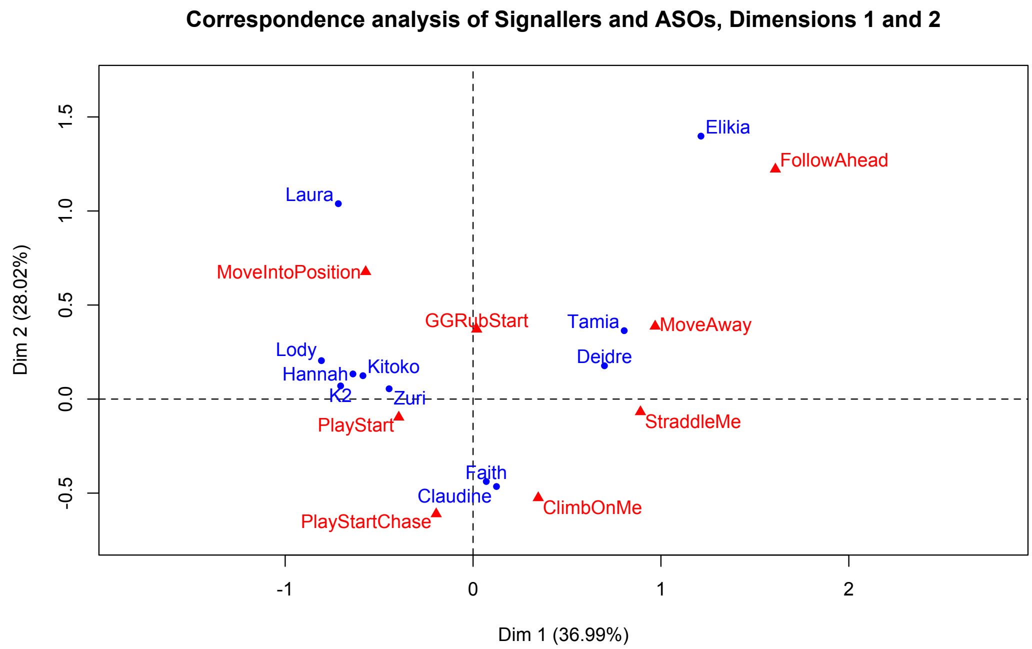
Figure 5.2 Hierarchical clustering of signallers by ASOs they used when gesturing. Values at branches are approximately unbiased p-values (AU, left side, labelled in red) and bootstrap probability (BP, right side, labelled in green). Red boxes indicate clusters with p-values less than 0.05 (i.e. AU > 95). Height on y-axis represents the Euclidian distance between the clusters that each node joins.

To identify associations between signallers and specific ASOs I ran a correspondence analysis, with signallers entered as the rows and ASOs as the columns. Twelve signallers and 12 ASOs qualified for analysis: signallers Claudine, Deidre, Elikia, Faith, Hannah, K2, Kitoko, Laura, Lody, Tamia, Zomi and Zuri; ASOs “climb on me”, “follow ahead”, “GG rub start”, “give affiliation”, “grab on”, “groom me”, “move away”, “move into position”, “play start contact”, “play start chase”, “start sex” and “straddle me”. There was significant dependency between the rows and columns (Chi square = 600.5, df = 121, P-value <0.000). The initial CA showed 5 outliers: 1 signaller Zomi; 4 ASOs “give affiliation”, “grab on”, “groom me” and “start sex”. Outliers were re-entered as supplementary points for the final analysis. Out of 7 dimensions 5 accounted for over 90% of total inertia. Dimensions 1 through 5 had the following inertia levels: 37.0, 28.0, 16.1, 8.6 and 6.0. The first two dimensions are presented in graph 5.2. The third dimension is plotted against dimension 1 in graph 5.3. Each ASO's level of contribution to the total inertia for each dimension is presented in table 5.2. Signallers located near each other in graphs 5.2 and 5.3 have similar patterns of communication in terms of what types of ASOs they tend to use; signallers located far away from each other on the graph have dissimilar patterns of communication in terms of what types of ASOs they tend to use. ASOs located near each other have similar profiles of signallers; ASOs located away from each other on the graph have dissimilar profiles of signallers.

To interpret the meaning of the dimensions extracted, I examined which ASOs contributed most highly towards each dimension. Since 8 ASOs were entered for the final analysis, a high-contributing ASO was one that had a contribution higher than 12.5 to the total inertia of the dimension in question (see table 5.2). There were 4 ASOs that contributed more than average to dimension 1: "follow ahead" and "move away", which have positive dimension coordinates, and "move into position" and "play start contact", which have negative dimension coordinates. Older females (adults and adolescents) tended to be on the positive end of the spectrum while males and younger females (infants, juveniles) are found further to the negative end of the spectrum. Using chi square test of independence I find that older females (adults and adolescents) were more likely to communicate both "follow ahead" and "move away" than do males and younger females (Chi square test, X2 = 29.99, n = 163, $P < 0.000$).

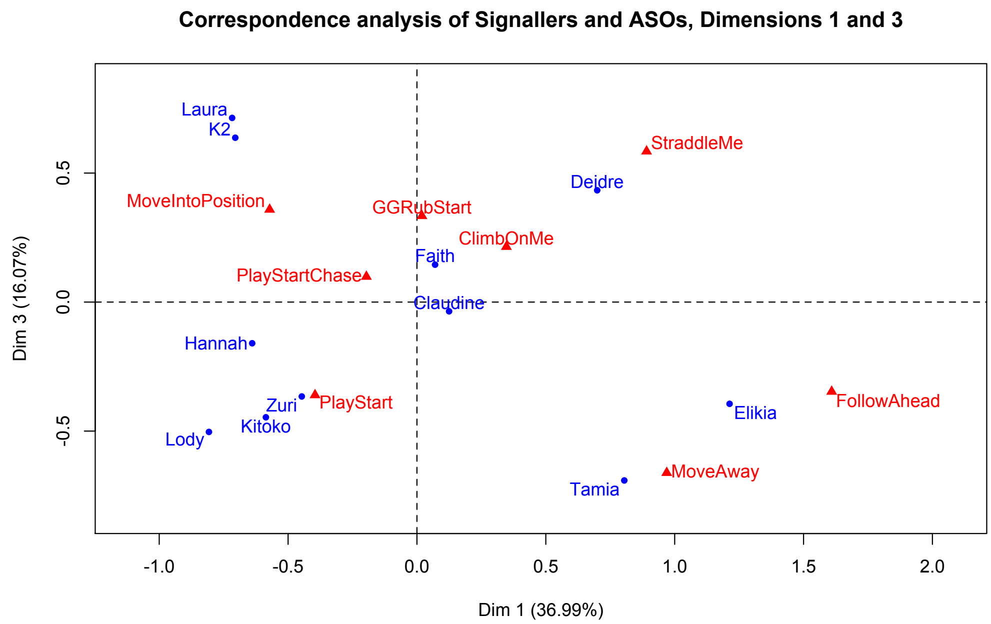
For dimension 2, there were 3 ASOs that contributed more than average towards the dimension: "move into position" which has a positive dimension coordinate, and "climb on me" and "follow ahead" which have negative dimension coordinates. Two bonobos, Claudine and Faith, are located on the negative end of dimension 2 whereas all other signallers are located on the positive end. Note that Claudine and Faith, an adult and an adolescent female, were also isolated in their own cluster (cluster 9, see figure 5.2) in the hierarchical clustering analysis. Using a binomial test I found that Claudine and Faith were more likely to use "climb on me" and "follow ahead" as compared to "move into position (Exact binomial test, number of instances where Claudine and Faith used "climb on me" and "follow ahead" = 38, number of trials = 43, $P < 0.001$). However, Claudine and Faith never used “follow ahead” and therefore are mapping strongly onto the negative side of dimension 2 solely for their relatively heavy use of “climb on me” as compared to “move into position”.

For dimension 3, there were 3 ASOs that contributed more than average towards the dimension: “move into position” which has a positive dimension coordinate, and “move away” and “play start contact” which have negative dimension coordinates (see Graph 5.3). No clear age or sex grouping appears in dimension 3. All three dimensions are presented together in a single 3D plot in Graph 5.4.



Graph 5.2 The first two dimensions of the correspondence analysis of signallers and their respective use of ASOs.

Signallers and ASOs are plotted by their dimension coordinates. Signallers are coloured blue. ASOs are coloured red.

