The Development of Gestural Communication in Non-Human Great Apes

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TABLE OF CONTENTS

1. GENERAL INTRODUCTION

> “*To understand the nature of any species fully,*
> *we need to know more than the ways of its adults.*
> *We need to know how its young are brought from initial,*
> *infantile inadequacy to mature, species-typical functioning.*”
> Bruner (1972, p. 687)

1.1. Setting the scene

Gesturing in the form of moving limbs or body is an integral part of day-to-day communication throughout human cultures (Feyereisen & de Lannoy, 1991; Kendon, 2004; Mead, 1934). We use our gestures in various ways; from facilitating the description of objects and actions to the more abstract expression of thoughts and emotions. In doing so, gestures are more likely to occur when talking (McNeill, 1992), but, whether it is a wave of the hand or a head shake, also often appear when not speaking (Kendon, 1988).

The importance and robustness of gesturing in adults and childrens’ communication has been highlighted through previous work in this field. Research has shown, for example, how our speech flow is compromised if we are told not to, or prevented from, gesturing (Cohen & Borsoi, 1996; Morsella & Krauss, 2004); and, how gestures are used more frequently if speaking is impaired (e.g., Stefanini, Caselli & Volterra, 2007). Further evidence comes from observations of people with visual and hearing impairments. People blind from birth gesture while speaking, even when their communicational partner is blind (Iverson & Goldin-Meadow, 1998; Iverson, Tencer, Lany & Goldin-Meadow, 2000). Likewise, congenitally deaf people, unable to talk and never exposed to sign language, have been observed to create a gestural system to communicate (Goldin-Meadow, Butcher, Mylander & Dodge, 1994; Goldin-Meadow &

Morford, 1985; Morford, 1998). It has also been shown that gesturing has a facilitative effect in learning contexts. While engaged in problem-tasks (such as mathematical equations), children reveal important knowledge with their gesturing which they may not express with words (e.g., Alibali & Goldin-Meadow, 1993; Church & Goldin-Meadow, 1986).

Previous research therefore has demonstrated that gesturing plays a vital role in the communication process, not only by helping the 'listener' but also by assisting the 'producer' in developing and articulating the information they wish to impart (Goldin-Meadow, 1999).

1.1.1. Gestural development in preverbal human children

The importance of gesturing in the early language development and socialisation of children is well established (Bates, Benigni, Bretherton, Camaioni & Volterra, 1979; Capone & McGregor, 2004; Crais, 2007; Goldin-Meadow, 1999; Gullberg, de Bot & Volterra, 2008; Iverson & Goldin-Meadow, 2005; Kendon, 1988; McNeill, 1992; Tellier, 2009). Gestures appear early in infancy; they are observed in and around the end of the first year of life (Bates, 1976; Bates et al., 1979; Carpenter, Nagell & Tomasello, 1998; Masur, 1980), and are used to effectively communicate with others before spoken words materialise (Acredolo & Goodwyn, 1988; Bates, 1976).

From the study of gestures, various definitions and terminologies have emerged. Iverson and Thal (1998, p. 60) defined gestures as intentional communicative actions that "... typically involve fingers, hands, and arms (e.g., in pointing) and also may employ facial features (e.g., lip smacking for cookies) or even the entire body (e.g., bouncing up and down for horse)."

Two main groups of gestures have been distinguished in early life, ‘deictic’ and ‘representational’ (Bates et al., 1979; Iverson & Thal, 1998). The earliest gestures are likely to be deictic (Bates et al., 1979; Iverson & Thal, 1998). These signals are used to indicate or request something of interest in the environment. An infant, for example, holds up an object to share their interest by tacitly saying, “Look at this!” Deictics are divided into, ‘contact’ signals (that involve physical contact with object or social partner) and ‘distal’ signals (where no physical contact is involved; Bates, Camaioni & Volterra, 1975; Crais, Douglas & Campbell, 2004). Representational signals temporally follow deictics in their development. Like deictics they are referential, but they also abstractly symbolise things or actions that are absent while gesturing. Signals of the representational category include ‘symbolic’ gestures (e.g., pretend eating while lifting the hand to the mouth and holding a virtual spoon), as well as culturally defined, ‘conventional’ gestures (e.g., waving a hand to say goodbye). These signals start to appear around the first birthday (Acredolo & Goodwyn, 1988; Bates et al., 1979) and, unlike deictic signals, only play a minor role in preverbal children (Liszkowski, 2008).

In respect to their communicative function, deictics have been categorised into two groups; signals which are used for imperative purposes (e.g., to request an object of interest) and those which have declarative purposes (e.g., to refer to an object to share their interest). Both are produced early on in their communicative development (Bates et al., 1975; Crais et al., 2004).

Little is known about how infants learn their gestures. Under the broad heading of socialisation (see Liszkowski, 2008; Liszkowski, 2011; Liszkowski & Tomasello, 2011), authors have suggested that some are learned through observation, while others are learned through socio-pragmatic or directed ritualisation processes whereby gestures are adopted in joint social activity (Clark, 1978; Cochet & Vauclair, 2010; Corballis, 2002; Tomasello, 1996; Tomasello & Camaioni, 1997). For example, some conventional gestures, such as waving the hand to say goodbye, do seem to be acquired via a form of imitation (Crais, 2007; Liszkowski, 2008; Masur, 1980). Other deictic signals appear to need a more obvious interaction for them to emerge. Theorists, for example, have posited differing origins of the *pointing* gesture; some claiming that it stems from a reaching action, while others believe it derives from a communicative negotiation or a joint social activity (Bates et al., 1975; Bruner, 1983; Vygotsky, 1978; Werner & Kaplan, 1963).

1.1.2. Gestures and the evolution of communication

In their search for the evolutionary roots of human language, researchers for many years have been interested in the communication systems of various mammal species. In his book *The Expression of the Emotions in Man and Animals* (1872), Charles Darwin, for example, was concerned with the evolutionary origin of non-vocal expressions in humans and various animal species. Non-human primates, because of their complex social structures and cognitive skills, and their close relatedness to humans, are of particular interest to more contemporary researchers (Whiten & Byrne, 1997).

One school of thought suggests that language evolved from primate vocalisations (Aiello & Dunbar, 1993; Burling, 1993; Dunbar, 1996; Zuberbühler, 2005). Based on the intuitive link between vocalisation and spoken language, research efforts here have tended to focus on vocal communication in monkey species and, more recently, non-human great apes (e.g., Cheney & Seyfarth, 1988; Crockford & Boesch, 2003; Engh, Hoffmeier, Cheney & Seyfarth, 2006; Hammerschmidt & Fischer, 1998; Kudo, 1987; Slocombe & Zuberbühler, 2005). It has been proposed, however, that the vocal domain of non-human primates is rather rigid (see Tomasello & Zuberbühler, 2002). While call perception may be more variable (e.g., distinct alarm calls inform about different predators; Seyfarth, Cheney & Marler, 1980; Snowdon, Elowson & Roush, 1997), flexibility in call production seems to be comparatively limited (e.g., members of a species share the same vocalisations).

The complex role that gesture plays in communication among non-human primates, and its intertwined nature with speech in humans, has led a number of other theorists to propose that language evolved from the manual rather than the vocal domain (Armstrong, Stokoe & Wilcox, 1995; Corballis, 2002, 2010; Hewes, 1973; Kendon, 2004; Kimura, 1993). Hence, increasing attention is now being paid to the gesturing of non-human great apes and monkeys (e.g., Call & Tomasello, 2007b; Cartmill & Byrne, 2010; Genty, Breuer, Hobaiter & Byrne, 2009; Laidre, 2008; Maestripieri, 1996a, 1996b; Meguerditchian & Vauclair, 2006, 2009; Meguerditchian, Vauclair & Hopkins, 2010; Pollick & de Waal, 2007; Tanner, 2004). Our closest living relatives do not speak and yet gesture in complex ways. Similar to humans, their gesturing involves variable behavioural strategies. New gestures are invented, used for multiple purposes and adjusted to allow for the attentional state of the receiver (Call & Tomasello, 2007b; Genty et al., 2009; Pollick & de Waal, 2007; Tomasello & Zuberbühler, 2002).

Other theorists have proposed that gestures and vocalisations are more likely to have coevolved to form language competences that humans have today. Arbib (2005) argues that although there was an early stage where communication was predominantly gestural, ‘protosign’ and ‘protospeech’ developed through an ‘expanding spiral’ until speech became the more dominant. While the debate concerning the precursor continues (Cheney & Seyfarth, 2005; King, 2004), future research is undoubtedly needed to further our understanding of the role that both vocal and gestural modes have played in the evolution of human language. For these ends the investigation of the gestural communication of human children and non-human great apes has been considered a fruitful way of learning more about the evolutionary foundations of human language (Bard, 2009).

Before turning to a more detailed account of non-human apes gestural communication, I will introduce each species by providing information on their taxonomic classification, on the habitat they populate, and the social systems they live in. To understand apes' non-vocal communicational abilities, it is essential to consider the varying socio-ecological factors that they are likely to encounter.

1.2. Taxonomy, habitat and social structure of non-human great apes

Besides the genus *Homo* (including modern humans), the great apes (Family Hominidae) include three extant genera; orangutans (*Pongo*), gorillas (*Gorilla*), and chimpanzees (*Pan*; Groves, 2005). The members within the Family Hominidae share a number of biological and behavioural features; a long lifespan, large body sizes, long dependence of offspring, as well as a rich behavioural repertoire and complex social organisations (Kelley, 1997; Smuts, Cheney, Wrangham & Struhsaker, 1987; van Schaik, 2004). While the taxonomic classification of the non-human great apes is debated (Enard & Pääbo, 2004), in the present research I distinguish the following four great ape species: bonobo (*Pan paniscus*), chimpanzee (*Pan troglodytes*), gorilla (*Gorilla gorilla*), and orangutan (*Pongo pygmaeus*).

The *Pan* species, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), are humans' phylogenetic closest relative. It is estimated that genus *Pan* split from the human lineage about four to six million years ago (Chen, Vallender, Wang, Tzeng & Li, 2001), while bonobos and chimpanzees are thought to have separated from each other about one to three million years ago (Enard & Pääbo, 2004; cf., Fischer, Wiebe, Pääbo & Przeworski, 2004). Gorillas diverged from the human lineage approximately five to eight million years ago, and orangutans approximately 12 to 16 million years ago (Chen et al., 2001; Wildman, Uddin, Liu, Grossman & Goodman, 2003). Orangutans are humans' phylogenetic most distant relative. It should be noted that the conservation status of the extant non-human great apes has been categorised 'endangered' and 'critically endangered' respectively (International Union for Conservation of Nature [IUCN], 2010).

In terms of habitat, bonobos live in primary, secondary and swampy rainforests in the Democratic Republic of Congo (Kano, 1992; Kortlandt, 1995), while chimpanzees populate a variety of regions in Equatorial Africa; from dry grassland to mountainous rainforests (Fruth, Hohmann & McGrew, 1999; Goodall, 1986). Both species are arboreal (tree-living) and terrestrial (ground-living) - although bonobos are thought to spend more time in trees than chimpanzees (Doran, 1993, 1996). Gorillas live in swampy to mountainous forests in Western and Eastern Central Africa and are primarily terrestrial (Parker, 1999). In contrast, orangutans are native to the Indonesian islands, Borneo and Sumatra, and inhabit wide plateaus and mountainous areas as well as lowland swampy areas (Kaplan & Rogers, 1994; Rijksen & Meijaard, 1999). Unlike African apes, they show an almost exclusively arboreal lifestyle (van Schaik, Monk & Robertson, 2001).

In relation to social structure, again bonobos and chimpanzees share the most commonalities. Both species form multi-male, multi-female groups in which individuals might separate into sub-groups only to later rejoin the original group (referred to as the fission-fusion system; Badrian & Badrian, 1984; Goodall, 1986). In chimpanzees, females occasionally form so called ‘nursery groups’ with their offspring and other mother-infant dyads (Pepper, Mitani & Watts, 1999). Gorillas on the other hand form small cohesive groups which usually include one silverback, several females and offspring (Robbins, 1999; Schaller, 1963). Orangutans are less socially inclined than African apes (but see Meijaard, Welsh, Ancrenaz, Wich, Nijman & Marshall, 2010). They tend to live semi-solitary lifestyles, forming individual-based fission-fusion groups where individuals only associate with other parties from time to time (van Schaik, 1999). For orangutans the strongest and most salient relationships involve females and dependant offspring (Watts & Pusey, 2002).

All non-human great ape species exhibit a prolonged maturation period (Kuroda, 1989). The mother-infant relationship is intense and they form a long-lasting alliance (Hoff, Nadler & Maple, 1981; van Schaik, 2004). Bonobo and chimpanzee offspring are weaned between four and six years (Boesch & Boesch-Achermann, 2000; Kuroda, 1989; Watts & Pusey, 2002), while for gorillas it is between three to four years (Robbins, Robbins, Gerald-Steklis & Steklis, 2007; Watts & Pusey, 2002). For orangutans five to eight years is reported as the period when the offspring begins to be prevented from sucking (van Noordwijk, Sauren, Nuzuar, Abulani, Morrogh-Bernard, Utami Atmoko & van Schaik, 2009). In all species, the mother fulfils the majority of parental care and is essential for the offspring’s survival (Goodall, 1986; Watts, 1989). They provide nutrition, protection, transportation and social company (van Noordwijk et al., 2009). During the first months of life, all ape infants are in constant contact with their mothers (Bard, 1995; Rijksen, 1978; Stewart, 2001), although it is proposed that the orangutan mother-infant dyad manifests the tightest bond out of all species (van Noordwijk et al., 2009).

1.3. Gesturing in non-human great apes

All four non-human great ape species (bonobo, chimpanzee, gorilla, and orangutan) use gestures to communicate with their conspecifics. Our existing knowledge of gesturing in non-human great apes is based on the pioneering and extensive observational studies of mainly wild, but also captive, individuals (de Waal, 1988; MacKinnon, 1974; Rijksen, 1978; Nishida, Kano, Goodall, McGrew & Nakamura, 1999; Schaller, 1963; van Hooff, 1973; van Lawick-Goodall, 1968). More recently attention has been devoted to the comprehensive analysis of gesturing, using observational as well as experimental methods, usually, though not exclusively, of apes in captivity (e.g., Call & Tomasello, 2007b; Cartmill & Byrne, 2007, 2010; Genty & Byrne, 2010; Genty et al., 2009; Liebal, Call & Tomasello, 2004a; Liebal, Pika, Call & Tomasello, 2004b; Liebal, Pika & Tomasello, 2006; Pika, Liebal & Tomasello, 2003, 2005b; Pollick, 2006; Povinelli & O'Neill, 2000; Povinelli, Theall, Reaux & Dunphy-Lelii, 2003; Tanner, 2004).

According to Call and Tomasello (2007b) non-vocal behaviour is considered a gesture when it is goal-directed towards a communicatory partner, there is anticipation of a behavioural response by the sender, and thereby shows an understanding of its potential influence and the context it appears in. Through moving limbs, head, or postures of the whole body, apes utilise gesture in different sensory domains. They do so either by making physical body contact with the communicational partner, e.g., placing an arm on the shoulder of the recipient (tactile domain); by undertaking signals that are understood visually, e.g., throwing the arms in the air (visual domain); or by producing a noise, e.g., slapping the ground (auditory domain). Across the four species, it is the tactile and visual modes that are the more dominant (Tomasello et al., 1997; van Lawick-Goodall, 1967). Auditory gestures have been observed less in the African species and not at all in orangutans (Liebal et al., 2006; Pika, Liebal, Call & Tomasello, 2005a).

While vocalisations are generally used to inform wider audiences, e.g., to communicate the presence of predators or the discovery of food, gestures are used in more intimate dyadic interactions and are likely to occur in less biologically important situations (Pika et al., 2005a; Tomasello, 2008; Tomasello & Zuberbühler, 2002). Gestures are adapted to a number of different behavioural contexts (Call & Tomasello, 2007b; Genty et al., 2009; Pollick & de Waal, 2007), most notable play, in African species, and food negotiation situations, in orangutans (Call & Tomasello, 2007a; cf., Pollick, 2006). Most gestures are used imperatively and are thought to initiate or announce a forthcoming action, e.g., slapping the ground in front of a conspecific to invite a play interaction (Call & Tomasello 2007b; Cartmill & Byrne, 2010; Pika et al., 2005a; Plooij, 1978; Tomasello & Camioni, 1997).

Gestural communication in non-human great apes continues to receive increasing attention, yet the period of infancy still remains poorly understood. To date research on our closest relatives has tended to focus on adolescent and adult apes. So far there has been no comparative systematic analysis on infants' gestural abilities and how signals are learned across the four ape species. In line with Bruner (1972), I propose that the dynamics of the gestural developmental process must place fundamental constraints on the form that fully mature behaviour can take. Hence, advanced knowledge of the early communicative skills of non-human great apes is crucial, if we are to gain a fuller and more holistic understanding of their communicational capacities.

1.4. Focus and aims

The overarching goal of this dissertation was to develop our understanding of the emergence of natural gestural communication in our closest living relatives, the non-human great apes. To do so I drew mainly on two principles that are judged to be fundamental to a comprehensive analysis of naturally occurring animal behaviour; ontogeny and phylogeny (Tinbergen, 1963). Ontogeny is described as the genetic and environmental factors responsible for the formation of a particular behaviour during an individual's lifetime, while phylogeny describes what the behaviour looks like in close related species, and how it might have developed through evolution. In particular, I wanted to learn more about the onset and early use of gesturing, how ape infants learn their gestures, and how head gestures are utilised across species.

