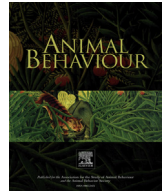




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Special Issue: Communicative Complexity

## Gestural development of chimpanzees in the wild: the impact of interactional experience

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To understand the complexity involved in animal signalling, studies have mainly focused on repertoire size and information conveyed in vocalizations of birds and nonhuman primates. However, recent studies on gestural abilities of nonhuman primates have shown that we also need a detailed understanding of other communicative modalities and underlying cognitive skills to grasp this phenomenon in detail. Here, we thus examined gestural signalling of chimpanzees, *Pan troglodytes*, living in two communities in the wild (Kanyawara, Uganda; Tai South, Côte d'Ivoire) with a special focus on the influence of the social environment on signal development. Specifically, we investigated to what extent specific social factors, namely behavioural context, interaction rates and maternal proximity, affect gestural production (i.e. gesture frequency, sequences and repertoire size). We used a combination of video recordings and focal scans obtained from 11 infants aged between 9 and 69 months during 1145 h of observation throughout two consecutive field periods. Overall, we found that social play was the context in which the highest number of gestures occurred. While gesture frequency and repertoire size increased with higher interaction rates with nonmaternal conspecifics and the number of previous interaction partners, no effect was found for interaction rates with mothers. Our results thus imply that infants of social mothers may have a head start in life. Moreover, we provide hitherto undocumented evidence for sex differences in gestural signalling, which may reflect the differential importance of early socialization for chimpanzee males and females. Gestural development thus relies heavily on interactional experiences with conspecifics, which adds support for gestural acquisition via the learning mechanism of 'social negotiation' in great apes.

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Communication systems vary greatly in the animal kingdom with respect to their degree of complexity, with human language representing one of the most sophisticated signalling systems (Hauser, Chomsky, & Fitch, 2002; Tomasello, 2008). Communicative complexity has been characterized in terms of the number of structurally and functionally distinct elements (e.g. repertoire sizes) or the number of information bits involved (Freeberg, Dunbar, & Ord, 2012). Studies have been strongly biased towards the vocal modality and have focused on repertoires, combinations (i.e. compositional syntax) and referential use as well as learning and modification of signals (for a review see Pollard & Blumstein,

2012). However, in recent years there has been a considerable increase of research interest concerning the production and use of multimodal and nonvocal signalling (Call & Tomasello, 2007; Liebal, Waller, Burrows, & Slocumbe, 2013; Pika & Liebal, 2012), suggesting that communicative complexity should be interpreted and tested in relation to 'the number [usage and application] of capabilities that have to be coordinated' (after Oller & Griebel, 2008, p. 141).

Concerning gestural signalling, it has been well established that all great ape species use open-ended, multifaceted gestural repertoires, consisting of species-distinctive and species-indistinctive gestures (Call & Tomasello, 2007; Pika, 2015). Gestures are employed as intentional (e.g. Hobaiter & Byrne, 2011a; Leavens, Russell, & Hopkins, 2005; Pika, Liebal, Call, & Tomasello, 2005; Roberts, Roberts, & Vick, 2014) and flexibly produced

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communicative strategies, as demonstrated by means-ends dissociation and adjustments to audience effects (Call & Tomasello, 2007; Cartmill & Byrne, 2007), and may in some cases have a referential function (e.g. Douglas & Moscovice, 2015; Pika & Mitani, 2006). Moreover, evidence exists for the production of idiosyncratic and dyad-specific gesture types, implying that individual and social learning processes are involved in the acquisition of gestures (Fröhlich, Wittig, & Pika, 2016b; Halina, Rossano, & Tomasello, 2013; Pika et al., 2005; Tomasello, Call, Nagell, Olguin, & Carpenter, 1994; but see Hobaiter & Byrne 2011a, 2011b for different views).