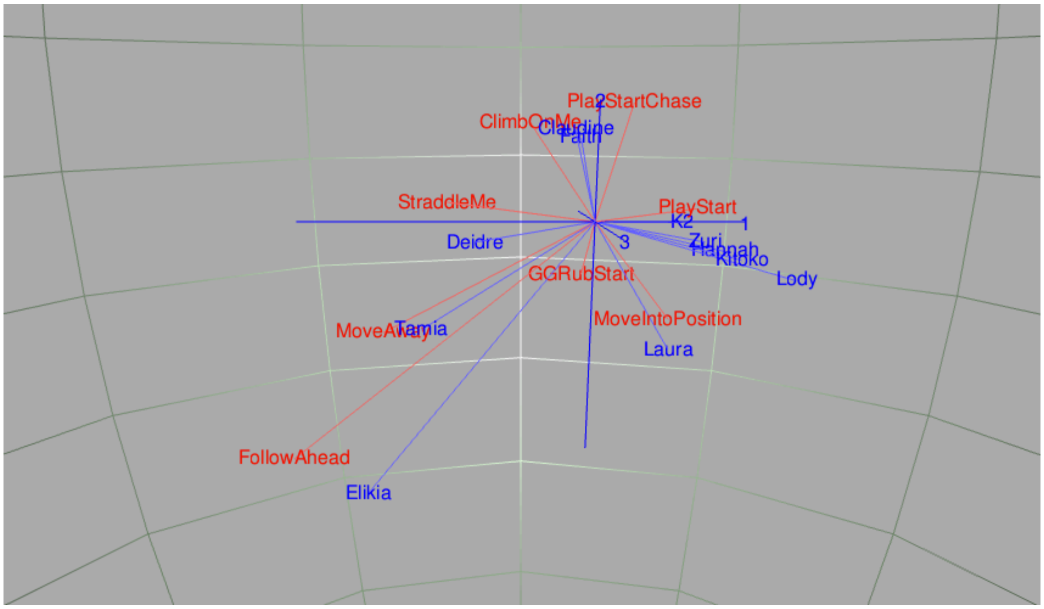


Graph 5.3 The first and third dimensions of the correspondence analysis of signallers and their respective use of ASOs.

Signallers and ASOs are plotted by dimension coordinates. Signallers are coloured blue, ASOs are coloured red.

Table 5.2 Contribution of each ASO towards the first three dimensions (per cent)

ASO	Contribution towards Dimension 1	Contribution towards Dimension 2	Contribution towards Dimension 3
Climb on me	9.16	27.67	8.05
Follow ahead	25.05	19.08	2.68
GG rub start	0.01	6.03	8.52
Move away	19.47	4.10	20.90
Move into position	16.25	30.12	14.73
Play start contact	17.08	1.34	32.65
Play start chase	0.90	11.57	0.53
Straddle me	12.07	0.09	11.95



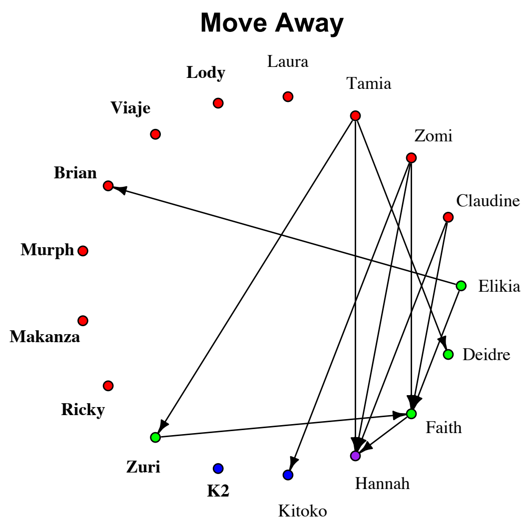
Graph 5.4 Plot of dimensions 1, 2 and 3 from the correspondence analysis of signallers and ASOs.

X-axis represents dimension 1, Y-axis represents dimensions 2, Z-axis represents dimension 3. Signallers and ASOs are plotted by dimension coordinates. Signallers are coloured blue. ASOs are coloured red.

5.3.3 Do signallers use specific ASOs for specific recipients?

The clearest demonstration of social group differences in the use of gestural communication appeared in dimension 1 of the correspondence analysis of ASOs is (see graph 5.2). Using a chi square test I found that older females (adults and adolescents) were more likely to communicate both “follow ahead” and “move away” than either males or younger females. To visualize the communicative differences between bonobo signallers I plotted social networks for both “follow ahead” and “move away”. For these social networks I included all 17 bonobos observed during the course of the study. In the social network graphs nodes represent individual bonobos and edges represent the direction of communication going from signaller to recipient. From the social networks it appears that older females are more likely to use both “follow ahead” and “move away’ as compared to younger females and males, confirming what was found in dimension 1 of the correspondence analysis.

From the social network diagrams there appears to be directionality involved in the use of “move away” and “follow ahead”. It turns out that these ASOs are used almost exclusively by older bonobos towards younger bonobos (Exact binomial test, number of instances where the signaller was older than recipient = 36, number of trials = 50, $P < 0.001$). The 14 exceptions all involved communication events where females signalled towards males.


Move Away
Lody
Laura
Tamia
Viaje
Zomi
Brian
Claudine
Murph
Elikia
Makanza
Deidre
Ricky
Faith
Zuri
K2
Kitoko
Hannah

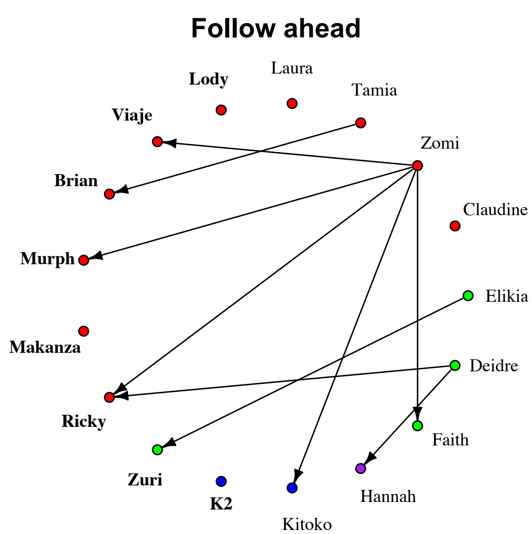

Follow ahead
Lody
Laura
Tamia
Viaje
Zomi
Brian
Claudine
Murph
Elikia
Makanza
Deidre
Ricky
Faith
Zuri
K2
Kitoko
Hannah

Diagram 5.1 Social networks of the 5 ASOs from dimension 1 of the correspondence analysis between Signallers and ASOs.

Arrows represent the direction of communication from the signaller towards the recipient. Bonobos are coloured by age group: red for adults, green for adolescents, purple for juveniles, blue for infants. Males are marked by bold font. Older animals are located towards the top of each diagram. Males are located to the left.

5.4 Discussion

This study demonstrated that signallers vary in their use of gestures based on both their age and sex. Through multivariate analysis I found that signallers use gestures for different ASOs and within different contexts based on their age or sex. Further, I found that particular signallers use particular ASOs and direct those ASOs towards particular recipients. These findings present preliminary evidence that bonobos are able to deploy their gestures flexibly depending upon social context of the communication event. By using gestures flexibly among recipients then signallers may be capable of using those gestures to manage their social relationships.

I first analysed signallers and their use of gestures for different contexts. Hierarchical clustering analysis split the bonobos into two clusters: one cluster consisted mostly of males and the other cluster consisted mostly of females. I next used correspondence analysis to find specific associations between signallers and contexts. I found that older bonobos are more likely to use gestures in the context of grooming while younger bonobos are more likely to use gestures in the context of play. I also found that infants and mothers with dependent offspring were more likely to use gestures within the context of travelling than they were to use gestures within the context of play.

I next analysed signallers and their use of gestures for different ASOs. Hierarchical clustering analysis split the bonobos into 4 clusters of mixed age and sex. The result indicates that bonobo use of ASOs is not necessarily based on the age and sex of the signaller. I next used correspondence analysis to find specific associations between signallers and ASOx. I found that older females were more likely to use gestures for the ASOs “follow ahead” and “move away” as compared to males and younger females. I also found that two females, Claudine and Faith, were more likely to use ASOs “climb on me” and as compared to the ASO “move into position”.

Although my study did not include an analysis of hierarchy among Milwaukee bonobos there may have been an effect of rank on signalling. "Move away", one of the two non-affiliative ASOs present in the bonobo repertoire, was used almost exclusively by the typically dominant members of bonobo communities: older females. Dominance studies of bonobo hierarchies are based on who displaces whom (Stevens et al., 2005, 2007; Vervaecke et al., 2000) with higher rank assigned to apes that are more likely to displace others rather than being displaced themselves. In bonobo society, females tend to gain higher rank as compared to other ape species and so older females using the ASO "move away" may be indicative of their generally higher status among conspecifics.

Rank may also influence gestural communication for bonobos that fall on the lower end of the hierarchical spectrum. Claudine and Faith fell into the same cluster in the hierarchical cluster analysis of ASOs and they were found to have a similar communication patterns based on their use of ASOs. Claudine and Faith tended to use the ASO "climb on me" whereas they rarely ever used the ASO "move into position". Although I do not know their relative rank within the Milwaukee bonobo community I will speculate that they are both low ranking individuals based on my observations of their interactions with others. If Claudine and Faith represent lower-ranking female bonobos then their use of ASOs might also represent general communication patterns of lower-ranking female bonobos.

Rank would be an excellent addition to the study of gestural communication and should be considered in future observations and analysis. Unfortunately, I was unable to analyse rank directly during my study of Milwaukee bonobos. Although many instances of displacement were captured on camera, observations of displacement were not done systematically and so do not qualify for linear rank analysis.