First, I undertook a systematic analysis of early gesturing in infants (Chapter 2). I conducted a longitudinal study of bonobos, chimpanzees, gorillas, and orangutans and systematically documented their gesturing during the first 20 months of life. In particular, I aimed to investigate; i) when infants start to gesture; ii) the order in which gestures of each sensory modality (tactile, visual, auditory) appear; iii) the extent that infants make use of these modalities in their early signalling; and, iv) the behavioural contexts where gestures are employed.

Second, I explored the role that bonobo and chimpanzee mothers, as the main social partner, played in their offsprings gestural learning (Chapter 3). Specifically, I aimed to assess the extent that gestural repertoires were shared within dyads (in terms of signal types used and their frequency performance). I contrasted, within and between *Pan* species (bonobo and chimpanzee), the following dyads: infant- mother, infant-unrelated adult females; infant-infant; and mother-mother. In doing so, I intended to learn more about the interplay of phylogenetic and ontogenetic mechanisms that might underlie gestural acquisition and development.

Finally, based on the observational data of the previous two studies I recorded the prevalence and diversity of head gestures across the four ape species (Chapter 4). In this regard, I presented a detailed description of head shaking episodes in bonobos, apparently aimed at preventing the recipient from doing something.

2. THE ONSET AND EARLY USE OF GESTURAL COMMUNICATION

2.1. Introduction

Most of what we know about the communicative abilities of our closest living relatives derives from studies on subadult and adult individuals (e.g., Call & Tomasello, 2007b; Cartmill, 2008; Genty et al., 2009; Genty & Byrne, 2010; Liebal et al., 2006; Pika et al., 2003, 2005b; Pollick, 2006; Tanner, 2004). Little attention has been paid to the emergence and early characteristics of their signalling, and, hence, the period of infancy is still poorly understood. Plooij (1978, 1984) has been the only researcher to date to systematically study the onset and early use of gestural signalling. Observing six wild mother-infant chimpanzee dyads with infants' ranging from 0 – 30 months, he found first gestures to appear around nine months of age. Only *ad hoc* observations on the gestural onset exist in other ape species. Bard (1988, 1992) observed free-ranging orangutans and their gesturing in food-sharing contexts within mother-infant dyads. Five infants (aged one month to five years) were followed for nine consecutive months. The author reported gestures from two years on – note, however, there were no infants observed between 11 months and two years of age. Liebal et al. (2006), while studying gestural communication in a predominant adult group of captive orangutans, reported gesturing in an 11-month-old infant. Finally, Pika et al. (2003, 2005b) observed a single bonobo, aged 13 months, and two gorillas, aged 16 and 20 months, employ gestures in their social interactions. The authors concluded that the ability to communicate via gestures was fully developed in captive bonobos and gorillas between one and two years of life. Collectively, these observations suggest that gestural behaviour emerges in the four ape species between 1 – 1.5 years of age.

The onset of gestural communication is of particular interest with respect to the varying life histories (i.e., the time-frame for important ontogenetic markers that characterise a course of life) of non-human apes. Although all great apes share slow life histories and long periods of dependent offspring when compared to other primates (Read & Harvey, 1989; Kelley, 1997); research suggests developmental rates still differ among species. This is particularly true for orangutans and gorillas who straddle the performance of bonobos and chimpanzees. Orangutans are thought to be the slowest among the non-human apes to reach their ontogenetic markers, e.g., gestation duration, weaning age, interbirth interval (Wich, Utami-Atmoko, Mitra Setia, Rijksen, Schürmann, van Hooff & van Schaik, 2004; Wich, de Vries, Ancrenaz, Perkins, Shumaker, Suzuki & van Schaik, 2009) and gorillas the fastest, showing the shortest infancy and juvenile stages (Bogin, 1999; Horwich, 1989; Watts & Pusey, 2002; Wich et al., 2009).

To date no comparative study has been carried out on the early gestural interactions in all four non-human great ape species. This is surprising given that for several decades authors have considered such an approach to be essential to our overall understanding of communication and its evolutionary roots (Cheney & Seyfarth, 1990; Marler, 1976; Plooij, 1979). The current study addressed this shortcoming. I performed a longitudinal, observational study of bonobos, chimpanzees, gorillas, and orangutans and systematically documented their gesturing during the first 20 months of life. More specifically, my aim was to investigate; i) when infants start to gesture; ii) the order in which signals of each sensory modality (tactile, visual, auditory) appear; iii) the extent to which infants make use of these modalities in their early signalling; and, iv) the behavioural contexts where signals are employed. Given the varying life histories in the four species, I expected the ages of gestural onset to differ; with gorillas showing the earliest and orangutans the latest onset across species. Onset differences were not expected in the two genus *Pan* species. Finally, no predictions were made concerning infants early use of signal modalities or the behavioural contexts where signals were employed.

2.2. Methods

2.2.1. Subjects

I observed six bonobos (*Pan paniscus*), eight chimpanzees (*Pan troglodytes*), three gorillas (*Gorilla gorilla*), and eight orangutans (*Pongo pygmaeus*), ranging between one and 20 months of age. They were born in captivity and lived in socially housed groups in six European zoos. All infants, except one, were reared by their biological mothers. The orangutan Dayang was raised by a foster mother from the group. The zoo facilities and their arrangements varied, but all enclosures contained climbing as well as resting opportunities, and several enrichment materials were provided (e.g., wood wool). The daily routines of the apes were not disrupted by the present research. Table 1 presents the sex, date of birth, species, and zoo affiliation of each infant.

Table 1. Infant characteristics.

Species	***Infant***	***Sex***	***Date of Birth***	***Zoo***
Bonobo	Habari	Male	29/01/06	Dierenpark Planckendael (B)
	Hongo	Male	25/02/06	Dierenpark Planckendael (B)
	Huenda	Female	06/07/06	Dierenpark Planckendael (B)
	Kivu	Male	24/02/07	Berlin Zoo (D)
	Luiza	Female	27/01/05	Leipzig Zoo (D)
	Nayembi	Female	26/04/06	Apenheul (NL)
Chimpanzee	Gihneau	Male	29/12/05	Burgers' Zoo (NL)
	Kara	Female	23/06/05	Leipzig Zoo (D)
	Kofi	Male	07/07/05	Leipzig Zoo (D)
	Lobo	Male	21/04/04	Leipzig Zoo (D)
	Lome	Male	11/08/01	Leipzig Zoo (D)
	Mora[†]	Female	23/06/07	Leipzig Zoo (D)
	Nafia	Female	10/06/06	Allwetterzoo Münster (D)
	Tai	Female	12/08/02	Leipzig Zoo (D)
Gorilla	Kibara	Female	13/01/04	Leipzig Zoo (D)
	Louna	Female	13/07/06	Leipzig Zoo (D)
	Shaila	Female	25/12/06	Burgers' Zoo (NL)
Orangutan	Dayang[‡]	Female	01/12/05	Apenheul (NL)
	Güsa	Male	09/06/06	Burgers' Zoo (NL)
	Ito	Male	26/12/06	Allwetterzoo Münster (D)
	Kila	Female	02/06/00	Leipzig Zoo (D)
	Maia	Female	07/12/07	Leipzig Zoo (D)
	Merah	Female	27/03/06	Apenheul (NL)
	Pagai	Male	06/12/03	Leipzig Zoo (D)
	Raja	Female	26/09/03	Leipzig Zoo (D)

[†] Infant died after suffering a bone fracture during observations; [‡] Infant was rejected by her mother soon after birth and was raised by a foster mother.

2.2.2. Observational procedure

The author and research assistants videotaped the observations between July 2001 and August 2008. Each infant was observed for four sessions per month (four calendar weeks) using focal animal sampling (Altmann, 1974). A session lasted five minutes and was undertaken either once every week or twice every second week. This resulted in 20 minutes of video footage per individual per month. The time of observations varied throughout the day (between 8:30 a.m. and 7 p.m.), with sessions for every subject distributed across the apes' diurnal activity. Infants were followed for a minimum of four consecutive months and a maximum of 20, i.e., the total observation time per infant ranged between 1.33 and 6.67 hours. On average, each species was observed for 27 hours. Table 2 presents detailed information of the protocol for observations and the analyses in which infants were included.

Table 2. Protocol for observations and analyses.

Species	*Infant*	*Frequency of observation*	*Observation period (initial-final age, in months)*	*Total observation time in hours*	*Analyses considered*	
					General & modality onset	*Modality & context use over*
Bonobo	Habari	Biweekly	13 – 20	2.7		✓
	Hongo	Biweekly	12 – 20	3		✓
	Huenda	Biweekly	7 – 16	3.3	✓	✓
	Kivu	Biweekly	2 – 20	6.3	✓	✓
	Luiza	Weekly	2 – 20	6.3	✓	✓
	Nayembi	Biweekly	12 – 19	2.2		✓
Chimpanzee	Gihneau	Biweekly	14 – 19	2		✓
	Kara	Weekly	2 – 20	6.3	✓	✓
	Kofi	Weekly	2 – 20	6.3	✓	✓
	Lobo	Weekly	1 – 20	6.7	✓	✓
	Lome	Weekly	2 – 20	6.3	✓	✓
	Mora	Weekly	1 – 11	3.7	✓	
	Nafia	Weekly	10 – 20	3.7	✓	✓
	Tai	Weekly	1 – 20	6.7	✓	✓
Gorilla	Kibara	Weekly	2 – 20	6.3	✓	✓
	Louna	Weekly	1 – 20	6.7	✓	✓
	Shaila	Biweekly	2 – 10	3	✓	
Orangutan	Dayang	Biweekly	17 – 20	1.3		✓
	Güsa	Biweekly	8 – 13	2	✓	
	Ito	Weekly	3 – 20	6	✓	✓
	Kila	Weekly	16 – 19	1.3	✓	✓
	Maia	Weekly	2 – 8	2.3		
	Merah	Biweekly	13 – 20	2.7	✓	✓
	Pagai	Weekly	4 – 20	5.7	✓	✓
	Raja	Weekly	6 – 19	4.7	✓	✓

2.2.3. Operational definitions and coding procedure

The operational definition of communication was adopted from Kimura (1993, p. 3) and refers to "… the behaviors by which one member of a species conveys information to another member of the species". I thereby focused on non-vocal signals that served to achieve a social goal and aimed to change the immediate behaviour of the recipient. A gesture constituted the sender directing a motoric action (using head, limb, or body movements) toward a recipient with anticipation of a reaction (adopted from Call & Tomasello, 2007b; Wetherby, Cain, Yonclas & Walker, 1988). The senders' action was accompanied by orienting their body towards the recipient, gazing at them (before, during or after signal) or by physical contact with them. The senders' anticipation of a reaction was evidenced by gaze alignment, waiting, or persisting in the communicative interaction (Bates et al., 1975; Bruner, 1981; Tomasello, Call, Nagell, Olguin & Carpenter, 1994). This definition excludes simple mechanical actions produced to complete a desired outcome without leaving the recipient the choice of action, e.g., to relocate another individual by applying physical force (Call & Tomasello, 2007b). Gestures were clustered into three sensory categories (Tomasello et al., 1997): tactile (signals were transferred by sharing body contact with recipient, e.g., nudging), visual (signals were realised over distance via particular body movements or postures, e.g., arm raising), and auditory (signals were transmitted via an acoustic yet non-vocal sound, e.g., chest beating). If a gesture incorporated more than one sensory mode, the tactile or auditory category was assigned rather than visual, i.e., these gestures could be perceived even if the recipient was not visually attending to them (Liebal, 2004).

For analysis, I played the footage through media player software and recorded the coding in a spreadsheet application. The applied coding scheme was based upon Tomasello, George, Kruger, Farrar and Evans (1985), and Liebal et al. (2006), but was further adapted in respect to the current research objectives. For each gesture, I gathered the following information: sex of sender, sex and age-class (infant: 0 – 2.5 years; juvenile: 2.6 – 5 years; subadult: 6 – 9 years; adult: ≥ 10 years) of recipient, gesture modality (tactile, visual, and auditory), gesture type, and behavioural context as judged by the available pre- and post information that accompanied the senders' signal. Table 3 presents detailed descriptions of gesture types identified and the behavioural contexts in which they were observed.

Table 3. Gesture types identified and behavioural contexts distinguished across the four ape species.

Coding category	*Associated subcategories*	*Description*
Gesture type & Modality		
Tactile	Arm on	Finger(s), hand(s), arm(s) were placed on any body part of the recipient; possibly holding on to recipients' body
	Body beat	Repeated, consecutive hits (see 'hit' description) executed with the same body part (i.e., hand(s), arm(s), or foot (feet))
	Formal bite	Gentle bite of recipients' body (executed with mouth)
	Gentle touch	Very gentle touch or hold of recipients' body with finger(s), or hand(s)
	Hit	Single and forceful hit of recipients' body with hand(s), arm(s), or foot (feet)
	Lip-lip touch	Touch recipients' mouth with one's own mouth
	Nudge	Brief movement towards recipients' body with single finger(s), hand, or foot; also kind of pinch
	Push	Exert pressure on recipients' body with hand(s), arm(s), or foot (feet)
	Rest head	Place one's own head on recipients' body
	Touch with genitals	Touch recipients' body with genital region
Visual	Arm raise	Lift arm(s) up in the air, approximately perpendicular to the ground
	Extend arm	Hold out one's hand(s), or arm(s) to recipient
	Hands around head	Lift arms up and place them around the head
	Head shake	Move head or head and upper part of body rhythmically or only once (either vertical or horizontal; included *nodding* and *bowing*)
	Lay back	Lay down on the ground and raise limbs in the air
	Move object	Move object (e.g., jute bag) on the ground
	Peer	Closely approach recipient and stare at its mouth or hands (while recipient is holding something of interest, e.g., food, or performing a certain action)
	Running back	Move backwards
	Shake	Shake limb(s) or whole body rhythmically; includes also kind of swinging around rope or bar
	Shake object	Wave object (e.g., rope) mainly with one's hand(s)
	Somersault	Turn a somersault on the ground
	Swagger	Move body rhythmically sidewise or back and forth while standing or sitting
Auditory	Beat object	Repeated, consecutive hits on ground, wall, or object (see 'hit object' description) executed with the same body part (i.e., hand(s), arm(s), or foot (feet))
	Body slap	Single hit of one's own body (except chest region) with hand(s)
	Chest beat	Repeated hits with alternating hand(s) on one's own chest
	Foot stomp	Single and forceful step on the ground with one foot or both feet
	Hit object	Single and forceful hit on ground, wall, or object with hand(s), or arm(s)
Behavioural context		
	Access	Behaviour related to the access of objects, such as offer access or prevent from access to an object
	Affiliation	Unaggressive approaches towards other individuals with the objective of decreasing distance and possibly establishing body contact), such as greeting events or requesting 'body closeness'
	Agonism	Aggressive behaviour, possibly including physical contact, e.g., threatening or antagonistic encounters; also included less obvious aggressive behaviour with the objective to increase distance between two individuals, such as displaying
	Ingestion	Behaviour concerning food intake, e.g., begging behaviour; includes solid and fluid food
	Playing	Behaviour to initiate or continue social play interactions, e.g., wrestling, chasing, or rough-and-tumble play, often accompanied by play face expression
	Sexual	Behaviour accompanying mating interaction, e.g., presenting genitals
	Locomotion	Behaviour accompanying the locomotion in the enclosure, e.g., initiating locomotion after a period of rest

2.2.4. Interobserver reliability and analysis

The author coded all video footage. To ensure reliability, 20% of the data were randomly chosen and coded by a naïve second person. I used Cohen's Kappa to measure the degree of concordance between the two observers for gesture modality, type, and behavioural context (Altman, 1991). The resulting Kappa values 0.89 (for modality), 0.84 (type), and 0.79 (context), according to Altman (1991) equate to a 'good' and 'very good' level of agreement.

To analyse the order in which signal modalities appeared, I used a ranking procedure. I assigned the ranks 1 – 3 to African apes (with '1' being the earliest and '3' the latest), and ranks 1 and 2 to orangutans (since they displayed no auditory signals). This also ensured that infants who had not displayed gestures in all possible modalities were incorporated in the analysis. If an African infant only showed a single sensory domain while being observed, I assigned the unseen modalities tied ranks. For example, the gorilla Shaila (observed between 2 – 10 months) showed visual but no tactile or auditory signals. I ranked her as follows: visual = 1, tactile and auditory = 2.5.

I used non-parametric tests for analyses. The Friedman and Wilcoxon tests compared dependant samples, while the Kruskal-Wallis and Mann-Whitney U-tests compared independent groups (Siegel & Castellan, 1988). All *p*-values were two-tailed and a null hypothesis was rejected at an alpha-level of 5%. As sample sizes were small, I reported exact significances (Mundry & Fischer, 1998). Moreover, I reported effect sizes (using Pearson's correlation coefficient *r*) for the Wilcoxon and Mann-Whitney U-tests (Field, 2005). An effect size of .10 represents a small effect, .30 a medium effect, and .50 a large effect (Cohen, 1988).

Sample sizes differed for particular analyses (see Table 2); more detailed information about these variations, and their rationale, is given in each respective results subsection. The median was the chosen form of central tendency unless otherwise stated.

2.3. Results

2.3.1. Overview of gestures

I identified twenty-seven gesture types (10 tactile, 12 visual, and 5 auditory) incorporating 298 gestures across the four ape species. No orangutan utilised any auditory signal. Since the auditory mode has also not been observed in older orangutans (Liebal et al., 2006; Pika et al., 2005a), I did not include this species in any analyses considering this domain. One out of the eight orangutans, Maia, observed from two to eight months, did not show any signals. Table 4 presents the number of gesture types observed (and their overall occurrences) per sensory modality and species.

Table 4. Number of gesture types observed in the four ape species (in brackets: total number of occurrences).