In this chapter I demonstrated that certain variables associated with signallers and recipients can influence how gestural communication is used. In the next chapter I focus on how the resuting interactions that occur between two bonobos may shape the communication that precedes it.

Chapter 6: Dialog

6.1 Introduction

In chapters 3 and 4 I described bonobos using gestures intentionally and for particular goals. What the goal of a gesture was could be determined through recording the behaviour of the recipient that effectively satisfied the signaller (i.e. the Apparently Satisfactory Outcome, ASO). But what about the case where the recipient bonobo responded only with another gesture of his or her own? In this case, the interaction may be termed a dialog.

As the intentional use of gestures implies that each signaller has a particular goal in mind, the question of 'success' in the case of dialog must be determined through the behavioural reaction by one of the bonobos towards the other. If both bonobos are attempting to change the behaviour of their target recipient, then only one of the bonobos can be labelled as successful within this type of dialog. However, a gestural response might itself be the goal of the original signaller. Take the example of piggyback riding in humans. An adult offers a child a piggyback ride by turning her back to him, bending her knees slightly and holding her arms out to either side. If the child understands this gesture he will jump onto the adult's back, wrapping his arms around her shoulders and his legs around her torso. But what if the child wishes to initiate a piggyback ride from the adult? The child might indicate this intention by tapping on the shoulders of the adult while standing behind her. If the adult understood the child's intention she would respond by dipping her knees and holding her arms out on either side, effectively performing the same gesture as she had done when she initially offered a piggyback ride. Ultimately there are two paths for initiating a piggyback ride. When the adult initiates the event only one gesture is needed, namely an Action Request gesture. The adult is requesting an action from the child, namely to jump onto her back. When the child initiates the event, two gestures are performed in a dialog. First a Permission Request gesture is used by the child, signalling the desire for a response from the adult in the form of a gesture. Then a Permission Grant gesture is used by the adult, signalling the acceptance of the child's original intent and allowing for the piggyback interaction to proceed. The Action Request gesture and the Permission Grant gesture in both of these scenarios are the same gesture: turn back to smaller human, dip knees, hold arms out to side.

As with piggyback riding in humans, bonobos are also observed engaging in behaviours that are both physically interactive (involving contact between the two engaging bonobos) and asymmetrical, in that the two bonobos do two different things during the interaction and one bonobo's actions depends on the previous actions of another bonobo. Other interactions initiated through gestural communication such as "groom me" or "travel together" fulfil only one of the two criteria: "groom me" involves physical interaction but only one individual, the groomer, is physically active, while "travel together" involves both individuals actively participating however they are both doing basically the same thing, travelling in tandem.

ASOs "climb on me", "GG rub start", and "start sex" are three examples of asymmetrical interactions (see table 4.1 for definitions); indeed, "climb on me" very closely resembles piggyback riding in humans except that the bonobo being ridden is most commonly walking quadrupedally. In GG rubbing, one of the two bonobos must move into a specific position so that the other bonobo may wrap her legs around the torso of her prone companion. During sex, a female must wait for the presentation of an erect penis before sex can commence. All three types of interaction can theoretically be initiated either through the communicative effort of a single bonobo or through a dialog of Permission Requests and Permission Grants. If a single bonobo uses gestures to initiate the physical interaction then he or she can only take one of the two roles within the resulting interaction. Those roles, deemed the executor role, are as follows: in "climb on me" it will be the animal who carries the other bonobo; in "GG rub start" it will be the animal that supports the weight of her companion; and in "start sex" it will be the male bonobo. If the bonobo wishes to initiate one of the previously listed interactions but intends for other bonobo to take on the executor role then he or she must use a Permission Request.

In the following analysis I re-evaluated the dataset of bonobo communication events for instances of dialog.

6.2 Specific method

In chapters 3 and 4 I reviewed all instances of gestural communication observed in Milwaukee bonobos including the types of gestures bonobos used and what they used them for. In this chapter I consider two different types of communication events: non-dialog communication events where bonobos use gestures towards one another with the goal of influencing each other's behaviour and dialog communication events where bonobos use gestures towards one another with the intention of eliciting a gestural response from the target recipient. See diagram 6.1 for a schematic of the progression of either type of communication event. To be classified as a dialog, the communication event should (1) have both bonobos direct gestures towards each other during the interaction; (2) end with an ASO that is an asymmetrical physical interaction; and (3) have the bonobo who ends up in the executor role of the physical interaction be the last to perform a gesture during the communication event. Further, the gestures used as Permission Grants should also be regularly used as Action Request gestures for the same ASO. For clarity I will label the two bonobos within the interaction as either the requestor (i.e. the bonobo using the Permission Request gesture) or the grantor (i.e. the bonobo using the Permission Grant gesture).

For the analysis of dialog it is important to have clear definition of a communication event. A communication event starts when a bonobo directs a gesture towards his or her recipient. When two bonobos use gestures towards one another then both sets of gestures are considered as part of the same communication event. A communication event ends when either an ASO is performed by one of the two interacting bonobos or else when communication has failed to elicit a satisfactory response (see section 2.4.4 on Apparently Satisfactory Outcomes).

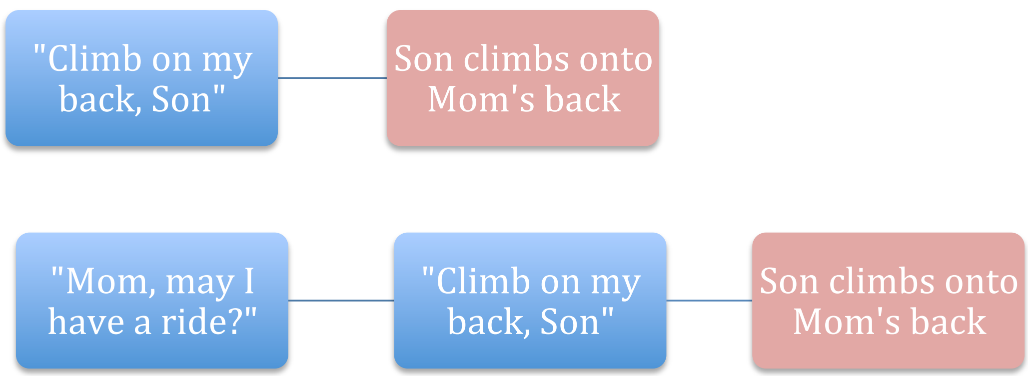


Diagram 6.1. The progression of gestural communication as it occurs within a non-dialog communication event and in a dialog communication event. Blue boxes represent verbal requests between a mother and son dyad. Pink boxes represent the different outcomes (i.e. ASOs) expected from the different forms of communication. The top set of boxes represent non-dialog. Here the Mother says "climb on my back, son" to which the son responds by climbing onto his Mother's back. The bottom set of boxes represent a dialog. Here the son initiates the interaction by first asking "Mom, may I have a ride?" and thereby using a Permission Request. Once this Permission Request has been made Mom responds with a Permission Grant, "climb on my back, son" to which the son responds by climbing onto her back.

As a third-party observer I cannot determine whether a gesture is being used as an Action Request or a Permission Request at the outset. Because I assume that Permission Requests are used with the goal of eliciting a gestural response I expect that only a particular gesture (or a small range of particular gestures) will satisfy the signaller after the performance of which she will end her communicative efforts. It follows that once the Permission Grant gesture is given the original signaller should respond behaviourally, and that this behaviour should in turn satisfy the other bonobo.

6.3 Results

Out of 1103 observed communication events, there were 36 separate occasions where two bonobos directed gestures towards each other within the same communication event. Twenty-two of the 36 communication events had successful outcomes where an ASO was performed by one of the two bonobos. Of the 22 successful communication events, there were 18 events where the sequence of gestures ended in an ASO in which the two bonobos played asymmetrical roles: “start sex”, “climb on me” or “GG rub start”. Five events ended with the ASO “start sex”, 5 events ended with the ASO “climb on me” and 8 events ended with “GG rub start”. These 18 communication events are potential examples of dialog. Although few in number, these examples present an opportunity for an initial analysis into whether bonobos are using gestures in dialog.

For each of these 18 communication events I identified the requestor and the grantor in the interaction. The grantor is the bonobo who performed the gesture that led to the other bonobo responding with an ASO. The gesture that the grantor used was identified as the Permission Grant gesture. The requestor is the bonobo who used the gesture that led to the other bonobo responding with a Permission Grant gesture. The gesture that the requestor used was identified as the Permission Request gesture. In the following analysis only the Permission Request gesture that led directly to a Permission Grant gestural response are included in further analysis (i.e. if the requestor persisted in gestural communication only the last gesture used as a Permission Request is included in further analysis).

6.3.1 "Start sex" dialog

There were 5 communication events where the ASO "start sex" was the final result of a dialog. The gestures used as Permission Requests and Permission Grants leading to the ASO "start sex" are presented in diagram 6.2. Milwaukee bonobos used the gestures *rocking* and *head shake* as Permission Requests and the gestures *display chest* and *rack pose* as Permission Grants during "start sex" dialog.

When the gestures used as Permission Grants were used as Action Requests in other communication events, were those gestures used for the same ASO, "start sex"? Diagrams 6.3 and 6.4 present gestures *display chest* and *rack pose* as they are used as Action Requests and the ASOs they were used for. According to diagram 6.3 the primary use of *display chest* as an Action Request was for the ASO "start sex" and according to diagram 6.4 the secondary use of *rack pose* as an Action Request was for the ASO "start sex". These results confirm the prediction that the Permission Grant gestures used to initiate "start sex" are also used as Action Requests for the same purpose.

Does the grantor bonobo (i.e. the bonobo who used the Permission Grant gesture) take the executor role during the resulting physical interaction? In all 5 communication events involving "start sex" the grantor bonobo was the male bonobo and therefore performed the executor role during the physical interaction. This result confirms the prediction that dialogs involving "start sex" occur when the bonobo initiating the interaction (i.e. the requestor bonobo) intends for her target recipient to take the executor role.

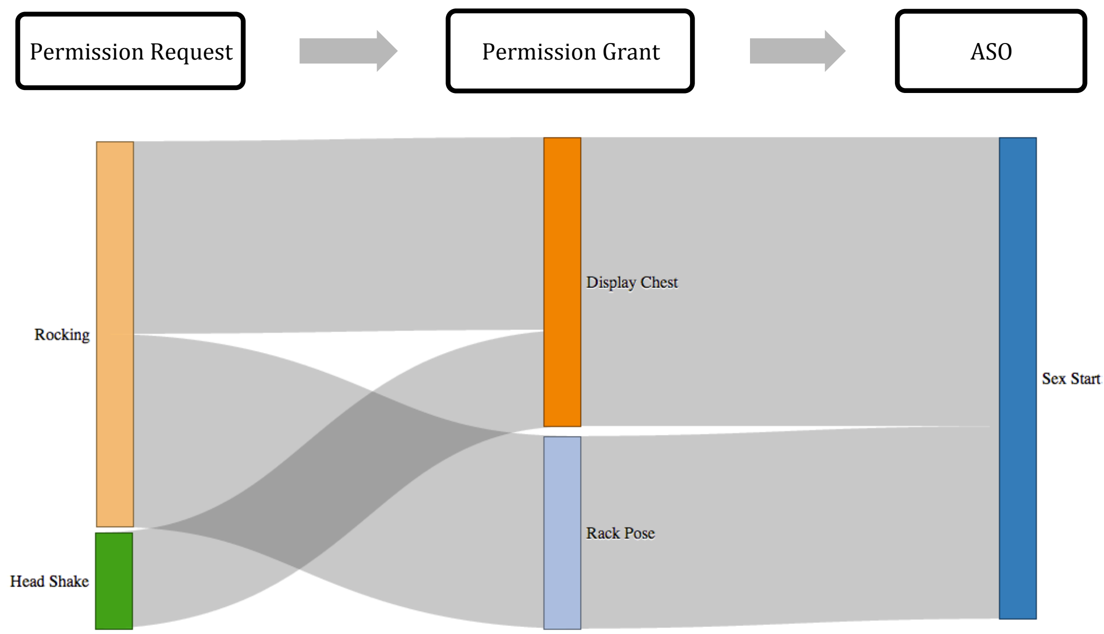


Diagram 6.2. This diagram presents the progression of 5 dialogs involving the ASO "start sex".

On the left are the Permission Request gestures performed by one bonobo in a dyad. The middle gestures are performed by the second bonobo to the first as a Permission Grant. On the right hand side is the resulting ASO ("start sex") occurring after both the Permission Request and Permission Grant have been performed. The grey bars connecting Permission Request gestures to Permission Grant gestures represent the number of times those particular gestures were observed in this particular sequence within the same communication event. Those numbers are as follows: *rocking* to *display chest*, 2; *rocking* to *rack pose*, 2; *head shake* to *display chest*, 1. The grey bars connecting Permission Grant gestures to the ASO "start sex" represent the number of times those particular gestures were observed being used to elicit the ASO "start sex" during dialogs. Those numbers are as follows: *display chest* to "start sex", 3; *rack pose* to "start sex", 2.

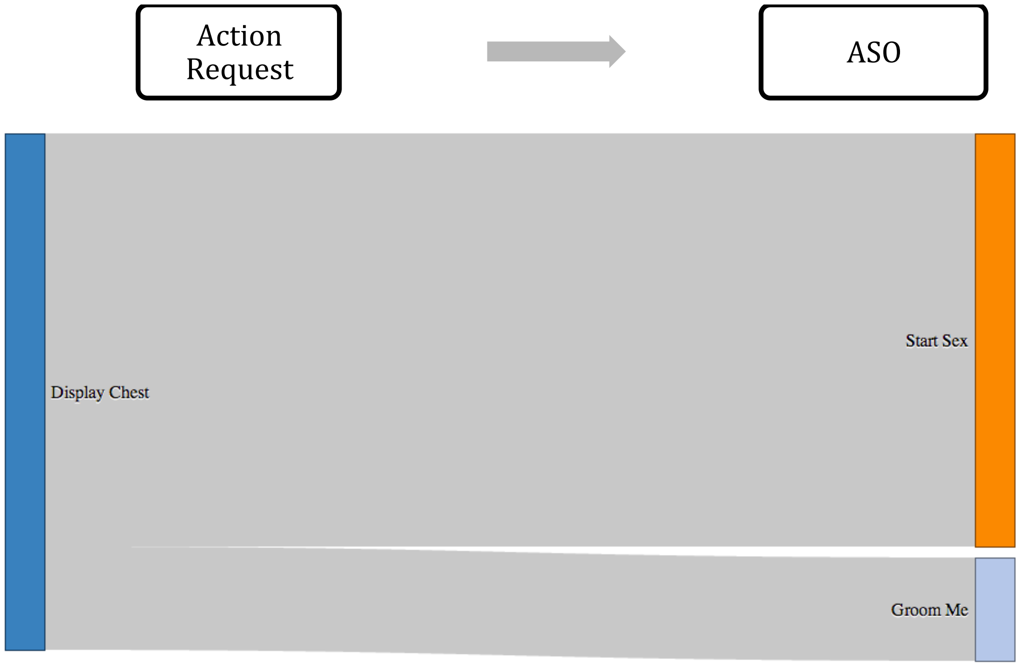


Diagram 6.3. This diagram presents the gesture display chest and the ASOs it was used for when used as an Action Request. 10 examples presented.

On the left side of the diagram is the gesture display chest as performed by one bonobo in a dyad. On the right side of the diagram are the resulting ASOs as performed by the recipient bonobo in the dyad. The grey bars connecting the display chest gesture to the ASOs on the right represent the number of times display chest was used for each ASO. Those numbers are as follows: *Display chest* to "start sex", 8; *display chest* to "groom me", 2. *Display chest* was used primarily for the ASO "start sex" and secondarily for the ASO "groom me".

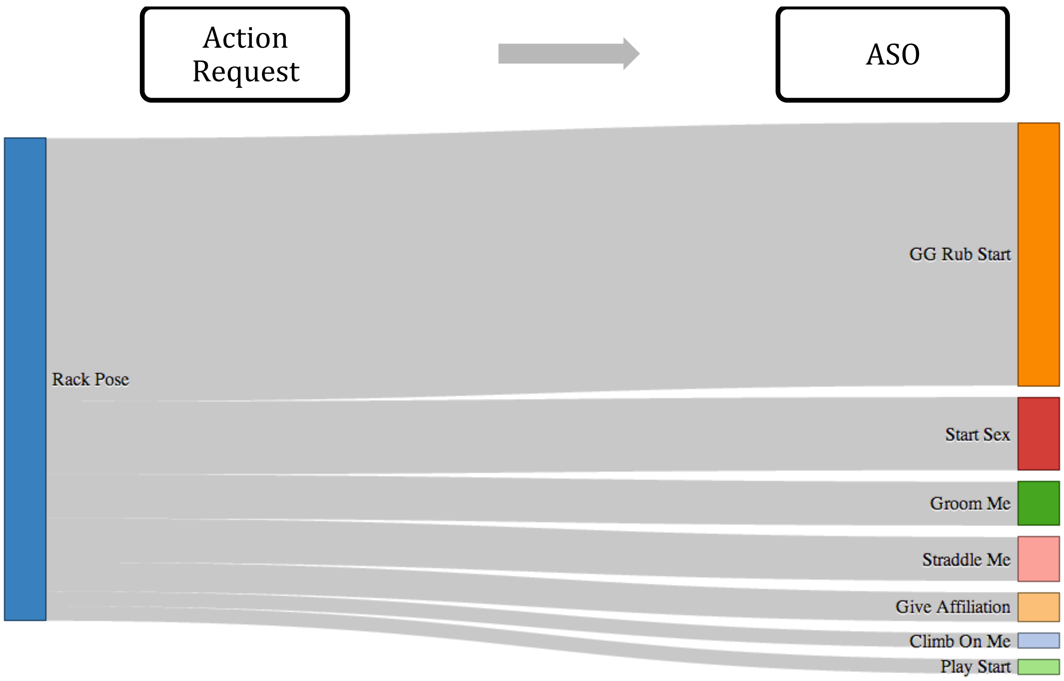


Diagram 6.4. This diagram presents the gesture rack pose and the ASOs it was used for when used as an Action Request. 33 examples presented.