Species	***Gesture types***			***TOTAL***
	Tactile	**visual**	**auditory**	
Bonobo (*N* = 6)	4 (19)	9 (58)	2 (7)	15 (84)
Chimpanzee (*N* = 8)	5 (46)	10 (58)	2 (6)	17 (110)
Gorilla (*N* = 3)	3 (12)	5 (18)	4 (12)	12 (42)
Orangutan (*N* = 7*)	8 (35)	5 (27)	-	13 (62)

* One subject excluded.

2.3.2. Gestural onset

To determine the gestural onset, I considered only subjects observed for at least two consecutive months prior to their potential first gesture. This subsample included 19 subjects (three bonobos, seven chimpanzees, three gorillas, six orangutans; see Table 2).

Figure 1 presents the age of each infant when their first gesture appeared (irrespective of sensory modality). I found differences between species (Kruskal-Wallis test: $H(3) = 10.59$, $p = 0.004$; $N = 19$). *Post hoc* examinations yielded a significant delayed onset in orangutans when compared with the three African ape species (Mann-Whitney U-tests: gorilla, $U = 0$, $p = 0.012$, $r = -.80$; chimpanzee, $U = 4$, $p = 0.012$, $r = -.69$; bonobo, $U = 0.5$, $p = 0.024$, $r = -.75$). The three African species displayed, however, their first gesture at a similar age (bonobo versus chimpanzee: $U = 6.5$, $p = 0.467$, $r = -.30$; chimpanzee versus gorilla: $U = 9$, $p = 0.800$, $r = -.11$; bonobo versus gorilla: $U = 0$, $p = 0.100$, $r = -.87$, note in this last comparison the small sample sizes for both species and high effect size).

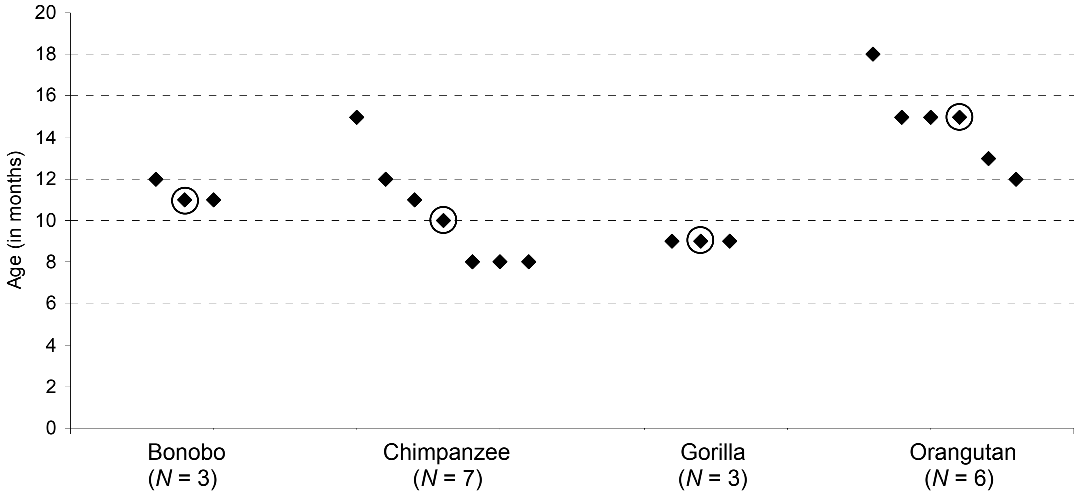


Figure 1. Infants' gestural onset (*N* = 19; circle represents median onset age in each species).

2.3.3. Emergence of tactile, visual and auditory gesturing

Figure 2 shows detailed information about the age at which gestures of each sensory modality (tactile, visual, and auditory) were first observed in the 19 infants who qualified for the onset analysis. By conducting the ranking procedure, I observed that the ranks at which the tactile and visual modality appeared were similar in all species ($N = 19$; tactile: $H(3) = 0.63$, $p = 0.921$; visual: $H(3) = 1.6$, $p = 0.676$). Auditory gestures (considering only the African species) also emerged at similar positions in the ranking system ($H(2) = 3.05$, $p = 0.266$; $N = 13$).

For African apes, some gesture modalities appeared earlier than others (Friedman test: $\chi^2(2) = 14.94$, $p < 0.001$; $N = 13$). *Post hoc* testing revealed that auditory signals were produced significantly later than both tactile (Wilcoxon test: $T = 0$, $p < 0.001$, $r = -.61$) and visual signals ($T = 3$, $p = 0.006$, $r = -.53$). The order that the tactile and visual modalities appeared was similar ($T = 21$, $p = 0.339$, $r = -.22$). This result was confirmed when orangutans were added to the analysis ($T = 53$, $p = 0.450$, $r = -.13$; $N = 19$).

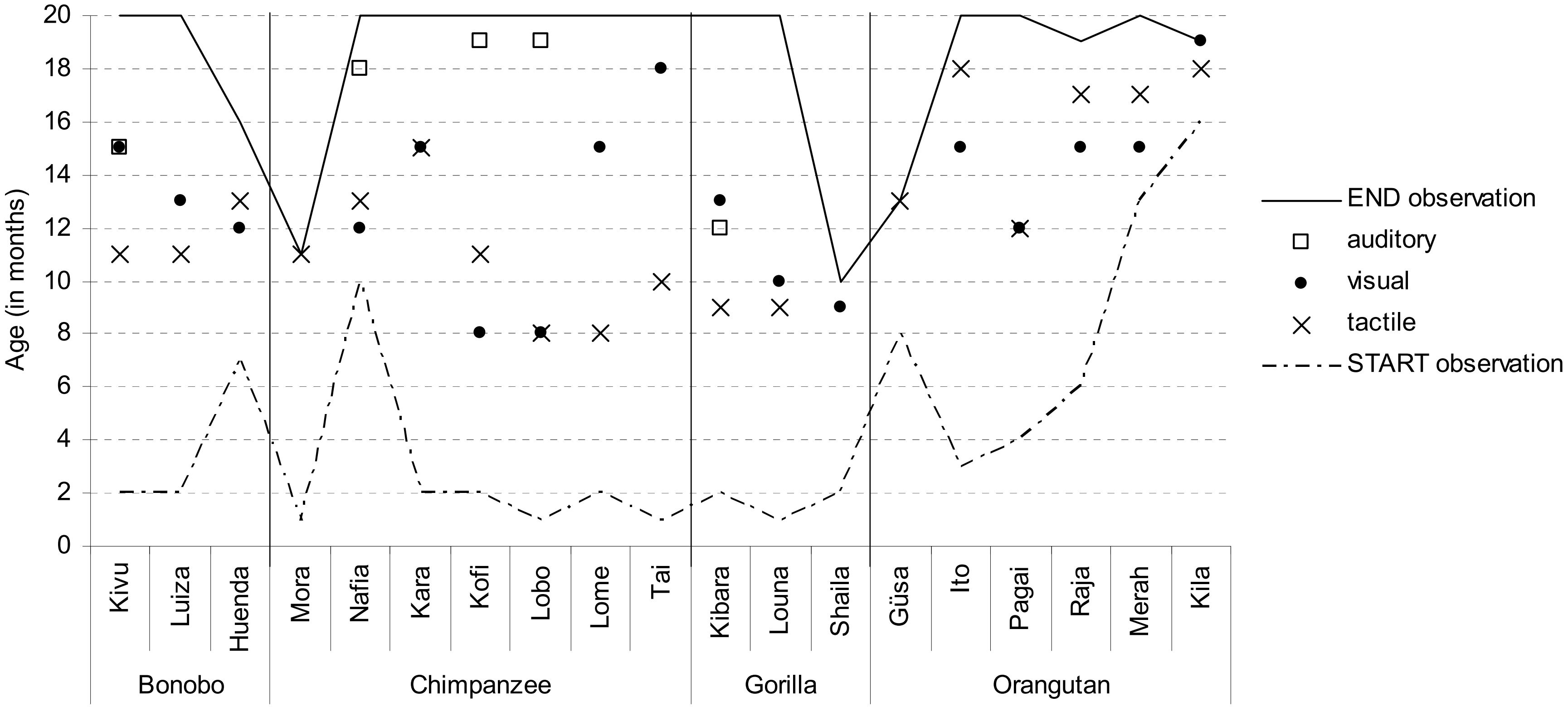


Figure 2. First appearance of gestures in the four species broken down by the three sensory modalities ($N = 19$).

2.3.4. Use of gestures over time

2.3.4.1. Sensory modality

To explore the role of sensory modality in the production of gestures over time (regardless of the respective signal types), I divided the observation period, of 9 months (the earliest median onset age for any species) to 20 months, into two time periods; 9 – 14 months inclusive and 15 – 20 months inclusive. Here, I considered only those individuals who were observed for at least one month in each time-block.

Since the three African species were similar in the order in which they first displayed all three sensory modalities (tactile and visual together, auditory significantly later), I compared them collectively over the two time-periods. Orangutans, who did not start gesturing until a median age of 15 months, could only be considered in the latter period 15 – 20 months. I contrasted their performances with those of African apes in the earlier 9 – 14 months period. Overall these analyses incorporated six orangutans and 15 African apes (six bonobos, seven chimpanzees, two gorillas; see Table 2).

Figure 3 presents the mean percentages of signals used in each domain for African apes and orangutans over the specified time periods. In African apes the proportion of visual signals that were displayed increased significantly over the two periods ($T = 25$, $p = 0.047$, $r = -.36$), while tactile gesturing significantly decreased ($T = 23$, $p = 0.035$, $r = -.38$). For the auditory domain, I found a trend for an increase ($T = 3$, $p = 0.078$, $r = -.34$).

Between 15 and 20 months of life, orangutans displayed a similar percentage of tactile ($U = 38.5$, $p = 0.631$, $r = -.11$) and visual signals ($U = 42$, $p = 0.834$, $r = -.05$) to that of African apes between 9 and 14 months (Figure 3).

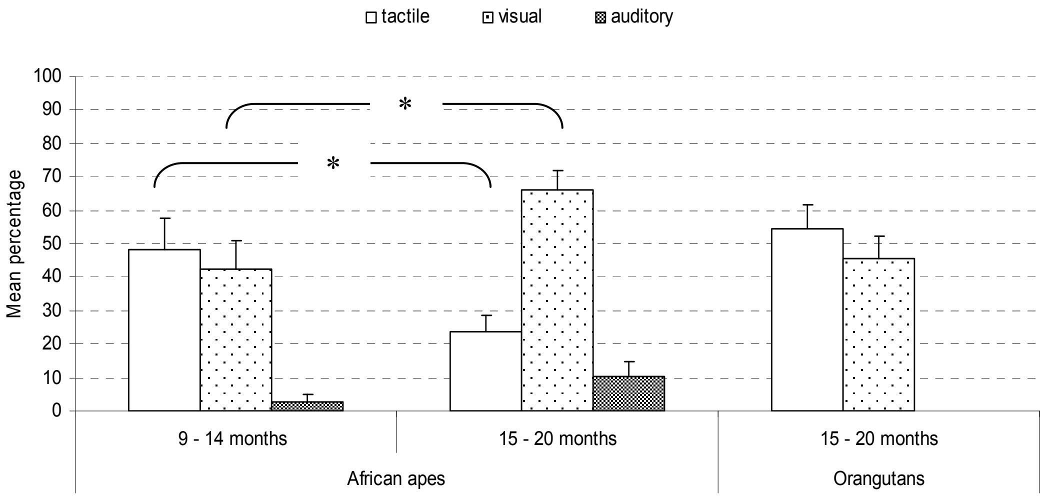


Figure 3. Mean percentages (plus standard error bar) for the three sensory modalities utilised by African apes (*N* = 15) and orangutans (*N* = 6) in the specified time-periods (* *p* < 0.05).

2.3.4.2. Behavioural context

I focused on the three main behavioural contexts in which infants employed their gestures: play, ingestion, and affiliation. Single cases of additional contexts - access, agonism, sexual, and locomotion - were assigned to the category ‘other’.

As described above, African apes were compared across the two time periods, while orangutans (15 – 20 months) were contrasted with the early performance of African apes (9 – 14 months). Figure 4 presents the mean percentages of signals employed in the behavioural contexts observed for African apes and orangutans.

African apes did not reveal any significant context differences over time (play: $T = 29$, $p = 0.273$, $r = -.21$; ingestion: $T = 13$, $p = 0.160$, $r = -.27$), although I found a clear trend for a lower percentage of affiliation-related signals in slightly older apes ($T = 11$, $p = 0.054$, $r = -.36$). Within each time-block, however, more signals were proportionally produced in certain contexts (9 – 14 months: $\chi^2(3) = 12.34$, $p = 0.004$; 15

– 20 months: $\chi^2(3) = 20.88, p < 0.001$). *Post hoc* testing revealed that infants produced a significantly greater percentage of signals in the play context than in the ingestion ($T = 5, p = 0.039, r = -.38$) and than in 'other' contexts ($T = 0, p = 0.002, r = -.52$) between 9 and 14 months. The proportion of play- and affiliation-related gestures that were shown did not differ ($T = 21.5, p = 0.318, r = -.19$). Between 15 and 20 months of life, signals were significantly more likely to be produced in play encounters than in any other context (ingestion: $T = 15, p = 0.016, r = -.43$; affiliation: $T = 3, p = 0.001, r = -.57$; 'other': $T = 5, p = 0.001, r = -.57$).

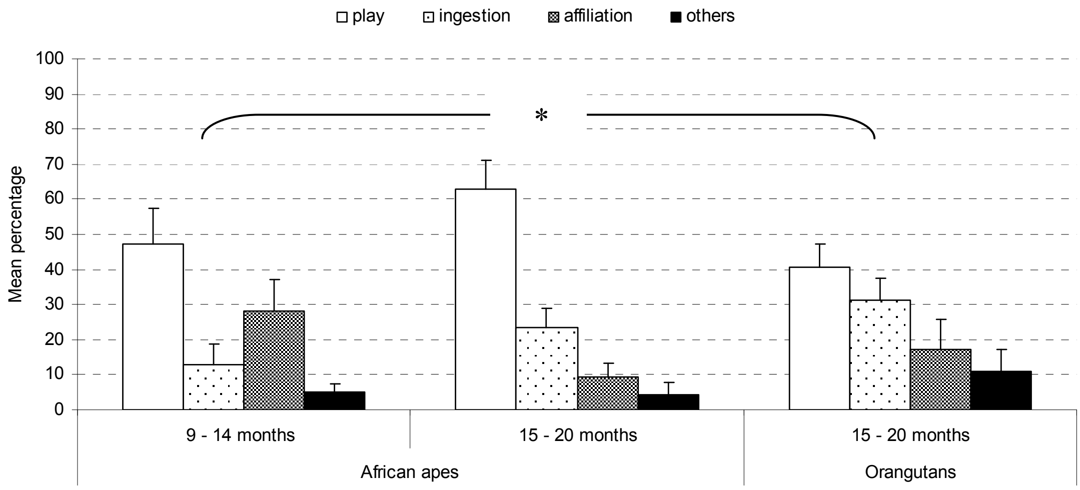


Figure 4. Mean percentages (plus standard error bar) of the gesturing context for African apes ($N = 15$) and orangutans ($N = 6$) in the specified time-periods (* $p < 0.05$).

Orangutans, in the 15 – 20 month period showed a greater percentage of food-related signals than African apes in the 9 – 14 month period ($U = 16, p = 0.018, r = -.51$). No differences were detected for the play ($U = 42, p = 0.834, r = -.05$) and affiliation context ($U = 40, p = 0.713, r = -.09$; Figure 4).

2.4. Discussion

In the present study I captured the onset of gestural communication in the four non-human great ape species. Orangutans started gesturing at least four months later than African apes, and, as previous research has also demonstrated (see Call & Tomasello, 2007a), did not show any auditory gestures. While African apes made use of all three signal modalities (tactile, visual, and auditory), auditory signals were only employed after the onset of tactile and visual. In their first six months of gesturing, the African species and orangutans displayed comparable proportions of tactile and visual signals. African apes, however, showed an increase of visual signals at the expense of tactile gestures with age. In terms of the behavioural contexts in which signals were employed, orangutans showed proportionally more food-related signals than African ape infants in their first six months of gesturing.

Regarding the gestural onset in chimpanzees, the data are largely consistent with Plooij's (1978, 1984) systematic observation of wild conspecifics. Plooij observed the first gestures around nine months, while in the current sample the median age was 10 months for chimpanzees. Compared with the African species, orangutans were the slowest to start gesturing. This finding supports my prediction that Asian apes would differ in their onset ages from other species as they are the slowest among the non-human apes to reach their ontogenetic markers (e.g., weaning age; Wich et al., 2004, 2009). The data also partially support the prediction that gorillas would be the fasted to gesture. Gorillas showed a possible accelerated onset when compared to bonobos, but not to chimpanzees (see Pika et al., 2003 for similar observations in gorillas). This coincides with our knowledge of gorilla's expedited developmental trajectory (Bogin, 1999; Horwich, 1989; Watts & Pusey, 2002; Wich et al., 2009). However, further research with larger sample sizes is needed to further verify this conclusion.

I propose that infant's motility played an important part in the recognised differences in gesturing development between the African ape species and orangutans. Congruent with this premise was the fact that distal (i.e., visual) gesturing increased over time at the expense of tactile signals in African apes. Tactile gestures appeared to be more important to the infant when they were still bodily close to the mother or were requesting 'comfort', but these were superseded by distal gestures as they matured and gained independence. The trend for a proportional decline in affiliation-related signals in these species (i.e., gestures that are used by infants to decrease distance from mother, such as *extend arm*), also supports the idea of a motility-gestural onset link. Further evidence of the importance of motility comes from my qualitative observations. Infants with less-advanced locomotion (hence, higher rates of close-body contact with their mother) displayed a slower gestural onset. Typically I observed this in orangutans (see Horwich, 1989; cf., Miller & Nadler, 1981); but also elsewhere. For example, one female chimpanzee (Kara) showed the latest gestural onset among her conspecifics (15 months versus 10 months median onset age in chimpanzees) and was observed to be the least independent from the mother.