On the left side of the diagram is the gesture rack pose as performed by one bonobo in a dyad. On the right side of the diagram are the resulting ASOs as performed by the recipient bonobo in the dyad. The grey bars connecting the rack pose gesture to the ASOs on the right represent the number of times rack pose was used for each ASO. Those numbers are as follows: *rack pose* to "GG rub start", 18; *rack pose* to "start sex", 5*;* *rack pose* to "groom me", 3; *rack pose* to "straddle me", 3; *rack pose* to "give affiliation", 2; *rack pose* to "climb on me", 1; *rack pose* to "play start", 1. *Rack pose* was used primarily for the ASO "gg rub start" and secondarily for the ASO "start sex".

6.3.2 "Climb on me" dialog

There were 5 communication events where the ASO "climb on me" was the final result of a dialog. The gestures used as Permission Requests and Permission Grants leading to the ASO "climb on me" are presented in diagram 6.5. Milwaukee bonobos used the gestures *arm raise*, *suspended hand* and *kick* as Permission Requests and the gestures *display back* and *body swing* as Permission Grants during "climb on me" dialogs.

When the gestures used as Permission Grants were used as Action Requests in other communication events, were those gestures used for the same ASO, "climb on me"? Diagrams 6.6 and 6.7 present gestures *display back* and *body swing* (used as Permission Grants in diagram 6.5) as they are used as Action Requests and the ASOs they were used for. According to diagram 6.6 the gesture *display back* was used as an Action Request primarily for the ASO "climb on me". This result supports the prediction that the Permission Grant gesture used to initiate "climb on me" was also used as Action Requests for the same purpose. According to diagram 6.7 the gesture *body swing* was never used for the ASO "climb on me". This result does not support the prediction that Permission Grant gestures are the same gestures used as Action Requests for the same purpose. However, the gesture *body swing* was observed being used successfully as an Action Request only 4 times making for a small sample size to compare the uses of body swing between communication event types.

Does the grantor bonobo (i.e. the bonobo who used the Permission Grant gesture) take the executor role during the resulting physical interaction? In all 5 communication events involving "climb on me" the grantor bonobo was the larger bonobo and therefore performed the executor role during the physical interaction. This result confirms the prediction that dialogs involving the ASO "climb on me" occur when the bonobo initiating the interaction (i.e. the requestor bonobo) intends for his or her target recipient to take the executor role.

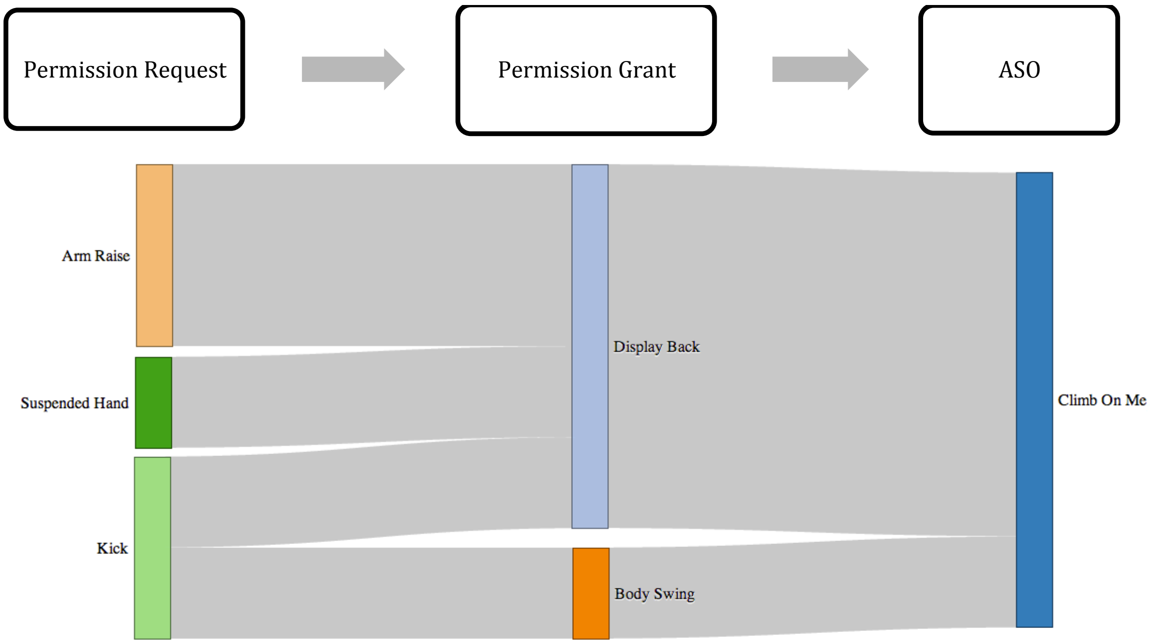


Diagram 6.5. This diagram presents the progression of 5 dialogs involving the ASO "climb on me".

On the left are the Permission Request gestures performed by one bonobo in a dyad. The middle gestures are performed by the second bonobo to the first as a Permission Grant. On the right hand side is the resulting ASO ("climb on me") occurring after both the Permission Request and Permission Grant have been performed. The grey bars connecting Permission Request gestures to Permission Grant gestures represent the number of times those particular gestures were observed in this particular sequence within the same communication event. Those numbers are as follows: *arm raise* to *display back*, 2; *suspended hand* to *display back*, 1; *kick* to *display back*, 1; *kick* to *body swing*, 1. The grey bars connecting Permission Grant gestures to the ASO "climb on me" represent the number of times those particular gestures were observed being used to elicit the ASO "climb on me" during dialogs. Those numbers are as follows: *display back* to "climb on me", 4; *body swing* to "climb on me", 1.

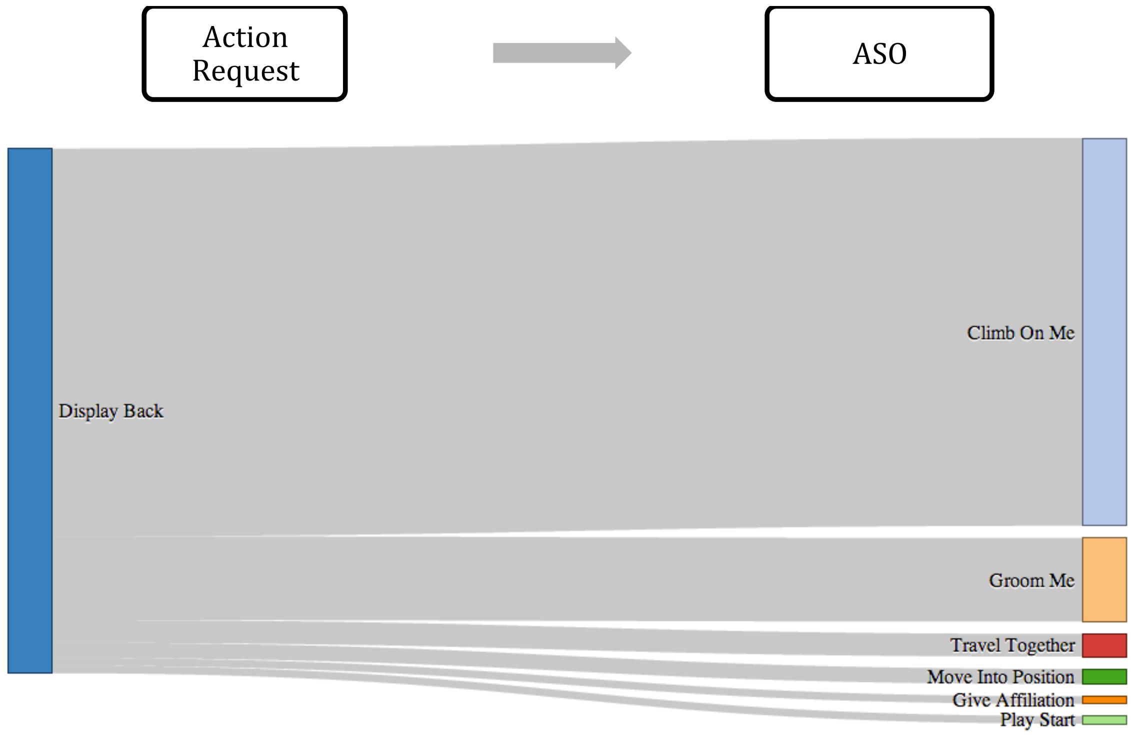


Diagram 6.6. This diagram presents the gesture display back and the ASOs it was used for when used as an Action Request. 69 examples presented.