As it has been hypothesised in human infants, the onset of locomotion has far-reaching implications on the maturation of the perceptual system and cognitive development in general (see Campos et al., 2000 for a review). Moreover, it has been proposed that the development of independent locomotion is intimately linked with the emerging ability for social referencing within the mother-infant dyad (Bertenthal &

Campos, 1990; Rochat, 2004). When starting to crawl, for example, infants use their mother's emotional reaction as an information source in potentially dangerous situations (Bertenthal & Campos, 1990). Social referencing might, therefore, serve as the connection between an infant's caregiver (who provides security) and the exploration of the environment (Rochat, 2004). I propose that further examining whether the emergence of gestures is temporally associated with the onset of independent locomotion, will enhance our knowledge of the processes involved in gestural acquisition for human and other ape species.

In regard to the behavioural contexts in which signals were employed in their first six months of gesturing, orangutans displayed a considerable higher proportion of signals in food-related interactions than African apes. Similar contextual patterns have been previously observed in older subjects (Call & Tomasello, 2007a). An explanation for this might be that African apes beg less for food as their mothers are more likely to share. Recent studies seem to indicate that bonobos, for example, are more tolerant and cooperative than other apes when it comes to food access and distribution (Hare, Melis, Woods, Hastings & Wrangham, 2007; Wobber, Wrangham & Hare, 2010; cf., Jaeggi, Stevens & van Schaik, 2010b).

Despite the different developmental trajectories of tactile and visual signals, both emerged close in time and were shown in similar proportions in the first six months of gesturing for the four species. These findings emphasise the importance of visual signalling in the apes' early life and thereby challenge the view that tactile signals are dominant in youngsters – as previously proposed for chimpanzees (Tomasello & Camioni, 1997). The current data indicate a similar early manifestation of visual gestures (and arguably underlying cognitive capacities) to that of human infants (see Crais, 2007). In regard to the visual domain, differing results have been reported in monkeys. Grigor'eva and Deryagina (1987), who examined the early gestural communication in stump-tailed macaques (*Macaca arctoides*) and hamadryas baboons (*Papio hamadryas*), found that visual gestures appeared later than tactile gestures in their ontogeny, in fact, in the early stages visual gestures were virtually non-existent. Overall, therefore, signals of the visual domain might have gained phylogenetic importance in human and non-human great ape species but not in monkeys.

Although the present research is the largest explorative study on ape infants' communication skills conducted to date, the data had various limitations. Most importantly, sample sizes were small. Time constraints and other logistical obstacles also meant that overall observation times for each species were limited, and individual observation times varied (i.e., infants were observed for differing time periods during their first 20 months). As a consequence, it was only possible to incorporate subsamples in the analyses (e.g., only 19 of 25 subjects were included in onset-analysis). Follow-up studies incorporating larger sample sizes and increased observation times per individual could help strengthen the generalisability of my findings.

In my exploration of apes' gestural beginnings, I found orangutans to differ markedly from African apes. Most notably, and in accordance with their proposed slow life history, orangutans were the slowest in gestural onset when compared with the African species. However, there were also similarities. Comparable to humans, and unlike monkeys, early gestures in all non-human ape species were likely to be visual or tactile. This may indicate the phylogenetic importance of the visual channel in early communication in human and non-human ape species. It is suggested that motility is an important ontogenetic antecedent embroiled in gestural acquisition and its development. The extent that this may be the case is one of the intriguing questions this research has raised and should be further explored.

Following the investigation of the onset and early use of gesturing in the four non-human great ape species, I now turn to the question: what role do genus *Pan* mothers' play in their offspring's gestural learning. I compare the gestural repertoires of six bonobo and four chimpanzee infants with their mothers to assess the signal overlap within these dyads. In addition, I contrast the repertoires between infant-infant, mother-mother dyad groups within and between species. From the derived findings I discuss possible mechanisms that might underlie the acquisition process.

3. WHAT ROLE DO MOTHERS PLAY IN THE GESTURAL ACQUISITION OF BONOBOS AND CHIMPANZEES?

3.1. Introduction

Proposed mechanisms that underlie the acquisition of gestural communication in non-human great apes are currently discussed in relation to the predominance of phylogenetic (evolutionary shaped) and ontogenetic (lifetime shaped) influences. In terms of the phylogeny, researchers have targeted the influence of biological inheritance, while those concentrating on ontogeny, have focused on how signals are either learnt via observing others (observational learning) or through progressive social interactions (ontogenetic ritualisation).

One form of evidence to support the biological inheritance of gestures comes through observing young apes who have developed species-typical gestures in the absence of role models (i.e., they were unable to observe older conspecifics). From these deprived contexts similar signals, e.g., *chest beat* in gorillas, have been found to strongly resemble those performed by conspecifics living in a more natural group composition (Redshaw & Locke, 1976). An alternative approach has been to comprehensively study distinct groups of a species (in their varying age-classes). For example, Genty et al. (2009) carried out a comprehensive analysis on the gestural repertoires of four separate gorilla groups (three captive and one wild). From their observations, the authors concluded that most gestures from gorillas belong to a (universal) species-typical pool of signals and that apparent repertoire differences between individuals and groups could be explained by varying ecological conditions.

From a series of studies on gestural communication and its genesis over a 12 year period in captive chimpanzee youngsters, Tomasello et al. (1985, 1989, 1994, 1997) have proposed that individual learning is the major mechanism at work in the gestural acquisition process. Through a process of ontogenetic ritualisation (described as 'conventionalization' by Smith, 1977) a signal develops as two individuals shape each other's behaviour in repeated interactions (Tomasello & Call, 1997). A non-communicative behaviour gains a communicative function through anticipation of the socially interacting individuals over time. For example, while playing with each other a chimpanzee youngster slaps her play partner. After several repetitions of this behaviour the conspecific recognises the signal and anticipates the play behaviour. The ritualisation is complete when the youngster raises its arm not to perform the physical act of slapping but to demonstrate an abbreviated *arm raise* gesture to invite play (Tomasello & Call, 1997). Support for this process underpinning gestural acquisition comes from studies that have witnessed the invention of new signals through social interactions and the highly variable repertoires observed among individuals in species groups (Call & Tomasello, 2007b). In all four non-human great ape species idiosyncratic gestures (performed by only one subject) have been observed in captivity; bonobos (Pika et al., 2005b); chimpanzees (Tomasello et al., 1985); gorillas (Pika et al., 2003); and orangutans (Liebal et al., 2006).

Another ontogenetic mechanism that has been discussed in relation to gesture acquisition is observational learning. Here individuals learn gestures by observing and subsequently replicating behaviours from; parents (parent-to-offspring transmission, called vertical transmission); peers (within same generation, called horizontal transmission); or non-related older to younger members (oblique transmission; Cavalli-

Sforza & Feldman, 1981). Hence, supportive evidence is provided by group-specific gestures, i.e., gestures that are used by members in one but not in other groups. For example, Liebal et al. (2006) observed the signal *offer arm with food pieces* in a single group of captive orangutans (see Pika et al., 2003, 2005b for similar observations in captive gorillas and bonobos).

One context that is likely to elucidate important information about the origin of gestures is the mother-infant dyad. Surprisingly little research has been conducted in this area. All great apes have extended periods of immaturity (Pereira & Fairbanks, 2002), and, hence, the mother-infant dyad is characterised by a long-lasting, and intensive relationship (Hoff et al., 1981; Plooij, 1978, 1984; van Lawick-Goodall, 1967). At the time infants begin to gesture (typically between 1 – 1.5 years of life in the four non-human great ape species; see Chapter 2 and Plooij, 1978), the mother is the most important social partner. In addition, several authors have suggested that the mother-infant relationship is essential to the communication basics that underlie an infant's socialisation process (King, 2004; Maestripieri & Call, 1996).

In the only systematic investigation of its kind, Cartmill (2008) compared the overlap of gestural repertoires among eight orangutan youngsters (seven, aged 10 – 25 months, and one, aged 30 – 48 months) and their mothers (including two foster, i.e., non-biological, mothers). The author reported that infants shared more gestures with their mother and adoptive mothers respectively, than they did with other adult female group members. It was concluded that the association between infant and caretaker was important to the observational learning of gestures. This is in contrast to chimpanzees, where, in comparison to peers, mothers are said to play only a minor role in the youngsters' gestural development (Tomasello et al., 1989, 1994).

Due to the lack of research in this area, the mother’s role in the development of an infant ape’s gestural repertoire remains unclear. The purpose of the present study was to increase our knowledge of the part mothers play in infants’ gestural acquisition, and, in doing so, further our understanding of the interplay of phylogeny and ontogeny in gestural development. I used an observational method to contrast, within and between *Pan* species (bonobo and chimpanzee), the following dyads: infant-(biological) mother, infant-unrelated adult females; infant-infant; and mother-mother. For each dyad observed, I recorded and compared the types of gestures exhibited and their frequency.

3.2. Methods

3.2.1. Subjects

I observed six bonobo (*Pan paniscus*) and four chimpanzee (*Pan troglodytes*) infants in their first 20 months of life (Table 5). All infants were born in captivity, lived in socially housed groups (in six European zoos), and were raised by their biological mothers. Mothers' age ranged between eight and 28 years in bonobos ($M = 19$, $SD = 9.59$), and between 21 and 43 years in chimpanzees ($M = 28.63$, $SD = 6.48$; Table 5).

Table 5. Infants observed.

Species	***Infant***	***Sex***	***Date of birth***	***Age of mother (at birth)***	***Location***
Bonobo	Habari	Male	29/01/06	11	Dierenpark Planckendael
	Hongo	Male	25/02/06	28[a]	Dierenpark Planckendael
	Huenda	Female	06/07/06	28[a]	Dierenpark Planckendael
	Kivu	Male	24/02/07	27	Berlin Zoo
	Luiza	Female	27/01/05	12	Leipzig Zoo
	Nayembi	Female	26/04/06	8	Apenheul
Chimpanzee	Gihneau	Male	29/12/05	21	Burgers' Zoo
	Kara	Female	23/06/05	29	Leipzig Zoo
	Kofi	Male	07/07/05	28	Leipzig Zoo
	Nafia	Female	10/06/06	43[a]	Münster Zoo

[a] Estimated age, as these mothers were born in the wild.

3.2.2. Observational and coding procedure

The author and research assistants videotaped the observations between July 2005 and August 2008. Focal animal sampling was used to record the infants and their social interactions (Altmann, 1974). Every infant was observed for four sessions per month with each session lasting 15 minutes. The sessions were undertaken either once every week or twice every second week and resulted in one hour of video footage per subject per month. Each infant was observed for a specific period of time during their first 20 months of life; the duration of the observed periods varied between eight and 19 months for bonobos and six and 19 months for chimpanzees (Table 6). Overall, bonobos were observed for 67 hours and chimpanzees for 55 hours. Note that the current study incorporated a subset of coded data (which accounted for one third of the whole dataset) from the previous study reported in Chapter 2.

Table 6. Observational information on each subject.

Species	***Infant***	***Observation regularity***	***Observation period*** *(age in months)*	***Total observation time in hours***
Bonobo	Habari	Biweekly	13 – 20	8
	Hongo	Biweekly	12 – 20	9
	Huenda	Biweekly	7 – 16	10
	Kivu	Biweekly	2 – 20	19
	Luiza	Weekly	8 – 20	13
	Nayembi	Biweekly	12 – 19	8
Chimpanzee	Gihneau	Biweekly	14 – 19	6
	Kara	Weekly	2 – 20	19
	Kofi	Weekly	2 – 20	19
	Nafia	Weekly	10 – 20	11

I recorded all signals produced by the focal animals (directed to mother or other group members) and their mothers (directed to infant or other group members). Mothers' gestures were noted whenever they were near the infant and therefore in the view of the camera. For each gesture I coded the following variables: sender and recipient (for both; sex, and age class: 0 – 2.5 years, 2.6 – 5 years, 6 – 9 years, ≥ 10 years), gesture modality (tactile: signal was transferred by initiating body contact with recipient; visual: signal was visually realised over distance via particular body movements or postures; auditory: signal was transferred via the acoustic channel but was non-vocal), and gesture type (see Appendix, Table 7 for definitions). For detailed operational definitions of gestural behaviour see Chapter 2 (section 2.2.3.).

3.2.3. Interobserver reliability

The author coded all video footage. To determine reliability, 20% of the infants' and mothers' gestures were randomly chosen and coded by a naïve second person. I used Cohen's Kappa to measure the degree of concordance between raters for modality and gesture type (Altman, 1991). In the case of unbalanced coding between raters, e.g., one rater used codes 1 – 3, whereas the other rater never used 1 at all, Kappa could not be computed because of the asymmetry in the table. In these cases, I used a permutation procedure to determine the coefficient (Manly, 1997; software written by R. Mundry). First, the original agreement between the two observers was established. Then the codes of one observer were randomised and the agreement was measured again. In total 1,000 randomisations were conducted (with the original data included as one permutation). Afterwards the original agreement was compared with the distribution of agreements derived from the permutations. The Kappa coefficient was determined as usual [K = (observed agreement - expected agreement) / (1 - expected agreement)], whereby the expected agreement was the average agreement revealed from truly permuted data. By applying this procedure, the information from every observation was retained and the Kappa was an appropriate measure of the reliability of the original codes. For the gesture modality, the Kappa values ranged between 0.86 (mother) and 0.91 (infant), and between 0.76 (mother) and 0.82 (infant) for the gesture types. According to Altman (1991) these values equate to a 'good' and 'very good' level of agreement.

3.2.4. Data analyses and statistics

I applied the Kendall rank correlation coefficient Tau (τ) to correlate the frequencies with which distinct gestures occurred in two individuals of a given dyad. I determined the correlation twice per dyad; once based on only those gestures which were shown by both individuals (in the following referred to as *only both* dataset) and once including each gesture which was shown by at least one of the two individuals, i.e., their entire repertoires (in the following referred to as *at least once* dataset). A τ of -1 indicates that gestures frequently performed by one individual were never shown by the other individual, whereas a τ of +1 indicates that relative frequencies by which the two individuals exhibited the gestures were in perfect agreement. I calculated the DICE-coefficient C_D (Dice, 1945) to obtain a measure of how similar the repertoires of two individuals were [with C_D = 2 x number of gestures common for subject A and B / (total number of gestures shown by subject A + total number of gestures shown by subject B)]. This coefficient indicates the proportion of shared gestures used in a dyad and ranges between 0 and 1; 0 indicates that two individuals did not share any gesture and 1 indicates a perfect match of gesture repertoires in a dyad.

In the case of the correlation datasets (*only both* and *at least once)*, I applied Fisher's omnibus tests (Haccou & Meelis, 1994) to ascertain whether single significant *p*-values were spurious. Here the *p*-values of the correlation coefficients were integrated into a single χ^2-distribution, where the degrees of freedom were twice the number of *p*-values incorporated. I then tested whether correlations between frequencies of gestures differed among dyad-types (infant-own mother *or* infant-other mothers) as well as among species. To do so, a repeated-measures ANOVA was undertaken for the proportions of shared gestures (DICE) and for each correlation dataset (*only both* and *at least once*), into which species was included as a between-subjects factor and dyad-type as a within-subjects factor.

Next, I compared the similarities between repertoires among different groups of dyads (DICE-coefficients of shared gestures as well as correlations between gesture frequencies). Firstly, I conducted comparisons between infant-infant, mother-mother, and infant-mother (own and other) dyads. I considered only bonobos for this analysis as they were the only species with a large enough sample size. If such a test reveals significance it could, for instance, indicate that repertoires of infants are particularly homogeneous (i.e., show larger similarity with one another rather than with mothers, or mothers with one another). Secondly, I conducted a comparison of infant species by contrasting bonobo-bonobo, chimpanzee-chimpanzee, and bonobo-chimpanzee dyads. Lastly, I repeated this comparison for mothers (bonobo-bonobo, chimpanzee-chimpanzee, and bonobo-chimpanzee). These three analyses could not be carried out using standard tests since the data were non-independent (i.e., each individual was involved in several dyadic measures of similarity). Hence, I used a permutation test (Adams & Anthony, 1996; Manly, 1997), similar to a Mantel-test for matrix correlation (Sokal & Rohlf, 1995). In the present analysis, one matrix denoted the dyadic similarity (e.g., the correlation between frequencies by which gestures occurred in the two subjects of a dyad); the other matrix represented the dyad-type (e.g., infant-mother, mother-mother, etc.). The test statistic consisted of the sum of the squared differences between mean similarity measures per dyad-type and the mean similarity measures of all dyads. Permutations were achieved by simultaneously randomising rows and columns of one of the two matrices. By conducting 1,000 permutations (into which the original data was included as one permutation) the sampling distribution of the test statistic was obtained under the assumption of a true null hypothesis. Finally, the *p*-value was estimated as the proportion of test statistics in the sampling distribution being at least as large as that of the original data.

I calculated the repeated-measures ANOVAs using SPSS 15.0. Fisher's omnibus test was calculated by hand, and for the matrix permutation test, a script (written by R. Mundry) for R 2.9.1 (R Development Core Team, 2009) was used.

3.3. Results

3.3.1. Description of mother-infant gestural repertoires

A total of 1,269 gestures (comprising 39 distinct gesture types) were analysed. The six bonobo infants produced 247 gestures (consisting of 21 types) and their mothers 561 gestures (26 types). The four chimpanzee infants employed 184 gestures (25 types) and their mothers 277 gestures (22 types; see Appendix, Table 7 for signal types and corresponding sensory domain observed in infants and mothers of each species).

Infant repertoires ranged from five to 17 gesture types in bonobos and from ten to 17 gesture types in chimpanzees. Mother repertoires consisted of 11 to 18 gesture types in bonobos and nine to 14 in chimpanzees (Table 8).

Table 8. Repertoire sizes of infants and mothers in bonobos ($N = 6$) and chimpanzees ($N = 4$); and the number of gesture types shown by each individual alone, and the numbers common to both.

Species	***Mother-Infant dyad***	***Repertoire size***		***Infant only***	***Mother Only***	***Both***
		Infant	***Mother***			
Bonobo	Djanoa-Habari	17	14	8	5	9
	Hermien-Huenda	5	13	2	10	3
	Hortense-Hongo	10	13	8	11	2
	Liboso-Nayembi	10	12	6	8	4
	Ulindi-Luiza	12	18	5	11	7
	Yala-Kivu	8	11	7	10	1
Chimpanzee	Fraukje-Kara	11	14	5	8	6
	Gaby-Gihneau	14	9	10	5	4
	Ulla-Kofi	17	12	11	6	6
	Yola-Nafia	10	10	5	5	5

3.3.2. Similarity of repertoires within mother-infant dyads

Overall, *p*-values derived from the Kendall correlation coefficients (Table 9) were significantly related in all genus *Pan* infant-own mother and infant-other mothers dyad types (Fisher's omnibus test: $\chi^2 = 108.79$, $df = 78$, $p = 0.012$). Infants were dissimilar from their own mothers and other mothers concerning the frequency of gestures that were employed by at least one dyad member (*at least once* dataset). The coefficients ranged from 0.01 to -0.58 (infant-own mother) and -0.14 to -0.54 (infant-other mothers); the corresponding *p*-values were significantly related when infants were compared with their own mothers (Fisher's omnibus test: $\chi^2 = 43.07$, $df = 20$, $p = 0.002$) and other mothers ($\chi^2 = 41.61$, $df = 20$, $p = 0.003$; Table 9). The correlations for gestures that were employed by both members of a dyad (*only both* dataset), however, were non-significantly related when infant-own mother dyads (Fisher's omnibus test: $\chi^2 = 14.79$, $df = 18$, $p = 0.676$) and infant-other mothers dyads ($\chi^2 = 9.32$, $df = 20$, $p = 0.979$; Table 9) were compared. Here, the corresponding coefficients ranged from 0.33 to -1.00 (infant-own mother) and 0.38 to -0.61 (infant-other mothers).

Table 9. Kendall rank correlation coefficients (T) and corresponding *p*-values between infant-own mother and infant-other mothers.

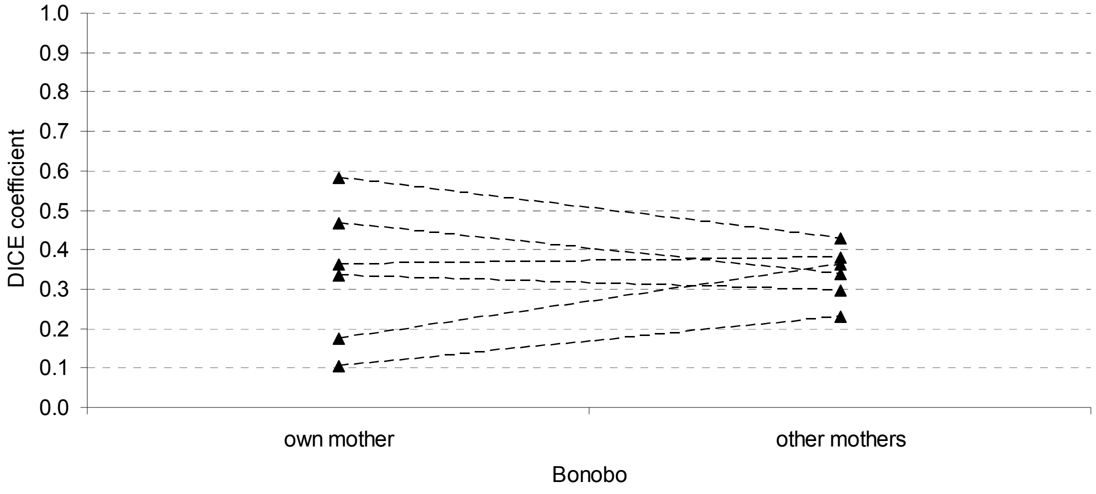
		At least once ***dataset***				**Only both** ***dataset***			
		Own mother		***Other mothers***[a]		***Own mother***		***Other mothers***[a]	
Species	***Infant***	**T**	**p**	**T**	**p**	**T**	**p**	**T**	**p**
Bonobo	Habari	0.01	0.976	-0.41	0.034	-0.10	0.741	-0.24	0.549
	Hongo	-0.53	0.003	-0.38	0.182	-1.00	1.000	-0.21	0.269
	Huenda	-0.10	0.664	-0.14	0.288	0.33	1.000	0.38	0.806
	Kivu[b]	-0.58	0.003	-0.47	0.101	-	-	-0.33	1.000
	Luiza	-0.19	0.272	-0.30	0.226	-0.16	0.634	-0.10	0.583
	Nayembi	-0.30	0.124	-0.23	0.261	-0.91	0.071	-0.23	0.837
Chimpanzee	Gihneau	-0.35	0.068	-0.38	0.073	0.24	0.655	-0.16	0.535
	Kara	-0.21	0.259	-0.54	0.007	-0.39	0.304	-0.61	0.740
	Kofi	-0.21	0.226	-0.14	0.463	0.21	0.559	0.00	0.671
	Nafia	-0.16	0.460	-0.25	0.345	-0.60	0.166	-0.22	0.613

[a] The reported significance levels are based on the mean values for all possible infant-other mothers dyads (bonobos: $N = 5$, chimpanzees: $N = 3$).

[b] The bonobo infant Kivu shared only one single gesture with his mother. He was therefore excluded from all *only both* analyses as a coefficient could not be calculated.

A repeated-measures ANOVA on each correlation dataset (*only both* and *at least once*) with the factors species (bonobo versus chimpanzee) and type of dyad (infant-own mother versus infant-other mothers), indicated no differences between bonobo and chimpanzees (*only both*: $F(1,7) = .022, p = 0.887$; *at least once*: $F(1,8) = .069, p = 0.800$), or dyad-type (*only both*: $F(1,7) = .459, p = 0.520$; *at least once*: $F(1,8) = 1.137, p = 0.317$). There was also no significant interaction between these factors (*only both*: $F(1,7) = 2.29, p = 0.174$; *at least once*: $F(1,8) = .202, p = 0.665$). Infants of both species showed a similar frequency of gesture occurrences (concerning gestures that occurred in both individuals or in at least one dyad-member) with unrelated adult females as they did with their own mothers (Table 9). Concerning the proportions of shared gestures, a further repeated-measures ANOVA with the factors; species (bonobo versus chimpanzee) and type of dyad (infant-own mother versus infant-other mothers), indicated also no difference between bonobos and chimpanzees ($F(1,8) = 1.009$, $p = 0.345$), or dyad-types ($F(1,8) = .430$, $p = 0.530$; Figure 5). Again, there was also no significant interaction between these factors ($F(1,8) = .493$, $p = 0.503$).

(a)



(b)

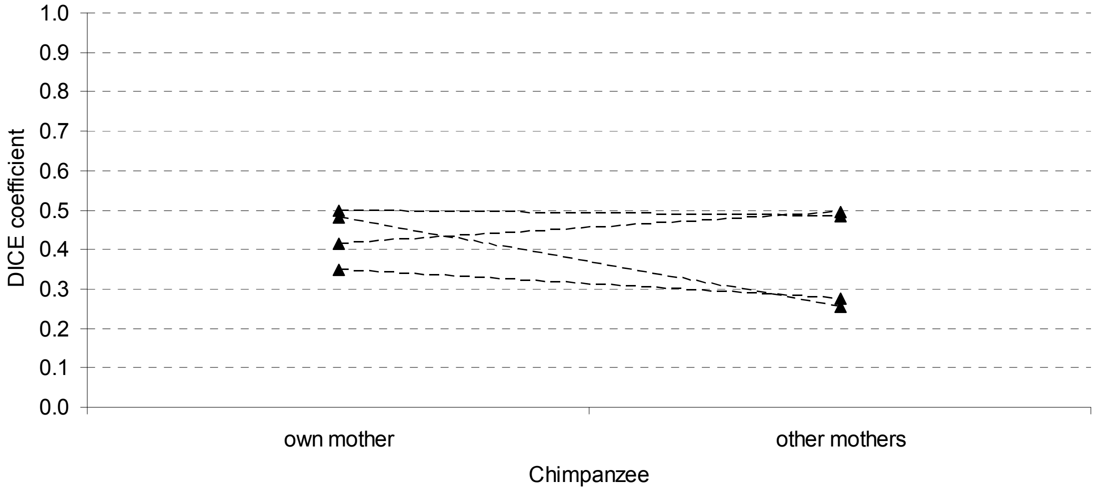


Figure 5. Overlap of gestural repertoires of infant-own mother and infant-other mothers dyads for (a) bonobos, *N* = 6 and (b) chimpanzees, *N* = 4. Indicated are the DICE-coefficients. Each infant is represented by a pair of triangles connected by a dashed line.

3.3.3. Further comparison of dyad-groups

For bonobos, I compared the shared repertoires and gestural frequency correlations of the dyad-groups (infant-infant, mother-mother, and infant-mother). A permutation analysis (based on 1,000 permutations) revealed no significant differences in terms of similar frequencies of occurrence (correlations based on *only both* data) of gestures for both individuals of a dyad ($p = 0.221$). However, the comparison of repertoires yielded a significant overall effect when analysing proportions of shared gestures in a dyad ($p = 0.001$; Figure 6a), as well as the correlations between frequencies of gestures which were shown by at least one of two dyad-members ($p = 0.004$; Figure 6b). For both datasets, *post hoc* analysis revealed that infant-infant and mother-mother dyads showed more homogeneity than mother-infant dyads. A similar pattern was observed in chimpanzees (Figure 7) but due to the small sample size it was not possible to test for significance.

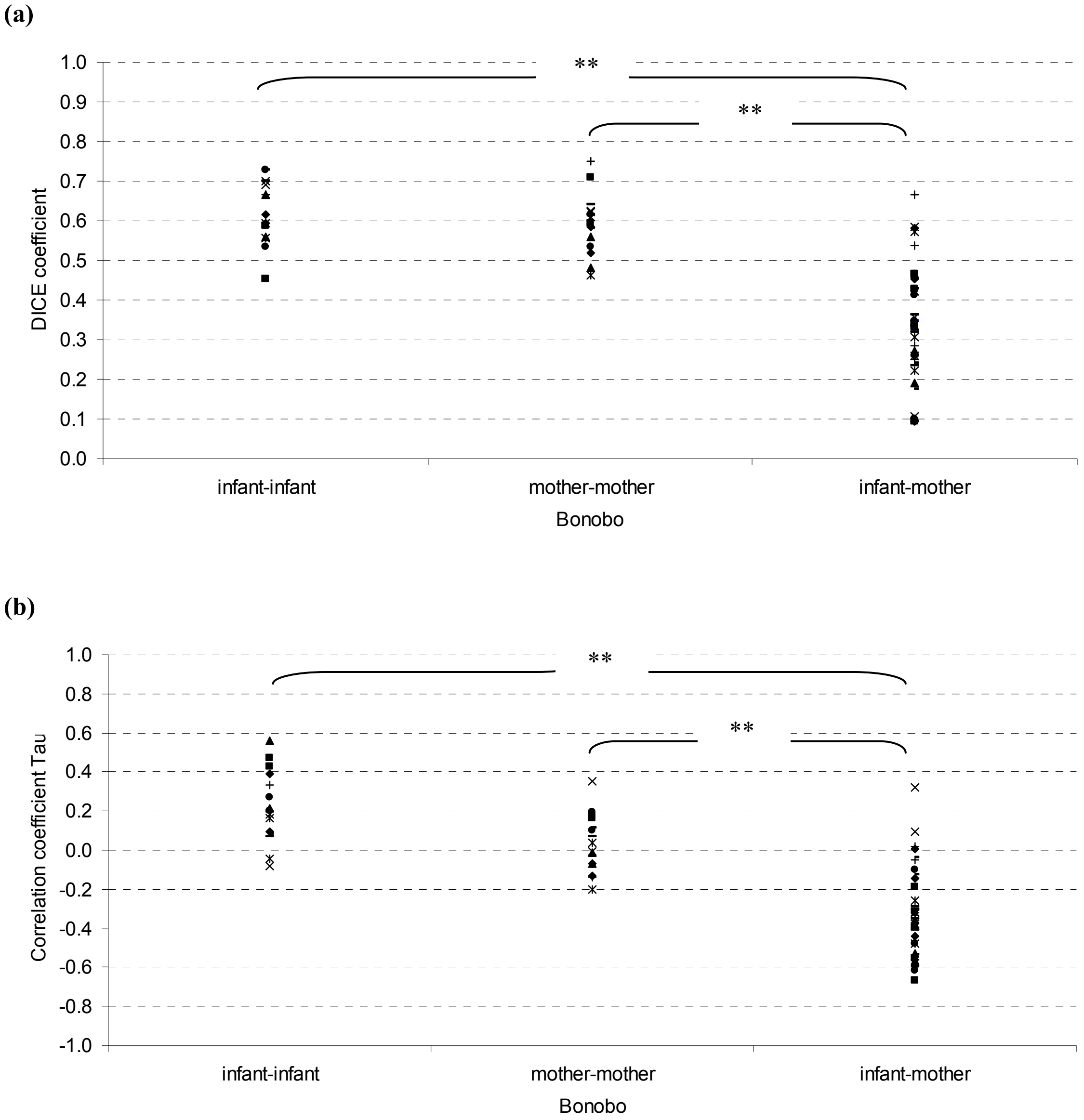


Figure 6. Repertoire similarities for bonobos in the three dyad-groups infant-infant (N = 15), mother-mother (N = 15) and infant-mother (N = 36). Indicated are (a) DICE-coefficients and (b) coefficients of *at least once* dataset. *Post hoc* permutation tests revealed that the homogeneity in terms of shared gestures and gesture frequency in the infant-infant group differed significantly from that in the infant-mother group (DICE: p = 0.001; *at least once*: p = 0.003). Likewise, mother-mother relationships differed in their homogeneity from that of the infant-mother group for each dataset (DICE: p = 0.001; *at least once*: p = 0.008). The infant-infant and mother-mother groups, however, did not differ significantly from each other (DICE: p = 0.649; *at least once*: p = 0.171).

(a)

(b)

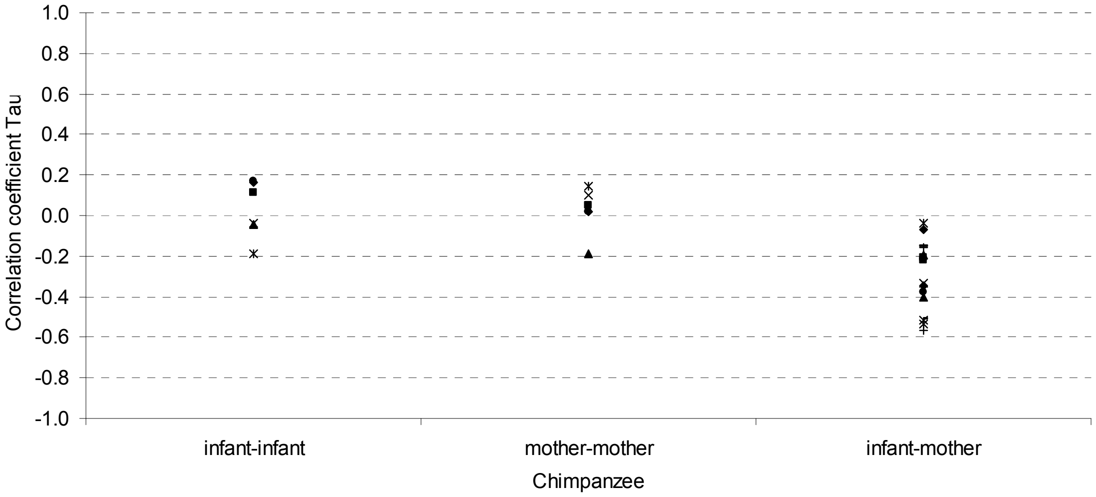


Figure 7. Repertoire similarities for chimpanzees among infant-infant (*N* = 6), mother-mother (*N* = 6) and infant-mother dyads (*N* = 16). Indicated are (a) DICE-coefficients and (b) coefficients of *at least once* dataset.

Comparisons of the bonobo-bonobo, chimpanzee-chimpanzee, and bonobo-chimpanzee infant dyad-groups indicated no significant differences for any of the three datasets (*only both*: $p = 0.256$; *at least once*: $p = 0.194$; DICE: $p = 0.189$; Table 10). The shared types and frequencies of gestures for bonobo and chimpanzee infants did not differ significantly between the three groups, i.e., neither of the two species were more homogeneous than the other or the between species dyads. In addition, when performing the same analyses (for each of the three coefficient-datasets) for the mothers there was no indication of a significant effect (*only both*: $p = 0.416$; *at least once*: $p = 0.956$; DICE: $p = 0.911$; Table 10).

Table 10. Mean coefficient values for *only both*- and *at least once*-correlations and DICE dataset.