On the left side of the diagram is the gesture display back as performed by one bonobo in a dyad. On the right side of the diagram are the resulting ASOs as performed by the recipient bonobo in the dyad. The grey bars connecting the display back gesture to the ASOs on the right represent the number of times display back was used for each ASO. Those numbers are as follows: *display back* to "climb on me", 51; *display back* to "groom me", 11; *display back* to "travel together", 3; *display back* to "move into position", 2; *display back* to "give affiliation", 1; *display back* to "play start", 1. *Display back* was used primarily for the ASO "climb on me" and secondarily for the ASO "groom me".

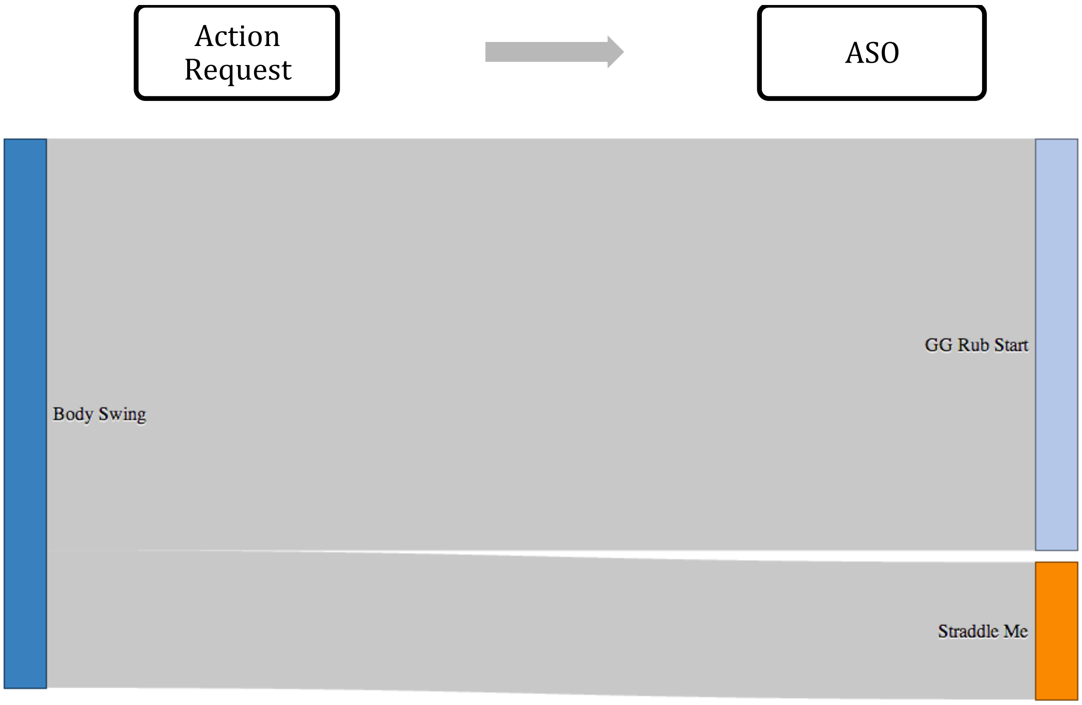


Diagram 6.7. This diagram presents the gesture body swing and the ASOs it was used for when used as an Action Request. 4 examples presented.

On the left side of the diagram is the gesture body swing as performed by one bonobo in a dyad. On the right side of the diagram are the resulting ASOs as performed by the recipient bonobo in the dyad. The grey bars connecting the body swing gesture to the ASOs on the right represent the number of times body swing was used for each ASO. Those numbers are as follows: *body swing* to "GG rub start", 3; *body swing* to "straddle me", 1. *Body swing* was used primarily for the ASO "GG rub start" and secondarily for the ASO "straddle me".

6.3.3 "GG rub start" dialog

There were 8 communication events where the ASO "GG rub start" was the final result of a dialog. The gestures used as Permission Requests and Permission Grants leading to the ASO "climb on me" are presented in diagram 6.8. Milwaukee bonobos used the gestures *rack pose*, *touch other*, *body shake* and *embrace* as Permission Requests and the gesture *rack pose* as a Permission Grant during "GG rub start" dialogs.

When the gesture used as a Permission Grant was used as an Action Request in other communication events, was that gesture used for the same ASO, "GG rub start"? Diagram 6.4 presents the gesture *rack pose* (used as a Permission Grant in diagram 6.8) as it was used as an Action Request and the ASOs it were used for. According to diagram 6.4 *rack pose* was used primarily for the ASO "GG rub start". This result confirms the prediction that the Permission Grant gesture used to initiate "GG rub start" was also used as Action Requests for the same purpose.

Does the grantor bonobo (i.e. the bonobo who used the Permission Grant gesture) take the executor role during the resulting physical interaction? In 6 of the 8 communication events the grantor was also the bonobo who performed the executor role during GG rubbing (i.e. being the bonobo who supported the weight of the other bonobo). In 2 of the 8 communication events the requestor performed the executor role during GG rubbing. This result partially confirms the prediction that dialogs involving the ASO "GG rub start" occur when the bonobo initiating the interaction (i.e. the requestor bonobo) intends for his or her target recipient to take the executor role.

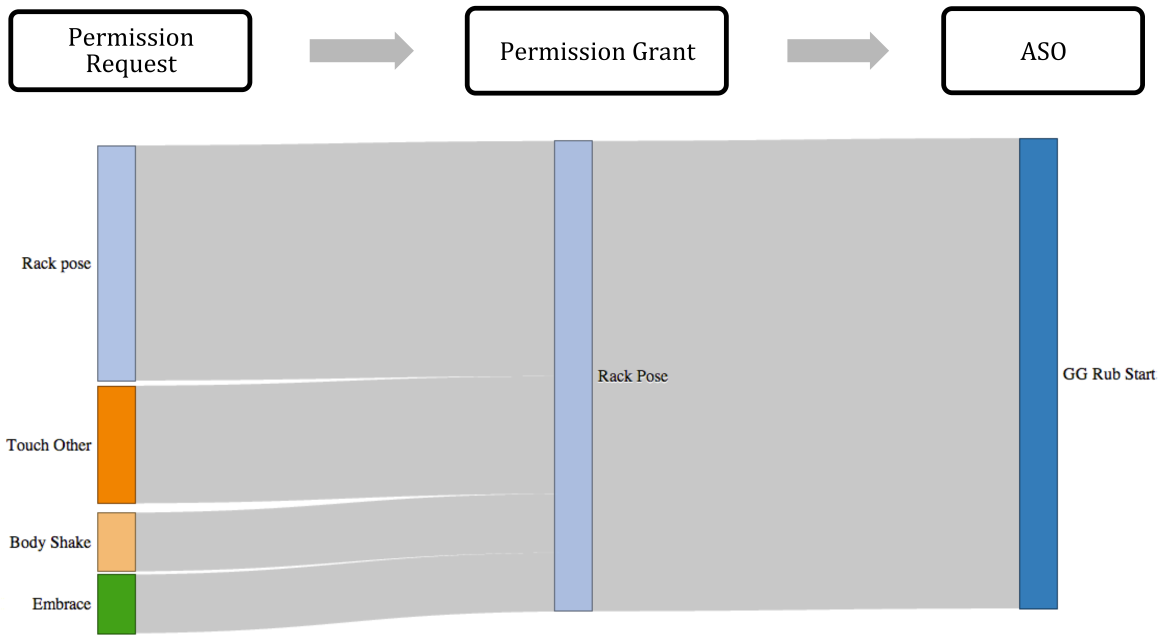


Diagram 6.8. In this diagram presents the progression of 8 dialogs involving the ASO "GG rub start".

On the left are the Permission Request gestures performed by one bonobo in a dyad. The middle gestures are performed by the second bonobo to the first as a Permission Grant. On the right hand side is the resulting ASO ("GG rub start") occurring after both the Permission Request and Permission Grant have been performed. The grey bars connecting Permission Request gestures to Permission Grant gestures represent the number of times those particular gestures were observed in this particular sequence within the same communication event. Those numbers are as follows: *rack pose* to *rack pose*, 4; *touch other* to *rack pose*, 2; *body shake* to *rack pose*, 1; *embrace* to *rack pose*, 1. The grey bars connecting Permission Grant gestures to the ASO "GG rub start" represent the number of times those particular gestures were observed being used to elicit the ASO "GG rub start" during dialogs. Those numbers are as follows: *Rack pose* to "GG rub start", 8.

6.4 Discussion

This study demonstrated that bonobos use gestures within a dialog in order to coordinate asymmetrical physical interactions. Asymmetrical interactions can sometimes depend on the use of dialog when a signaller wishes to take a specific role within the pending interaction. If she wishes to take on the executor role then she simply needs to inform her recipient of her desire. In the example of piggyback riding, the executor role involves carrying another individual. If, however, she wishes for the other bonobo to take on the executor role then she must "inquire" as to whether the other bonobo will agree to performing this role. In this scenario she is seeking a gestural response in which the recipient confirms that he will take the executor role.