		Species comparison		
	Dataset	**Bonobo-Bonobo**	**Chimpanzee-Chimpanzee**	**Bonobo-Chimpanzee**
Infants	Only both (Tau)	0.09	0.38	0.09
	At least once (Tau)	0.22	0.03	0.14
	DICE C_D	0.62	0.54	0.58
Mothers	Only both (Tau)	0.20	0.05	0.28
	At least once (Tau)	0.04	0.02	0.05
	DICE C_D	0.59	0.57	0.59

3.4. Discussion

Our findings suggest that the genus *Pan* infants did not learn their gestures by observing their mothers. In my comparison of infants and adult females there was no evidence to suggest that infants of either species shared gestures with their own or other mothers to any significant extent. In addition, gestures that were more prominently used by mothers and unrelated adult females were less likely (if at all) to be produced by infants and vice versa. Gestural sharing among individuals of the same age class was, on the other hand, prevalent. Bonobo infants were homogenous regarding the gestures they shared and, likewise, gestures within mother-dyads (similar observations were made for chimpanzees). A similar tendency was also observed across species. Both bonobo and chimpanzee infants, and bonobo and chimpanzee mothers performed similar types of gestures. However, in spite of the observed homogeneity of gesture types, infant and female adult peers (within and across species) demonstrated individual differences in the frequency that they used them.

The fact that infants and mothers shared few gestures indicates that vertical transmission through observational learning can be excluded as the main mechanism at work in the gestural acquisition of genus *Pan* (Tomasello et al., 1989, 1994). This is further supported by recent theoretical suggestions that uniparental transmission of knowledge is an unlikely source for observational learning within a group. Enquist, Strimling, Eriksson, Laland and Sjostrand (2010) have proposed that learning a behavioural trait is highly unlikely to occur through observing a single parent (or a specific individual); instead it is far more feasible that a trait is established through monitoring multiple individuals.

Uniparental observational learning may, however, be more important to the Asian ape species. Cartmill (2008) reported that orangutan infants may indeed learn their signals via observing the mother's repertoire. One explanation for this could be the intense relationship that exists in orangutan mother-infant dyads when compared with the genus *Pan* species (Watts & Pusey, 2002; Wich et al., 2004). Out of all non-human ape species, orangutans spend the longest period with their mother (Wich et al., 2004). In this time the mother is thought to have an important role in infant's early development, e.g., in the development and facilitation of foraging skills (Jaeggi et al., 2010a; van Schaik, 2004). Uniparental transmission may therefore be more common in orangutan mother-infant dyads than in other non-human ape species.

Although I can only conjecture from the current data how the observation of peers might have influenced gestural acquisition and development, I suggest that horizontal transmission is unlikely to be responsible for the reported gestural overlap in bonobo infant and adult age-classes. Three out of 15 investigated bonobo infant-infant dyads and one out of six chimpanzee infant-infant dyads were housed in the same zoo group. Comparative *post hoc* analyses of these dyads with those where members were housed in separate zoo groups revealed no marked differences in their relationship-coefficients (see Call & Tomasello, 2007a). I found similar results for bonobo and chimpanzee mothers (see Appendix, Table 11). Coupled with the fact that cross-species comparisons revealed no significant repertoire differences among infant and mother dyads, gestural similarity in the peer groups seems unlikely to have occurred solely through observing others.

Other group members might have, however, influenced infants' early gesturing in other ways. Despite the homogeneity with their peers, bonobo infants and adult females showed individual differences in the frequency that gestures were used; in other words, individuals prioritised gestures differently in the peer groups. The variability in how infants utilise their gestures could be explained by the individual learning processes *ritualised* in social encounters during their lifetime (Pika et al., 2003). Importantly, however, the variability, which derives from this process does not necessarily manifest from *different gesture types*, as previously proposed (e.g., Call & Tomasello, 2007b); but rather in their *different usage patterns*.

The fact that bonobo infants (and mothers) shared a considerable number of gestures with peers (despite the majority of individuals being housed in different zoos), and the cross-species similarities observed in bonobos and chimpanzees, suggests a substantial phylogenetic influence in gestural acquisition (Genty et al., 2009). Implicated in these influences might be the differing motives for communication, and the behavioural contexts, in which signals have evolved. For example, many gestures used by infants in the current sample were play-related or even play-specific (see also Chapter 2). The *arm raise* signal, for instance, was typically used in play interactions by almost all genus *Pan* infants (nine out of ten) observed, but was not observed in any adult individual of the present sample – their gestures were more likely to be concerned with affiliation, ingestion, and agonism (Tomasello et al., 1985, 1994). The importance of the behavioural contexts, however, again emphasises the role that conspecifics play in gestural development. I believe that it is unlikely that a signal like *arm raise* would develop in the absence of other play partners. The signal overlap among individuals of the same age class, and the differences between age groups, might be strongly shaped by evolutionary pathways, but in order to manifest social activity is needed.

Limitations in the present study should be acknowledged. While this was the first systematic investigation of the gestural repertoires of genus *Pan* mother-infant dyads, time and other resource limitations meant that sample sizes were generally small, particularly for chimpanzees. In addition, the infants were the focal animal under observation in the current study; with mothers only being observed in their close vicinity. However, *post* method analysis demonstrated that the individual repertoire sizes I observed in bonobo and chimpanzee mothers were at least as high or comparable to the repertoire sizes reported in other studies using similar coding procedures (Pika et al., 2005a). I am therefore confident that although the mothers were not focal animals, their repertoires at the time of observation were fully captured.

In conclusion, the genus *Pan* mothers played only a minor role in the gestural acquisition of their offspring. Bonobo and chimpanzee infants' early gestural repertoires would seem to be forged by evolutionary influences, and shaped by the social interactive experiences they encounter during life (Mason, 1963; Pika et al., 2003; Rogers & Kaplan, 2000). I suggest that rather than dichotomising the phylogenetic and ontogenetic mechanisms implicated in gestural acquisition (Call & Tomasello, 2007b; Cartmill, 2008; Genty et al., 2009), future research should aim to explore their relationship in more detail. An interesting place to start would be a systematic analysis of gorilla mother-infant dyads. Compared to other ape species, gorillas' gestural skills are said to have tighter evolutionary constraints (Redshaw & Locke, 1976; Call & Tomasello, 2007a). This would add to our understanding of how phylogenetic and developmental influences work together in the communicational abilities of non-human great apes.

After highlighting and discussing possible underlying mechanisms, and, in particular, the role of genus *Pan* mothers in their offsprings gestural learning, I now turn to the prevalence and use of a particular group of signals (i.e., head gestures) across species. Based on the observational data of the two previous studies (Chapter 2 and 3), I quantify the prevalence and diversity of head gestures across the four non-human ape species. In doing so, I report the first observation of head shaking behaviour in bonobos where the apparent aim was to prevent the communicational partner from performing a certain activity.

4. DO BONOBOS SAY ‘NO’ BY SHAKING THEIR HEAD?

4.1. Introduction

The head shake gesture (i.e., moving the head horizontally from side to side) is regularly used as a communicative signal in humans. Although head shaking can fulfil several communicative functions, e.g., feedback signal during conversation (Cassell, 2000; McClave, 2000), it has been generally associated with an explicit or implicit negative connotation in many parts of the world (Darwin, 1872; Kendon, 2002; Morris, 1994; see Cassell, 2000; Darwin, 1872 for cultural variations to this norm).

Head gestures have also been described in the African great apes but not in orangutans (e.g., Becker, 1984; Cartmill, 2008; Genty et al., 2009; Liebal et al., 2006; Pika et al., 2003, 2005b; Tanner, Patterson & Byrne, 2006; Tomasello et al., 1997; van Hooff, 1973; van Lawick-Goodall, 1968). More specifically, three main forms of head gestures have been identified: *bows* (moving the torso and the head back and forth), *nods* (moving the head vertically up and down), and *shakes* (moving the head horizontally from side to side). Except for two isolated reports of chimpanzees signalling ‘no’ through head shaking (de Waal, 1982; Kortlandt, 1969), head shakes in African great apes have been mainly associated with an affiliative function, for instance, in the context of play (e.g., bonobos: Pika, 2007; chimpanzees: van Hooff, 1973; gorillas: Tanner et al., 2006).

Here I report the first observations in bonobos of head shakes associated with situations that are best described as preventing (or trying to prevent) another individual from engaging (or re-engaging) in a certain activity. The study provides a quantitative estimate of the prevalence and diversity of head gestures across the four non-human ape species and presents a detailed description of observed episodes of ‘preventive’ head shaking in bonobos.

4.2. Methods

The current observations were made during the data collection for the two earlier reported studies (Chapter 2 and 3). I videotaped 25 great ape infants during their first 20 months of life: six bonobos (*Pan paniscus*), eight chimpanzees (*Pan troglodytes*), three gorillas (*Gorilla gorilla*), and eight orangutans (*Pongo pygmaeus*). The ape infants – housed in six European zoological parks – were observed at different time periods, based on their age and their accessibility for filming, between July 2001 and August 2008.

I videotaped the infants’ behaviour using focal animal sampling and scored all communicative behaviour shown by the infant, as well as any signal directed toward the infant by the mother or other group members. In addition, all signals produced by the mother and directed toward non-focal animals were also recorded whenever she was near the infant and therefore in the view of the camera. Overall, I obtained 190 hours of focal animal observations (bonobos = 69 hours, chimpanzees = 79 hours, gorillas = 16 hours, orangutans = 26 hours).

I used a standardised and validated ethogram to score the communicative signals (see Chapter 2, section 2.2.3. for definitions and criteria). Three forms of head gestures, as mentioned and defined above (bow, nod, and shake; section 4.1.), were identified. Additionally, I scored the following behavioural contexts in which the gestures occurred: access, affiliation, agonism, grooming, ingestion, play, locomotion, sexual, and submission (see Chapter 2, section 2.2.3. for definitions).

4.3. Results

Both bonobos and chimpanzees made use of head gestures, whereas gorillas and orangutans did not. Bonobos displayed three head gestures; bow (*n* = 29), nod (*n* = 57), and shake (*n* = 49), in nine distinct contexts: access, affiliation, agonism, grooming, ingestion, play, locomotion, sexual, and submission. Chimpanzees, however, only displayed bow (*n* = 6) and nod (*n* = 16) gestures in two behavioural contexts: play and affiliation.

Of the 49 head shakes observed in bonobos, 13 occurred while trying to inhibit or terminate a particular non-social behaviour of the recipient through active manipulation (e.g., pulling back an infant that was running away). These 13 preventive instances occurred during seven bouts of interactions and were primarily (in 11 out of the 13 occurrences) observed in mother-infant dyads, with the mother and infant adopting the sender and recipient role, respectively (see Table 12 for additional information). In one instance, an adult male showed a head shake after the infant reached for the male’s food, and in another instance, a mother employed head shaking after an adult female took food from her. The remaining 36 (non-preventive) head shakes were used to initiate or to maintain behaviour in various contexts. These were predominantly play (*n* = 25), e.g., to initiate play with a group member, and affiliation (*n* = 6), e.g., to approach and greet a group member. Singular head shakes were also observed in agonistic, food-related, and locomotion encounters, and two instances where I was unable to code the observed context were characterised as unknown.

Table 12. Number of preventive head shakes corresponding to dyad, location, and context of interaction bout.

Location	***Sender-recipient dyad***	***Number of head shakes per interaction bout***	***Context***
Leipzig Zoo	Mother → Offspring Ulindi Luiza	2	Affiliation[a]
		2	Affiliation
		2	Access[b]
		4	Ingestion
Dierenpark Planckendael	Adult Male → Infant Kidogo Habari	1	Ingestion
	Mother → Adult Female Djanoa Hortense	1	Ingestion
Berlin Zoo	Mother → Offspring Yala Kivu	1	Affiliation

[a]See '*Example 1*' in text. [b]See '*Example 2*' in text.

The preventive signals were performed by four individuals living in three different captive groups (the two communicators from Dierenpark Planckendael belonged to the same group). The mother-offspring dyad formed by Ulindi and Luiza produced a total of 16 head shakes by the mother (10 preventive). Yala produced 8 head shakes (1 preventive) toward her offspring Kivu, whereas Kidogo and Djanoa only produced a single head shake in their dyad (which was preventive in both cases). In 3 of the 7 interactions, 1 head shake occurred; in 3 interactions, 2 head shakes were performed; and in 1 interaction, 4 head shakes were displayed. No other head gestures in bonobos or chimpanzees were used with this preventive function. To illustrate the use of the preventive head shakes, I provide a description of two of the observed episodes.

Example 1

The mother and her female offspring were sitting next to each other on the ground. The offspring started crawling away toward a nearby tree trunk and proceeded to climb. The mother retrieved the infant and positioned her back to her side. The infant made continual efforts to climb the trunk, and each time the mother retrieved her. This culminated in the mother seizing the infant by the leg and shaking her head while looking towards her. The infant climbed once again, this time moving around the tree (now out of sight of the mother). After awhile the mother got up, moved around the tree, grabbed the infants’ arm, and pulled her to the place where they originally sat. When releasing the infant the mother looked at her and shook her head once more. The mother started grooming another group member, and the infant moved toward the tree again.

Example 2

The mother and her female offspring were sitting next to each other on the ground while the infant manipulated a piece of leek. After awhile, the mother took the leek from the infant and threw it to the side. Eventually, the infant retrieved the leek and the mother tried to recapture it. The mother shook her head twice while doing so and threw it away from her again. The infant continued to move toward the piece of leek.

4.4. Discussion

To date, African great apes have been observed to display head shakes mainly for initiating or resuming interactions such as play. Here, I report the first observations of head shakes in bonobos accompanying an active effort to terminate or prevent the recipient from engaging in a particular behaviour. Although I observed head gestures in both chimpanzees and bonobos, only the latter employed head shakes (cf., Liebal et al., 2004a; Tomasello et al., 1997; van Hooff, 1973). Moreover, bonobos produced head shaking for initiating, maintaining, and terminating interactions, and in general they used head gestures more frequently than chimpanzees and in a greater variety of contexts. These findings indicate that bonobos are more sophisticated in their use of the head as a signal medium when compared with the other ape species.

One possible explanation for bonobos' extensive variety of head gestures might stem from their higher levels of inter-individual tolerance and diffused hierarchical structures (Hare et al., 2007; Paoli, Palagi & Borgognini Tarli, 2006). For example, according to the 'emotional reactivity hypothesis' (Hare & Tomasello, 2005), bonobos differ from other apes in their social-problem-solving strategies because their emotional temperament affords more cooperative behaviour. In relation to this, Maestripieri (1999) proposed that species living in egalitarian-individualised societies, with diffused hierarchical structures, are more likely to develop greater sophistication in their communicational systems than despotic societies that have strict hierarchies. In this regard, bonobos might have developed communicational signals such as the preventive head shake to coordinate, and possibly negotiate, during situations of conflict.

Nevertheless, additional research is required. Single-case observations of head shaking with a negative connotation have been reported in chimpanzees (de Waal, 1982;

Kortlandt, 1969). Future research using a more systematic, cross-species approach could clarify whether the observed interspecies differences were due to small sample sizes or observation times. Furthermore, more detailed studies are needed to establish the functional role of all forms of head gestures (e.g., shake, nod, and bow) for each species.

Current research on gestural communication in great apes has shown that the use of the head as a communication device is more prevalent in African apes compared with orangutans and other primates (Becker, 1984; Cartmill, 2008; Liebal et al., 2006). Although some monkeys possess well-defined head gestures (e.g., head flagging in gray-cheeked mangabeys; Wallis, 1983), they appear more stereotyped and less diverse than those observed in African great apes. Calling attention to the preventive communicative function of a previously described gesture contributes to expand the variety of motives underlying gestural use in great apes. Until now, most great ape gestures, not just head gestures, have been interpreted as invitations to engage in various activities or as announcements of impending behaviour (Call & Tomasello, 2007b). It is true that some intention movements can inform recipients about the actor's intent to prevent some activity. For instance, a dominant animal can take a step in the direction of an object to inform others about its intent to claim it, thus preventing others from taking it. However, this is quite different from the head shaking gesture which, by itself, does not indicate any particular action. If the use of preventive head shaking is confirmed in genus *Pan*, this would raise a further, more speculative, evolutionary question: Do these gestures reflect a primitive precursor of the human head shake that denotes negation? This is an intriguing possibility, but additional data along the lines indicated above will be needed to provide an informed answer.

5. GENERAL DISCUSSION

The present research is the first explorative, comparative study on the ontogenetic origins of gestural communication in non-human great apes living in captivity. The findings thereby make a unique contribution to our current understanding of the early communication efforts of bonobos, chimpanzees, gorillas, and orangutans and lay important foundations for future research. My research aims were threefold. First, I undertook a systematic analysis of the gestural onset and early signal use across the four ape species (Chapter 2). Second, by examining the extent that gestures were shared within and across genus *Pan* infant-mother, infant-infant, and mother-mother dyads, I intended to learn more about the possible phylogenetic and ontogenetic factors that underlie gesture acquisition (Chapter 3). Lastly, I investigated the use of head gestures across the four ape species. By doing so, I reported the first ever observation of 'preventive' head shaking behaviour in bonobos (Chapter 4). Following a summary of the main findings in respect to each of the above aims, I will outline the underlying limitations of the project before returning to a generic discussion of the key findings and how they add to our current understanding of gesturing in non-human great apes.