To qualify as dialog a communication event had to conform to three outset parameters. First a communication event must have involved both bonobos directing gestures towards one another. Second, the communication event must have ended with an asymmetrical interaction. The communication events that conformed to both the first and second parameter ended in three types of ASOs: "climb on me," "GG rub start" and "start sex". The third parameter for determining whether a communication event could be classified as a dialog involved defining the different roles each bonobo took during the gestural exchange as well as during the resulting asymmetrical interaction. Because I assumed that the use of dialog occurs when the original signaller wishes for her recipient to take on the executor role then it should follow that episodes of dialog will follow this pattern. Therefore the grantor bonobo (i.e. the bonobo that used a permission grant gesture) must have performed the executor role within the resulting interaction. Out of 22 potential examples of dialog there were 16 communication events that conformed to all three parameters.

The evidence for dialog was supported by the similar use of gestures between communication events involving dialog and communication events not involving dialog. I predicted that the grantor bonobo within a dialog communication event will use the same gesture for the same ASO as a bonobo would if he was using gestures within a non-dialog communication event. As with the piggyback example, both dialog and non-dialog communication events end in the ASO "climb on me", do the same types of gestures get used to elicit that response between dialog and non-dialog? Of the 5 gesture types identified as being used as Permission Grants, 4 of them were used primarily as Action Request gestures for the same ASO during instances of non-dialog. This result confirms the prediction that Permission Grant gestures are also used as Action Requests for the same purpose.

Although I am the first to document the use of dialog in bonobos I do not believe that this is an exclusively bonobo use of gestural communication. Out of the three types of asymmetrical interactions involving dialog only one revolved around a bonobo specific behaviour (i.e. "GG rub me"). The other two asymmetrical interactions, "climb on me" and "start sex", are found in other species of apes and are also initiated through gestural communication. Referring back to chapter 4 and the table comparing the different ASOs observed in apes (table 4.1), both chimpanzees and gorillas use gestures to initiate "climb on me" interactions and both chimpanzees and orangutans use gestures to initiate "start sex" interactions (Hobaiter and Byrne, 2014; Genty et al., 2009; Cartmill and Byrne, 2010). Do these interactions observed in other apes sometimes involve dialog?

When I first began coding the gestures of bonobos my coding process was based on certain assumptions. First, that the gestures observed within a communication event were used solely to direct a behavioural response within a recipient. Second, that if the original recipient responded to the original signaller with a gesture of her own then that gesture was for a new objective on the original recipient's behalf and therefore unrelated to the original signaller's use of gestures. What I have demonstrated through my study of dialog is that gestures made in response to other gestures are sometimes the actual goal behind a original signaller's use of gestural communication. If you assume that gestures made in repose to other gestures are unrelated then you will consequently ignore all potential cases of dialog. I would therefore propose that dialog is occurring in other ape species and that the assumptions that went into previous studies of gestural communication effectively prevented researchers from identifying events of dialog. Through reviewing footage of gestural communication that involve “climb on me” and “start sex” interactions there may be evidence of dialog that was initially overlooked by the original coders.

In summary, this study has shown that ape gestural communication may vary from the one signaller – one recipient approach as seen in previous analyses of ape gestural communication. Going forward, studies of gestural communication should consider the possibility of dialog occurring between signallers. Specifically, researchers should pay close attention to communication surrounding physical interactions where apes play complimentary roles to one another.

Chapter 7: General Discussion

7.1 Review of findings of this thesis

7.1.1 Repertoire of gestures for Milwaukee bonobos

Milwaukee bonobos used 55 types of gestures over the course of a 12-month study. This is the largest group repertoire observed in a single study of bonobos. Of those 55 gestures, 45 have been observed in previous studies of bonobos. A further 15 gestures have been observed in previous studies of bonobos but were not observed in use by Milwaukee bonobos. Therefore, the total known gestural repertoire of bonobos is comprised of 70 gestures. From comparing the known repertoire of bonobos to that of other apes I concluded that there are 6 bonobo-specific gestures. Four of the six bonobo-specific gestures have been described in previous studies of bonobo gestural communication: *body shake*, *crab pose*, *knock other*, and *starfish pose*. Two bonobo-specific gestures were discovered during the course of this study and are therefore new to the study of ape gestures: *body swing* and *rack pose.*

Milwaukee bonobos used gestures in a highly flexible manner. Confirming the findings of previous studies of ape gestural communication I found that Milwaukee bonobos adjust their use of gestures depending on the attentional state of the audience (Pika et al., 2005; Genty et al., 2009; Liebal et al., 2006; Liebal et al., 2004). Also confirming findings from previous studies of ape gestures, Milwaukee bonobos use gestures flexibly between contexts in that they use multiple gestures within a single context and will use a single gesture across multiple contexts (Call and Tomasello, 2007; Liebal, 2007; Pika, 2007a; Pika, 2007b).

7.1.2 Meanings of gestures

Milwaukee bonobos use gestures for 16 Apparently Satisfactory Outcomes (ASOs). Of the 32 gestures that were most frequently used by Milwaukee bonobos, 20 were associated with a primary ASO. For example, the gestures *display back* was primarily used to mean "climb on me". As my study included a range of bonobo signallers, I considered whether individual bonobos tended to use the same gestures for the same meanings. Of the 7 gestures that qualified for analysis, 5 gestures were used for the same ASOs across signallers.

Having identified 6 bonobo-specific gestures, *body swing*, *rack pose, body shake*, *crab pose*, *knock other*, and *starfish pose*, what were those gestures used for? It turns out that bonobos use bonobo-specific gestures for bonobo-specific behaviours. Of the 6 bonobo-specific gestures, 3 qualified for the analysis of gestures and their associated primary ASO. Those 3 gestures, *body swing*, *rack pose* and *starfish pose*, were all primarily used for the ASO "GG rub start", itself a bonobo-specific behaviour. Of the 3 gestures that did not qualify for analysis (being used too infrequently during the study period), 2 were observed being used to mean "GG rub start": *crab pose* and *body shake.*

I found that bonobos tend to use multiple gestures for a single meaning and that a single gesture can be used for different meanings across communication events. As my study was the first to uncover the meanings of bonobo gestures then this study is also the first to demonstrate this type of flexibility within bonobo gestural communication. This finding follows Hobaiter and Byrne (2014) who revealed a similar pattern of flexibility in chimpanzee meanings of gestures.

7.1.3 Social context of gestural communication

Having established that bonobos use many gestures for a range of meanings I next investigated the influence signaller age or sex has upon gestural communication. I first analysed signaller age and sex and its influence on gestural communication through hierarchical cluster analysis. First I analysed signallers and their use of gestures for different contexts. The analysis split the bonobos into two clusters: one cluster consisted mostly of males and the other cluster consisted mostly of females. The result indicates that males and females tend to communicate within different contexts. I next analysed signallers and their use of gestures for different ASOs. Hierarchical clustering analysis split the bonobos into 4 clusters of mixed age and sex. The result indicates that bonobo use of ASOs is not necessarily based on the age and sex of the signaller.

I next analysed the association between signallers and their use of gestures for specific contexts or for specific ASOs. To do so I used correspondence analysis. First I analysed the association between signallers and the types of contexts in which they used gestural communication. I found that older bonobos are more likely to use gestures in the context of grooming while younger bonobos are more likely to use gestures in the context of play. I also found that infants and mothers with dependent offspring were more likely to use gestures within the context of travelling than they were to use gestures within the context of play.

I next analysed the association between signallers and the types of ASOs for which they use gestural communication. I again employed correspondence analysis. I found that older females were more likely to use gestures for the ASOs “follow ahead” and “move away” as compared to males and younger females. I also found that two females, Claudine and Faith, were more likely to use ASOs “climb on me” and as compared to the ASO “move into position”.

Following the correspondence analysis of signallers and their use of ASOs, I explored the direction of communication based on the age and sex of the signaller and the recipient. I plotted social networks of communication, where nodes represent bonobos, coded by age and sex, and edges represent instances of communication where the arrow indicates the direction of communication from signaller to recipient. Looking specifically at the use of the ASOs "follow ahead" and "move away" I found that older females tend to use those ASOs and that those ASOs are more likely to be directed from the older bonobos towards younger bonobos. The 14 exceptions to this rule all involved younger females signalling "follow ahead" or "move away" towards older males.

These results provide evidence for flexibility in the use of gestures between social contexts. In my analysis I found that older females tend to use gestures to mean "follow ahead" and "move away" and they use those gestures primarily towards specific recipients: males and younger females. This result provides preliminary evidence that signallers moderate their use of gesture depending on whom their target audience happens to be. As different bonobos use gestures for different contexts and for different ASOs then it becomes imperative that studies of gestures focus on a range signallers in both age and sex. If not, then the study of gestures will necessarily be limited in its representation of just how expansive and flexible gestural communication can be.

It has been proposed that the evolutionary function of a larger communicative repertoire is for the better management of a complex social network (Freeberg et al., 2012). How exactly do animals use large communicative systems to manage their social networks? Ape gestural communication is itself a large communicative system. Do apes manage their social networks through the use of gestural communication? In my study of I found that only certain signallers use gestures for certain meanings and that they direct those meanings towards certain recipients. This is the first evidence for the gestural communication system being used as a tool for social management. Future studies on social management should focus on whether relationship status influences the use of gestures and in reverse, whether the use of gestures influences relationship status.