5.1. Synopsis

Through the longitudinal observation of the first 20 months of life for bonobos, chimpanzees, gorillas, and orangutans, I captured the age of gestural onset in the four species and drew distinctions across species. Most notably, I found orangutans only started gesturing around 15 months of age, at least four months later than African ape species. Orangutans also differed in other gestural features. They employed no auditory signals (see also Call & Tomasello, 2007b; Liebal et al., 2006), and in their first six months of gesturing showed proportionally more signals in food-related interactions (e.g., to beg for food) than African apes. With respect to the onset of the two remaining sensory domains; tactile and visual, all four species were similar. Early gestures were equally as likely to be tactile as they were visual, and remained so for the six months that followed onset. For African apes, however, an increase in visual signals at the expense of tactile gestures was witnessed beyond the first six months period.

Comparisons between the type and frequency of gestural repertoires of mother-infant dyads, showed no indication that genus *Pan* infants learnt their gestures by observing the mother. Infants of both species differed from their mothers in their signal types and performed gestures with differing frequencies. Infant-infant and mother-mother groups, however, were homogenous regarding the gestures they shared (within and across species), but showed individual differences in the frequency that particular gestures were utilised. Hence, infants were more likely to share gestures with individuals of the same age class (including conspecifics housed in other zoo groups or other *Pan* species respectively) than they would share with their own mother.

A quantitative estimate of the prevalence and diversity of head gestures across the four ape species in the current sample revealed that while bonobos and chimpanzees used their head to gesture, gorillas and orangutans did not (cf., Genty et al., 2009; Pika et al., 2003; Tanner et al., 2006 for observations of head gestures in larger samples of gorillas). Out of genus *Pan*, bonobos were the most prolific in terms of their use of head gestures. They showed the greatest variety and frequency of head gestures, and employed them in more behavioural contexts than chimpanzees. In this regard, I observed a head shaking behaviour in bonobos that had never been reported before.

Most notably, during interactions with group members, four individual bonobos employed head shaking while trying to prevent the communicational partner from doing something.

Conclusively, the findings from the three studies highlight the complexity and interdependence of phylogenetic and ontogenetic factors in the development of gestural communication in our closest living relatives, the non-human great apes. However, before discussing these in more detail, I will address underlying methodological limitations and constraints to the research.

5.2. Limitations

Several logistical and practical complications emerged during the course of the research. The most important ones were the rarity of infants (at the time of observation) and the challenges of undertaking the observations in six European zoos. As a result sample sizes were generally small and individual observation times were low. However, despite these constraints, the fact that a single researcher analysed the gesturing across species was a methodological strength. Most importantly, coding methods were standardised throughout the studies. As a result I am confident the similarities and differences identified within and across species were internally reliable and valid.

Moreover, the employed observational procedure of focal animal sampling might have reduced the number of signals observed since the subject was recorded during different daily activities (e.g., playing, feeding, resting etc.; Cartmill & Byrne, 2010; see Martin & Bateson, 1993). Alternatively ad libitum sampling could have been used, focusing on specific periods of social activity, e.g., around feeding time, where gesturing was likely to be more prevalent (Cartmill & Byrne, 2010). However, this sampling method bore the risk of biasing observations to particular behavioural contexts and in doing so narrowing the communicational domains that could be observed (e.g., during feeding time, food-related signals are likely to be more prevalent). Hence, I believe that focal animal sampling was the appropriate method to capture fuller repertoires of communicational behaviour.

A further possible limitation to the research is that the current findings and their interpretations are based on captive individuals living in restricted and predetermined environments. The external validity of the reported communicational behaviour to conspecifics' in natural and expansive environments may be questionable. With respect to the gestural onset, however, it should be noted that the only existing observation of wild chimpanzees reported similar ages for gestural onset as the present study suggests (Plooij, 1978, 1984). This indicates that the results, on this feature at least, are valuable and externally valid.

The observation of infants or mother-infant dyads in captive settings also has considerable advantages. Research on gestural communication is difficult to carry out in the wild due to less than optimal observational conditions (Pollick, Jeneson & de Waal, 2008). In particular, infants are often hidden from the observer's view and consequently continuous observation of both mothers and their young offspring is very difficult (Bard, 1992; van Schaik, 2004). Hence, the examination of the communication of captive individuals has given us unique and invaluable insights into the emergence of gesturing which would not otherwise be possible. Inevitably there are limitations to this work and until verification through future research the present findings need to be treated with some caution. Nevertheless I believe that the current research has provided important foundations from which to develop our understanding of the early signalling in non-human great apes and that it has made a considerable contribution to work in the field from which future studies can only benefit.

5.3. The interdependence of phylogeny and ontogeny

5.3.1. Similarities and differences in early gesturing in non-human great ape species

Through the comparison of the apes' early gestural communication, I found considerable similarities and differences across species. Out of the four groups, bonobos and chimpanzees were the most similar in their early signalling, while orangutans were the most dissimilar. Genetic relatedness could be an explanation for these patterns (see Call & Tomasello, 2007a). Bonobos and chimpanzees are genetically the closest related species, while orangutans are genetically the most distant (Chen et al., 2001; Wildman et al., 2003). Inextricably linked with phylogeny are socio-structural and environmental factors. Here, orangutans also differ considerably from other apes, while the two genus *Pan* species are more similar. Unlike African apes, orangutans show an almost exclusive arboreal (tree-living) lifestyle and are the most solitary-living (van Schaik, 1999; van Schaik et al., 2001). In contrast, genus *Pan* inhabit a variety of arboreal and terrestrial (ground-living) habitats and live in comparable fission-fusion group structures (Badrian & Badrian, 1984; Doran, 1993, 1996; Goodall, 1986). In the following sections, I will discuss how this broader phylo-ontogenetic framework is implicated in the key findings of the present research.

5.3.1.1. Gestural onset

The delayed gestural onset observed in orangutans when compared with the three African species is consistent with what we know of their slow life history patterns (Wich et al., 2004, 2009). Habitat and socio-organisational factors are likely to be important co-factors in the maturity rates that have evolved and therefore cannot be neglected in the interpretation of the results. It has been proposed that since arboreal mammals encounter a smaller number of mortality risk factors compared to terrestrial mammal species, they take longer to reach developmental markers (van Schaik & Deaner, 2003; see also Shattuck & Williams, 2010). Orangutans are less likely to encounter predators or parasite infections in their more arboreal and solitary lifestyle (van Schaik & Deaner, 2003; Wich et al., 2009). In addition, their semi-solitary lifestyle might complement prolonged maturation periods; mothers, for example, only let their offspring venture alone when they are capable of sustaining themselves (van Schaik, 2004).

5.3.1.2. Early use of sensory modalities

In terms of infants signal modality use in the first six months of gesturing, I found tactile and visual gestures (regardless of respective signal types) to be equally important for African (9 – 14 months) and Asian apes (15 – 20 months). In African ape infants I observed a proportional increase of visual signalling at the expense of tactile signalling in the second six months of gesturing (15 – 20 months). While it was not possible to follow orangutans beyond their first six months of gesturing, previous studies investigating mainly subadult and adult individuals, have reported similar modality proportions within orangutans, yet more tactile gestures compared to African apes (Call & Tomasello, 2007a; note these observations were also carried out in captive environments).

The current study suggests that the different ontogenetic trajectories in African and Asian apes with respect to modalities have a strong phylogenetic base, particularly for orangutans. It is possible that in early infancy, all species share similar modality preferences given their ‘closer’ body contact with the mother. As motility increases in African apes so do distal gestures. This, however, does not seem to be the case in Asian apes (Call & Tomasello, 2007a). These modality differences have been previously related to varying habitats that species populate. Several authors have proposed that members of arboreal species employ more signals involving body contact than terrestrial species, due to the dense vegetation they live in (Call & Tomasello, 2007a; Liebal et al., 2006; Marler, 1965). Tactile signals that involve body contact with the recipient appear to be the most effective in habitats with obstructed view, and, hence, are the most frequently performed. This suggests considerable phylogenetic factors are implicated in tactile signalling.

5.3.1.3. Head gestures

While genus *Pan* shared numerous gestural features (i.e., onset age, use of sensory modalities, and the signal types displayed), bonobos demonstrated one interesting heterogenic feature that adds a new dimension to our current knowledge of the non-vocal signalling among non-human great apes. They showed a pronounced use of head gestures. Moreover, four individuals employed head shaking apparently aimed at preventing the social partner from engaging (or re-engaging) in a certain activity. As well as being the first recorded example of preventive head shaking in bonobos (see de

Waal, 1982; Kortlandt, 1969), the observations highlight a motive rarely observed before in apes' gesturing. To date, most gestures have been broadly interpreted as invitations to engage in various activities or as announcements of impending behaviour (e.g., grooming or play; Call & Tomasello, 2007b; Cartmill & Byrne, 2010). The head shaking behaviour observed in these cases seemed to indicate a specific purpose and preferred outcome.

The variety of head gestures observed exclusively in bonobos may be related to their more diffused hierarchical structures and higher levels of inter-individual tolerance when compared with other apes (de Waal, 1989; Hare et al., 2007; Kano, 1992; Paoli et al., 2006). This is in accordance with Maestripieri's (1999) proposal that species living in more egalitarian societies are likely to develop more sophisticated communication skills than species living in more despotic societies.

5.3.1.4. Gestural acquisition

A complex ontogenetic and phylogenetic relationship was also implicated in genus *Pan* infants gestural acquisition and development (Chapter 3). None of the previously proposed mechanisms: biological inheritance, observational learning or individual learning, seem to be solely responsible for gestural development (see Arbib, Liebal & Pika, 2008; Cartmill & Maestripieri, in press). While infants from the two genus *Pan* species were more likely to share gestures with each other than they were with their own mothers, they showed individual differences in the frequency that particular gestures were utilised. Hence, there was limited evidence to suggest that infants learned their gestures by observing the mother. Gestures seem to be predetermined by biological inheritance (and the evolved behavioural contexts in which signals emerge), but are ‘shaped’ in their application through individual learning processes during lifetime. These findings have important implications for our current knowledge of apes’ gestural acquisition (Call & Tomasello, 2007b; Cartmill, 2008; Genty et al., 2009). Rather than genus *Pan* infants showing extensive variability in their signal repertoires, the current findings highlight the overall gestural similarity across peers and the fact that most variability is observed in usage.

In regard to the role that mothers play in their offspring’s signal learning, orangutans might differ from genus *Pan* infants. It has been proposed that orangutans learn their gestures by observing the mother (Cartmill, 2008). The closeness in these mother-infant dyads, as well as the paucity of other conspecifics surrounding them, might lead to orangutan infants being more attuned to observe their mothers compared with other ape infants (Galdikas, 1978; MacKinnon, 1974; van Noordwijk et al., 2009; van Schaik, 1999; van Schaik, 2004; Watts & Pusey, 2002; Wich et al., 2004).

5.4. The role of the mother in genus *Pan* infant’s ‘communicative socialisation’

Undeniably, the mother is very important in an infant’s early life in terms of nourishment, security and comfort (Hoff et al., 1981; Plooij, 1978, 1984; van Lawick-Goodall, 1967). In chimpanzees, however, it has been proposed that other group members play a bigger role than mothers in the development of youngsters’ gestural communication (Tomasello et al., 1989, 1994). The current findings support this assertion and show that it can be extended to bonobos (and possibly gorillas) for two reasons. First, I highlighted the importance of motility in onset and early gesturing (Chapter 2). Gesturing in African apes became more sophisticated as they gained independence from the mother. As motility increased more visual and fewer tactile signals were observed, fewer ‘comfort-seeking’ gestures (i.e., affiliation-related signals) occurred, and play signals became most prominent in slightly older infants. Second, I demonstrated that while genus *Pan* mothers only had a small role in their offspring’s gestural acquisition, other group members were likely to play a more important role (Chapter 3).

The minimal involvement that mothers have in infants’ gesturing has also been observed in non-ape primates. In her investigation of stumptail macaques (*Macaca arctoides*), Chevalier-Skolnikoff (1974) emphasised the scarcity of mutually engaged mother-infant interactions when compared to other social encounters. She concluded that youngsters would consider “... the mother as a nourishing-tactile-comfort-transport object rather than a social being” (p. 52). It was also noted that youngsters only infrequently directed gestures towards the mother. From these observations, the author concluded that the mother, as opposed to other group members, has only a minor role in the youngsters’ socialisation.

An important question is why does the mother, the primary social partner, play such a small role in infants’ gestural development? A possible explanation might be that when infants venture away from the mother, they are exposed to highly complex and demanding social environments with potential dangers and negotiations. Living in a complex social system that is hierarchically organised, demands that individuals learn to recognise and differentiate their position in relation to others (Byrne & Whiten, 1988; Smuts et al., 1987). As infants begin roaming freely they are confronted with new social challenges. In these encounters they may start to use gestures to interact and possibly negotiate within the social network they are living in. In this regard, the importance of play in youngsters’ social development has been thoroughly discussed

(Bekoff, 1972; Bekoff & Allen, 1998; Maestripieri & Ross, 2004; Palagi, 2006; Pellis & Iwaniuk, 2000). It is possible that my observations have captured the prerequisites for apes to become competent social group members and have begun to determine the point at which these skills emerge in their development.

5.5. A tentative comparison of non-human apes and preverbal children

A comparison of ape and human gesturing needs to be treated with caution. Ape and preverbal human infants differ considerably in their gestures and motives for carrying them out (Bates et al., 1979; Bullinger, Zimmermann, Kaminski & Tomasello, 2011; Iverson & Thal, 1998). For example, in terms of the communicative function of signals, it has been proposed that human infants use their early signals for imperative (e.g., reaching to request an object of interest) and declarative purposes (e.g., pointing as a means of sharing interest in an object). Non-human apes, however, mainly use signals for imperative but not declarative purposes (Bates et al., 1975; Tomasello, 2006, 2008; Tomasello & Camaioni, 1997; cf., Leavens, 2004; Leavens, Hopkins & Bard, 2005). In addition, gesture definitions and terms often vary widely among and between research with humans and non-humans (e.g., Call & Tomasello, 2007b; Genty et al., 2009; Iverson & Thal, 1998; Pollick, 2006). Nevertheless, important findings have emerged from the present studies that may add to our understanding of human communicational systems and give us new directions for further research. In the following I will discuss the interrelated findings of: onset age of gesturing, significance of locomotion, and possible processes underlying gestural acquisition.

From the current findings we now know that African ape gestures appear in and around the end of the first year of life. This is comparable to human infants (Bates, 1976; Bates et al., 1979; Carpenter et al., 1998; Masur, 1980, 1983). The fact orangutans show a delay in their gestural onset compared to human and African apes, and are the slowest to gain independence from their mother, is one of the reasons why motility may be an important antecedent to gesturing in all species. An important discovery to emerge from the present study was that advanced motility related to faster onset and an increase in visual gestures. Again this is similar to human infants. Motility has far-reaching implications for human children's development in general, and, more specifically, for the emergence of communicative behaviour (Bertenthal & Campos, 1990; Campos et al., 2000; Rochat, 2004).

While the motility-gesture onset link is an intriguing observation which warrants further research, it should to be acknowledged that non-human apes have generally more advanced motor skills than human infants (Gómez, 2010). We might therefore expect ape infants to gesture earlier than they did. What may be as important, in this respect, is the link between motility and leaving the 'security range' that is provided by the mother. Infant apes are mobile at an earlier age compared to humans but they may still remain within 'arm's reach' of their mother. Hence, the acquisition and development of gestures may rely as much on the infant leaving the security zone and entering the social and hierarchical networks that surround them (see above, section 5.4.) than on their motility skills. Whether this is the case, and the extent that this differs from human infants again warrants further investigation.

Although, the similar gestural repertoires observed across genus *Pan* species implicate a substantial biological influence, we can rule out that infants learned their gestures through this single process (see also Arbib et al., 2008; Cartmill & Maestripieri, in press). Social processes were also vital. This finding is similar to what has been proposed for humans gestural acquisition, where under the broad heading of socialisation two main theories have been proposed (see Liszkowski, 2008; Liszkowski 2011; Liszkowski & Tomasello, 2011): observational learning (Crais, 2007; Liszkowski, 2008; Masur, 1980) and socio-pragmatic interaction (gestures are learned through joint social action; Bates et al., 1975; Bruner, 1983; Vygotsky, 1978; Werner & Kaplan, 1963). The current data suggest that, if the observational learning process is involved in genus *Pan* early gesture acquisition, it is unlikely to incorporate the mother-infant dyad. Infants shared only few, if any, gestures with their mothers. In this regard non-human apes are likely to differ from humans where certain gestures seem to be learnt via some form of observation process involving the caretaker (in particular representational gestures, such as hand waving to say goodbye; Crais, 2007; Liszkowski, 2008; Masur, 1980). However, the importance of socio-pragmatic interaction does seem to be comparably implicated in ape gestural acquisition. Most importantly, this was evidenced by the varied usage of particular gestures (in terms of their frequency) in individuals. Therefore, although, the similar gestural repertoires observed across genus *Pan* species implicate a substantial biological influence, these predisposed signals are unlikely to appear in the absence of a social communicative partner. In this sense, social interactions would appear to be essential for gestures to emerge and develop in both non-human and human great apes.

In sum, my comparative glance has revealed important parallels between non-human and human great ape infants that suggest shared foundations for early gestural features. However, disparities between species have also been revealed and therefore caution in our extrapolations is needed.

5.6. Future research

My work has inspired some important new directions for research. I have suggested that motility plays a significant role in the varying gestural onset times and maturity rates amongst the species and is therefore an integral component of the early socialisation processes. Although I regularly witnessed infants with advanced locomotion (resulting in earlier and increased independence from mother) to be more sophisticated in their communicational development, this was not part of my focal observations. To explore the roles that motility and conspecifics play in the socialisation process, a longitudinal observation with a more detailed time-frame analysis is needed. By applying such a framework we can systematically explore at what age infants leave their mothers in relation to onset of gesturing, when they start to interact with others, and, very importantly, to whom signals are directed (e.g., mother, other group member). Measurements concerning motor skills could be used to capture motility (e.g., manual reaching, independent sitting, quadruped walking, etc.); the proximity while gesturing between signaller and recipient; the respective signal modality; and the behavioural context. For such an extensive investigation, single or, if possible, multiple case study designs (Stake, 1995; Yin, 1994) where individual apes are intensely observed in their early social interactions, should be applied. Furthermore, comparing motility processes and outcomes to similarly measured ones in humans can also only add to our understanding of gestural development across species.

Another important future direction for research emerging from my work is a more extensive analysis of the role that peers and other conspecifics play in the shaping of gestural repertoires. How, for example, does this shaping process work? Does it involve singular or multiple dyads? How does the process differ, if at all, for particular gesture types? Answers to these questions can only add to our efforts to learn more about the gestural acquisition process in non-human great apes. Again due to the intensity of observations involved, case study methodologies appear the most appropriate approach to launch into this area of research.

The observation of the preventive head shake in bonobos has raised further questions. So far, only little research exists on the motives and varying functions of ape signalling. To capture the function or motive of a signal in animals is, for understandable reasons, a challenging task (Smith, 1965). I suggest that future research should focus on determining the function and motives of gestures by exploring behavioural parameters more precisely. Recently, a first step in this direction has been made by Cartmill and Byrne (2010) who, through a systematic approach, aimed to determine the goals of particular gestures in orangutans. Future research should follow this line and extend this to other ape species in order to learn more about the varying motives and functions of gesturing across species.

CONCLUSION

My dissertation provided the first systematic and comparative account of non-human great apes' early gestural communication. As such, it affords important knowledge about how gestures emerge in our closest relatives and offers a unique, fuller and holistic understanding of gestural communication.

Implicated in the story of when gestures first appear across species, and how they are learnt and utilised within the lifespan, are important socio-environmental and life history factors. In unearthing these, deep ontogenetic and phylogenetic roots which are difficult to disentangle were revealed. I suggested that further research is necessary to fully comprehend the role that motility plays in gestural development and socialisation and to provide further clues about how the communication mechanisms of non-human and human great apes are related. Moreover, I suggested that the genus *Pan* mother played a relatively small role in offspring's gestural learning and communicative socialisation. Further intensive and longitudinal analysis of singular gestures might unravel the complexities of the social mechanisms that underlie the acquisition of gestures.

Conclusively, the findings provide important foundations from which to develop our understanding of the early signalling in non-human great apes and, as such, offer a unique contribution to the field from which future studies can benefit.

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APPENDIX

Table 7. Gesture types (and behavioural descriptions) observed in genus *Pan* infants and mothers (in brackets: total number of occurrence).

Sensory Modality	***Gesture type***	***Behavioural description***	***Bonobo (N = 6)***		***Chimpanzee (N = 4)***	
			Infant	***Mother***	***Infant***	***Mother***
Tactile	Arm on (156)	Finger(s), hand(s) or arm(s) were placed on any body part of the recipient; possibly holding on to recipients' body	✓ (16)	✓ (76)	✓ (15)	✓ (49)
	Body beat (26)	Repeated, consecutive hits (see 'hit' description) executed with the same body part (i.e., hand(s), arm(s) or foot/feet)	✓ (20)	✓ (2)	✓ (4)	
	Formal bite (145)	Gentle bite of recipients' body	✓ (2)	✓ (73)	✓ (2)	✓ (68)
	Gentle touch (8)	Very gentle touch or hold of recipients' body with finger(s) or hand(s)		✓ (3)	✓ (1)	✓ (4)
	Hit (71)	Single and forceful hit of recipients' body with hand(s), arm(s) or foot/feet	✓ (38)	✓ (3)	✓ (27)	✓ (3)
	Hold chin (10)	Place hand around chin of recipient and hold		✓ (9)		✓ (1)
	Lead (19)	Place hand or arm around a body part (e.g., the neck) of the recipient and lead them in a certain direction		✓ (14)		✓ (5)
	Lip-lip touch (8)	Touch recipients' mouth with one's own mouth	✓ (2)		✓ (2)	✓ (4)
	Nudge (114)	Brief movement towards recipients' body with single finger(s), hand, or foot; also kind of pinch		✓ (52)	✓ (3)	✓ (59)
	Pull (26)	Grasp a part of recipients' body with hand or foot and perform a short (+/- forceful) movement	✓ (1)	✓ (20)		✓ (5)
	Push (63)	Exert pressure on recipients' body with hand(s), arm(s) or foot/feet		✓ (51)	✓ (2)	✓ (10)
	Push with object (7)	Poke or hit recipient with an object		✓ (4)		✓ (3)
	Rest head (3)	Place one's own head on recipients' body			✓ (3)	
	Shake body (10)	Shake a part (e.g., head, arm) or body of recipient (e.g., infant)		✓ (7)		✓ (3)
	Tap (80)	Tap or poke with knuckle(s), single finger(s) or whole hand repeatedly on recipients' body	✓ (1)	✓ (65)		✓ (14)
	Touch with genitals (1)	Touch recipients' body with genital region	✓ (1)			
		Number of tactile gesture types	8 (81)	13 (379)	9 (59)	13 (228)

APPENDIX

Table 7. *Continued*

Visual	Arm raise (52)	Lift arm(s) up in the air, approximately perpendicular to the ground	✓ (27)		✓ (25)	
	Extend arm (72)	Hold out one’s hand(s) or arm(s) to recipient	✓ (34)	✓ (15)	✓ (13)	✓ (10)
	Gallop (2)	Run toward recipient in an exaggerated manner		✓ (2)		
	Hands around head (3)	Lift arms up and place them around the head	✓ (2)		✓ (1)	
	Head shake (117)	Move head or head and upper part of body rhythmically or only once (either vertical or horizontal; included nodding and bowing)	✓ (5)	✓ (101)	✓ (4)	✓ (7)
	Headstand (1)	Turn vertically and stand on head and shoulders in front of recipient		✓ (1)		
	Ice skating (7)	Perform a pirouette in front of recipient		✓ (6)	✓ (1)	
	Lay back (10)	Lay down on the ground and raise limbs in the air	✓ (3)		✓ (7)	
	Move object (3)	Move object (e.g., jute bag) on the ground	✓ (1)	✓ (2)		
	Offer (6)	Present object, food or infant to recipient		✓ (5)		✓ (1)
	Offer body (24)	Present a body part (e.g., back, head) to recipient		✓ (11)		✓ (13)
	Peer (108)	Closely approach recipient and stare at its mouth or hands (while recipient is holding something of interest, e.g., food or performing a certain action)	✓ (48)	✓ (17)	✓ (33)	✓ (10)
	Present genitals (9)	Present genital region to recipient by raising the abdomen towards recipient		✓ (8)		✓ (1)
	Shake (26)	Shake limb(s) or whole body rhythmically; includes also kind of swinging around rope or bar	✓ (14)	✓ (4)	✓ (7)	✓ (1)
	Shake object (23)	Wave object (e.g., rope) mainly with one’s hand(s)	✓ (8)	✓ (5)	✓ (6)	✓ (4)
	Somersault (2)	Turn a somersault on the ground			✓ (2)	
	Swagger (5)	Move body rhythmically sidewise or back and forth while standing or sitting			✓ (5)	
	Throw object (1)	Throw object towards recipient without hitting them			✓ (1)	
		Number of visual gesture types	9 (142)	12 (177)	12 (105)	8 (47)

APPENDIX

Table 7. *Continued*

Auditory	Beat object (6)	Repeated, consecutive hits on ground, wall or object (see ‘hit object’ description) executed with the same body part (i.e., hand(s), arm(s) or foot/feet)	✓ (1)		✓ (3)	✓ (2)
	Body slap (1)	Single hit of one’s own body (except chest region) with hand(s)			✓ (1)	
	Foot stomp (27)	Single and forceful step on the ground with one foot or both feet	✓ (13)	✓ (5)	✓ (9)	
	Hit object (13)	Single and forceful hit on ground, wall, or object with hand(s) or arm(s)	✓ (6)		✓ (7)	
	Jump (4)	Jump in a quadrupedal manner up and down in front of recipient	✓ (4)			
		Number of auditory gesture types	4 (24)	1 (5)	4 (20)	1 (2)
		Total number of gesture types	**21 (247)**	**26 (561)**	**25 (184)**	**22 (277)**

APPENDIX

Table 11. Mean coefficient values for the three datasets of same zoo-housed and different zoo-housed dyads.

Species	***Dyads compared***	***Dataset***	***Same zoo group***		***Different zoo group***	
Bonobo	Infant-Infant	DICE C_D	0.53	*N* = 3	0.65	*N* = 12
		At least once (Tau)	0.34		0.19	
		Only both (Tau)	-0.12		0.15	
	Mother-Mother	DICE C_D	0.58	*N* = 3	0.60	*N* =12
		At least once (Tau)	0.08		0.03	
		Only both (Tau)	0.02		0.25	
Chimpanzee	Infant-Infant	DICE C_D	0.50	*N* = 1	0.54	*N* = 5
		At least once (Tau)	-0.04		0.04	
		Only both (Tau)	-0.05		0.47	
	Mother-Mother	DICE C_D	0.62	*N* = 1	0.57	*N* =5
		At least once (Tau)	0.10		0.01	
		Only both (Tau)	0.27		0.01	

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SUMMARY

Our closest living relatives, bonobos, chimpanzees, gorillas, and orangutans make regular use of gestures to communicate with their conspecifics. Although the gestural communication of non-human great apes continues to receive increasing attention due to its proposed implications for the evolution of human communication, little is known about the emergence of gesturing.

Focus of the current dissertation was the ontogenetic origin of gestural communication in the four non-human ape species. In particular I investigated: the onset and early use of gestures; the role mothers might play in regard to their offsprings' learning of gestures, and the use of head gestures across species. Using focal animal sampling, a total of 25 captive ape infants (six bonobos, eight chimpanzees, three gorillas, and eight orangutans) were observed periodically during their first 20 months of life. I primarily recorded the gestural behaviour (i.e., signals that were generated by the movement of the hand, arm, head or body position) of infants and peripherally the gestures of their mothers.

In the first study (Chapter 2), I conducted a systematic exploration of the onset and early use of gestural communication in bonobos, chimpanzees, gorillas, and orangutans. I investigated: i) the onset ages of gesturing, ii) the order in which signals of the different sensory modalities (tactile, visual, and auditory) appeared, iii) the extent to which infants made use of these modalities in their early signalling, and, iv) the behavioural contexts where signals were employed. I found orangutans to differ in several important gestural characteristics to that of African ape species. They showed the latest gestural onset; made no use of signals of the auditory sensory domain, and were more likely to use signals in food-related interactions in the first half a year of gesturing. In

all four species, both tactile and visual signals were the first to appear. Auditory gestures appeared only later in the African species. While visual gesturing gained prominence over time, tactile signalling decreased in African apes. The findings also indicated that motor ability, which encourages independence from caregivers, may be an important antecedent in gestural onset and development.

In the second study (Chapter 3), I explored the role that genus *Pan* mothers played in their offspring's learning of gestures. To do so, I examined the similarity of gestural repertoires (in terms of signal types and their frequency) in bonobo and chimpanzee mother-infant dyads. Comparisons across the age-groups revealed that infants of both species were unlikely to share gestures with their own or other mothers (i.e., unrelated adult females). Gestural sharing was, however, prevalent within respective age-groups. Within and across species, infant-infant and mother-mother groups were homogenous regarding the types of gestures they shared, but showed individual differences in the frequency that particular gestures were utilised. There was therefore limited evidence that infants learned their gestures by observing their mothers. I proposed that while infants' use of gestures is shaped by individual learning opportunities, biological inheritance plays an important role in their formation (including substantial impact of the behavioural contexts in which signals have evolved).

In my last study (Chapter 4), I provided a quantitative estimate of the prevalence and diversity of head gestures across the four ape species, and found bonobos to be the most prolific in terms of their variety of head signals and frequency. I also reported the first observations of 'preventive' head shaking in bonobos. Head shakes in these instances were associated with situations that are best described as the signal producer preventing (or trying to prevent) another individual from engaging (or re-engaging) in a certain activity. This observation underlined a yet rarely observed motive in non-human apes signalling.

The current findings have shown how biological, socio-environmental and life history factors are implicated in the story of when and how gestures first appear across species, and how they are learnt and utilised within the lifespan. The research affords unique knowledge about the emergence of gesturing in the non-human great apes and, in doing so, offers important foundations that future studies can build on.

ZUSAMMENFASSUNG

Bonobos, Schimpansen, Gorillas und Orangutans machen regelmäßig Gebrauch von Gesten, um mit ihren Artgenossen zu kommunizieren. Aufgrund der möglichen Bedeutung für die Evolution von Sprache, wurde der gestischen Kommunikation unserer nächsten Verwandten in der Vergangenheit viel Beachtung geschenkt. Dennoch ist bislang nur wenig über den Gestenerwerb von Menschenaffen bekannt.

Ziel der vorliegenden Arbeit war die Untersuchung der frühen Entwicklung gestischer Kommunikation in den vier Menschenaffenarten. Dazu beobachtete ich insgesamt 25 Jungtiere innerhalb ihrer ersten 20 Lebensmonate (sechs Bonobos, acht Schimpansen, drei Gorillas und acht Orangutans) in sechs Europäischen Zoologischen Gärten. Zusätzlich zu dem kommunikativen Verhalten der Jungtiere wurden auch die Gesten der Mütter aufgenommen.

In der ersten Studie (Kapitel 2) führte ich einen systematischen Vergleich der frühen gestischen Kommunikation aller vier Menschenaffenarten durch. Dabei untersuchte ich folgende Fragestellungen: Wann beginnen junge Menschenaffen zu gestikulieren? In welcher Reihenfolge treten die Gesten der verschiedenen Sinnesmodalitäten (taktil, visuell und auditorisch) auf? In welchem Umfang werden diese Modalitäten genutzt und in welchen Verhaltenskontexten werden Gesten in den ersten Monaten eingesetzt? Orangutans unterschieden sich in mehrerlei Hinsicht von den Afrikanischen Menschenaffen. Sie begannen später zu gestikulieren und setzten ihre kommunikativen Signale häufiger im Rahmen der Nahrungsaufnahme ein. Taktile und visuelle Gesten traten bei Jungtieren aller Arten von Beginn an auf, während auditorische Gesten erst zu einem späteren Zeitpunkt und nur von Afrikanischen Menschenaffen gezeigt wurden. Im Laufe des ersten Lebensjahres nahm die Bedeutung visueller Gesten für

Afrikanische Menschenaffen zu, während der Anteil taktiler Signale sank. Die Untersuchungsergebnisse deuteten darauf hin, dass die zunehmende Mobilität der Jungtiere (und die damit verbundene wachsende Unabhängigkeit von der Mutter) eine wichtige Rolle bei der Entstehung und Entwicklung gestischer Kommunikation spielt.

In der zweiten Studie (Kapitel 3) untersuchte ich, ob Bonobos und Schimpansen ihre Gesten durch Beobachtung der Mutter erlernen. Der Vergleich der Gestenrepertoire von Mutter-Kind-Paaren zeigte, dass Jungtiere beider Arten nur wenige Gesten mit ihren Müttern teilten. Größere Übereinstimmungen wurden hingegen innerhalb einer Altersgruppe beobachtet (d.h. unter Jungtieren und unter Müttern). Diese Ähnlichkeit innerhalb einer Altersgruppe zeigte sich auch nach einem Artvergleich von Bonobos und Schimpansen. Im Gegensatz dazu, zeigten die Mitglieder beider Altersgruppen keine Übereinstimmungen in der Häufigkeit mit der einzelne Gesten verwendet wurden (weder innerhalb einer Art noch über die beiden Arten hinweg). Diese Beobachtungen deuten darauf hin, dass in erster Linie genetisch verankerte Entwicklungsprozesse sowie individuelle Lernmechanismen für den Erwerb und den Gebrauch von Gesten in Bonobos und Schimpansen verantwortlich sind; wohingegen das Lernen durch Beobachtung der Mutter eine untergeordnete Rolle zu spielen scheint.

In der dritten Studie (Kapitel 4) untersuchte ich den Gebrauch von Gesten, die mit dem Kopf ausgeführt werden. Von allen vier Menschenaffenarten, zeigten Bonobos hierbei die größte Vielfalt (sowohl im Hinblick auf Anzahl der Gestentypen als auch deren Häufigkeiten). Darüber hinaus beobachtete ich einzelne Fälle von ‚präventivem' Kopfschütteln in Bonobos. Das ‚präventive' Kopfschütteln trat in Situation auf, in denen der Sender versuchte eine bestimmte Handlung des Empfänger zu unterbinden.

Diese Verwendung des Kopfschüttelns beschreibt ein bisher selten beobachtetes Motiv in Menschenaffen.

Die Ergebnisse der Studien deuten auf ein komplexes Zusammenspiel von biologischen, sozio-ökologischen und lebensgeschichtlichen Faktoren bei der Entwicklung gestischer Kommunikation in Menschenaffen hin. Die vorliegende Arbeit leistet damit einen wichtigen Beitrag zum besseren Verständnis der gestischen Kommunikation unserer nächsten Verwandten und bietet darüber hinaus eine Basis auf die zukünftige Studien aufbauen können.

Publications and manuscripts based upon this dissertation

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Curriculum Vitae

For reasons of data protection,
the curriculum vitae is not included in the online version.

Erklärung

Hiermit versichere ich, die vorliegende Arbeit selbständig verfasst und keine anderen als die angegebenen Hilfsmittel verwendet zu haben. Die Dissertation wurde in keinem früheren Promotionsverfahren angenommen oder abgelehnt.

Ort, Datum *Unterschrift*