7.1.4 Dialog in gestural communication

In my study of dialog I set out 3 parameters for whether a communication event qualified as dialog. First, both bonobos within a dyad must have used gestures towards each other during the same communication event. Out of the entire data set there were 36 instances where both bonobos used gestures towards each other during the same communication event. Secondly, the resulting interaction between the two bonobos must have been asymmetrical in that the two bonobos performed different roles. Out of the 36 instances of bonobos potentially engaging in dialog there were 18 communication events for which there was an identifiable ASO and that the ASO involved an asymmetrical interaction between the two bonobos. The third criterion for labelling a communication event as dialog was whether the grantor bonobo (i.e. using the Permission Grant gesture) took the executor role during the resulting interaction. For the 5 dialogs involving the ASO "climb on me" all events concluded with the grantor taking the executor role. For the 5 dialogs involving the ASO "Start Sex" all events concluded with the grantor taking the executor role. For the 8 dialogs involving the ASO "GG rub start" 6 events concluded with the grantor taking the executor role. I therefore conclude that there is evidence for dialog occurring within bonobo gestural communication having found 16 instances that conform to all three criteria.

Further evidence supports the case for dialog through the similar use of gestures during dialog and non-dialog communication events. Of the 5 gesture types identified as being used as Permission Grants, 4 of them were used primarily as Action Request gesture for the same ASO during instances of non-dialog. One of the gestures was used secondarily as an action request for the same ASO during instances of non-dialog. This result confirms the prediction that Permission Grant gestures are also used as Action Requests for the same purpose.

7.2 Implications of the findings of this thesis

7.2.1 Origins of language

My interest in gestural communication arose initially from reading about the sign-language capabilities of a few celebrity apes. Although popular media has misrepresented how apes use sign language (e.g. apes using sign language to coordinate the over-taking of the human race, "Rise of the Planet of the Apes" directed by Rupert Wyatt, 2011) they're ability to learn hundreds of signs, combine them in novel ways and use those signs to make imperative requests towards their captors or conspecifics tells us that apes have a unique capacity for gestural communication (Savage-Rumbaugh and Lewin, 1994, Gardner and Gardner, 1969, Gardner et al., 1989, Fouts et al., 1989).

The capacity for apes to learn sign language is only one of many lines of evidence that indicate that human language originated in gesture (e.g. infants begin gesturing before speaking, Petito and Marentette, 1991; humans employ manual gestures alongside speech, Iverson and Goldin-Meadow, 1998). To better understand the origins of language researchers have recently focussed on identifying the similarities between human language and ape gestural communication. One such comparison is of the levels of flexibility found in both systems. Flexibility is a defining feature of language as words can be combined to express an endless range of concepts (Hauser et al. 2002) and words are used freely between multiple contexts (Corballis, 2009). Gestural communication in apes is also highly flexible and therefore has been argued as a likely origin to modern language as compared to that of vocalizations (Arbib et al., 2008; Corballis, 2009; Call and Tomasello, 2007; Pollick and de Waal, 2007). My studies of bonobo gestures confirm the finding that gestural communication is a highly flexible system: Milwaukee bonobos use gestures flexibly between contexts, they use gestures for multiple meanings and many gestures can be used for the same meaning, and they adjust their use of gesture depending on the attentional state of their intended audience.

Beyond the similarities between language and ape gestural communication, researchers might also consider the evolutionary path gestural communication must have taken to arrive at modern language. If we consider the state of gestural communication as it exists now in modern apes, what constraints would force the system to become more language-like? In other words, to go from ape gestural communication to language, what were the intermediary steps? I propose that one initial step in forming more language-like communication would be in the development of dialog as it co-evolves with the development of more 'complicated' interactions (i.e. interactions where either party is playing a different yet complimentary role towards one another). In my studies of bonobos, dialog became a necessary descriptor of gestural communication as I coded more and more "climb on me" interactions. Mother and infant were expressing a common goal, that being conjoined travel, and they were organizing this interaction through the use of gestures. Rather than doing or not doing a reactive behaviour in response to a simple request, the respondent bonobo was instead agreeing or disagreeing to a laid out plan. This coordination of complementary behaviours I argue may be the stimulus for the development of more complex communicative strategies. Just as the steps to solving a problem increases as the problem becomes more complicated I argue that as interactions between interlocutors become more complex so must the communication that orchestrates it.

7.2.2 Gestural communication as a tool for social influence

I am also interested in the flexibility of gestural communication for it's potential use towards social management. Just as an ape will adjust her use of gestures depending on her recipient's state of attention I propose that the age or sex of that recipient will also influence the ape's use of gestures. It is therefore an important next step in the study of ape gestural communication that social variables such as age and sex and further rank and kinship are

One important next step in studies of gestural communication will be to focus on the influence the social environment has on patterns of communication. Living in a complex social environment where bonds between group members extend beyond kin and pair-bonds (Dunbar and Schultz 2007), an ape should respond differently to different social partners as well as have different goals behind those interactions. To express those different goals gestural communication comes to use as an ape can initiate specific interactions with specific social partners. Because social relationships are ever-changing, when approaching another group member one should take care in how one expresses what exactly he or she wishes to achieve.

What is the function of gestural communication? Most immediately, a bonobo uses a gesture to effect change in another bonobo's behaviour in a specific and goal-directed way. Ultimately, gestural communication is used to increase or decrease social contact, which in turn affects the kinds of relationships one has amongst her social partners. When a relationship changes, do bonobos perceive this change? In a study of reconciliation between bonobos who've recently engaged in an aggressive altercation, bonobos are more likely to engage in socio-sexual behaviours such as GG rubbing with each other after conflict than they were prior to the altercation (Hohmann and Fruth, 2000). Since changes within a relationship influences how bonobos behave towards one another, then there may also be a change in how individuals communicate before and after conflict.

My analysis of gestural communication suggests that social variables such as age and sex influences how bonobos use gestures. This leads to the question of whether the type of relationship the signaller has with her recipient affects her use of gestures. Cords and Aureli (2000) described three dimensions of relationship quality: value (a measure of direct benefits gained via association), security (how predictable interactions are over time) and compatibility (level of tolerance between social partners). Relationship measures have been useful in describing social behaviours in chimpanzees such as post-conflict affiliation (Fraser et al., 2010). Could the type of relationship two bonobos have with each other influence how they communicate? Gestural communication provides an excellent system for studying the influence apes have over their social environment. More than just intending for a particular behavioural reaction to occur, the signaller also intends for one particular recipient to perform that behaviour. The choice of whom one communicates with and what the signaller intends for the recipient to do may be based on previous interactions between the signaller and the recipient. If so then the communication event in and of itself could be used as a measure of relationship status.

7.2.3 Role taking in dialog

Why an episode of gestural communication occurs may have to do with any number of social or environmental circumstances. As those preceding circumstances are unknown to third-party observers, we instead describe communication events by the contexts in which they occur. Dialog, on the other hand, presents a sequence of cause-and-effect. In dialog, Bonobo A uses a gesture to which Bonobo B responds with her own gesture. In this instance we know exactly what caused Bonobo B to gesture: that being Bonobo A's gesture. In my studies of dialog there were two scenarios in which the identities of Bonobo A and Bonobo B were pre-determined. In piggy-back rides, the smaller bonobo always initiated dialog making her Bonobo A and her larger companion Bonobo B. This was due to the fact that the larger bonobo is the only one of the two who could take on the executor role (i.e. support the weight of her companion) and therefore must take on the role of the grantor bonobo (i.e. respond to the smaller bonobo with a Permission Grant gesture). In the same sense sex has pre-determined roles when it comes to dialog. As the male must take the executor role during heterogeneous sex then it will be the female who initiates sex through dialog.

However, if two bonobos intend to engage in GG rubbing it is not necessarily predictable as to which one will take the executor role. When there is a clear size discrepancy then the larger of the two will take the executor role and support the weight of the other. But what about the case where the to bonobos are of equivalent size? Without a clear size discrepancy, are there social circumstances that prescribe a pair of bonobos to either role within GG rubbing? Since the grantor bonobo is the one that will eventually perform the executor role then it is the requestor bonobo (i.e. the bonobo who begins the dialog) who will take the non-executor role. By using gestural communication the two bonobos are setting out their roles within the pending interaction. Does the relationship that exists between two bonobos determine the roles either one takes during GG rubbing?

In previous studies it has been found that when female bonobos engage in GG rubbing the higher-status female tends to take the "mounter" position (de Waal, 1987; Hohmann and Fruth, 2000) what in my study I called the non-executor role. From my study of dialog in GG rubbing the bonobo that gives the Permission Request gesture (i.e. the bonobo that initiates dialog) is more likely to end up in the mounter position which, based on patterns established in previous studies, should indicate that the dialog-inducing bonobo will be the dominant bonobo within the dyad. Further research into dialog should take into account the rank of individuals and how that attributes to patterns of gestural communication.

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