Research concerning different facets of communicative complexity and underlying cognitive mechanisms are thus crucial to grasp this phenomenon, if possible, in its full intricacy and develop a definition that is shared across species and communicative mediums. In addition, to understand the impact of ontogeny and socioecological factors, it is necessary to investigate the developmental trajectories of communicative signals. So far, it has been suggested that meaningful communicative signals develop first in interactions with the mother and are subsequently shaped in interactions with other members of the social community, such as siblings or peers (Maestriperieri & Call, 1996; Plooij, 1978). However, although it has been shown that social experiences strongly influence sociocognitive outcomes (for reviews see Bard & Leavens, 2009; Leavens & Bard, 2011) and communicative development (Snowdon & Hausberger, 1997), this vital aspect has rarely been considered in studies of great ape communication (Bard & Leavens, 2014). The existing studies on gestural development have provided fine-grained analyses on a hitherto undocumented level, focusing on the onset, developmental trajectories and contextual usage of gestural signals (Bard et al., 2014; Halina et al., 2013; Schneider, Call, & Liebal, 2012a; Tomasello et al., 1997). However, they have all focused on individuals in captive settings and it is thus not clear to what extent these findings may be representative of the behaviour of individuals and groups living in their natural environments (Boesch, 2007; Fröhlich, Wittig, et al., 2016b). To gain an in-depth understanding of gestural signalling in great apes, it is important to study gestural ontogeny in populations living in their natural environment where they are exposed to active selection pressures (see also Boesch, 2007; Fröhlich, Kuchenbuch, et al., 2016). In addition, longitudinal approaches are useful tools to enable both between- and within-subject comparisons (Pika, Liebal, & Tomasello, 2003; Tomasello et al., 1994; Tomasello, Gust, & Frost, 1989) but they have only recently been implemented for great apes in the wild (Fröhlich, Kuchenbuch, et al., 2016; Fröhlich, Wittig, et al., 2016b).

The aim of the present study was thus to investigate whether specific factors related to social exposure, namely behavioural context, interactional experience and maternal proximity, affect the development of gestural signalling. To do so, we implemented a combination of methods using both high-quality video recordings and focal animal scans. Focal scan data of chimpanzee, *Pan troglodytes*, infants enabled us to trace both their social (e.g. interaction rates and partners) and their spatial independence (e.g. maternal proximity), which complemented the fine-grained analysis of communicative development. Therefore, we had the opportunity to examine multiple domains of development simultaneously. Systematic studies on the sociocomotor development in chimpanzees in their natural environments are extremely rare and have mainly focused on sex differences (Lonsdorf, Markham, et al., 2014) while the trajectory of physical development and maternal proximity has been neglected (however, see Koops, Furuichi, & Hashimoto, 2015 for a study addressing the influence of this factor on tool use). Given the large intersite variability in chimpanzee

social behaviour in the wild (Boesch, 2007; Boesch, Hohmann, & Marchant, 2002), we included two communities of different subspecies to obtain a more representative sample of the whole species.

Specifically, we observed the communicative, social and locomotor behaviour of six infants living in a community of eastern chimpanzees, *P. t. schweinfurthii*, in Kibale National Park, Uganda and five infants living in a community of western chimpanzees, *P. t. verus*, in Taï National Park, Côte d'Ivoire. We examined factors influencing signalling behaviour in three distinct contexts: food sharing, mother–infant joint travel and social play. These three contexts were chosen since they are known to involve frequent communicative exchanges (van Lawick-Goodall, 1967; Plooij, 1978; Wilkinson, Leudar, & Pika, 2012). To investigate social influences on gestural development, we analysed gesture frequency, gestural production in sequences and repertoire sizes as established measures of gestural signalling (Call & Tomasello, 2007; Hobaiter & Byrne, 2011a, 2011b). Specifically, we turned our attention to three research questions. First, does gestural signalling of infant chimpanzees differ in relation to behavioural contexts? To address this question, we investigated gestural production and repertoire produced in the three different contexts.

Second, is gestural signalling influenced by the interactional experience of a given infant? To answer this question, we linked focal scan data collected on social interactions with mothers and other conspecifics (e.g. grooming, play, affiliation) to data on gesture frequency, sequence and repertoire sizes. Importantly, interactions with mothers and interactions with other conspecifics were considered and analysed separately. Following the 'social negotiation hypothesis' (Fröhlich, Wittig, et al., 2016b), we assumed that developmental experiences and learning will play a major role in gesture acquisition and predicted that gesture production should be substantially enhanced by higher rates of social interaction with mothers and conspecifics.

Third, to what extent is gestural signalling of chimpanzee infants influenced by maternal proximity? To answer this question, we linked focal scan data collected on maternal proximity to data on gestural signalling. It has been argued that gestural ontogeny might depend crucially on the chimpanzee infant becoming spatially independent and leaving the security range provided by the mother (Van Lawick-Goodall, 1968). If this hypothesis is true, we predicted we would find an increase in gestural production in relation to an increase of physical distance between mother and maturing offspring (Bard et al., 2005). On the other hand, infants might feel more confident to practise and employ their first gestural signals with conspecifics while being in close proximity to their mother (Fröhlich, Wittig, & Pika, 2016a). With respect to this hypothesis, we predicted that the proximity of the mother would have a positive influence on gesture use.

In addition to age effects we also controlled for other confounding effects by including infant's sex, mother's parity and study site as factors in our analyses. We included the effect of sex since male and female chimpanzee infants might differ in gestural signalling resulting from differential roles of early socialization (Fröhlich, Wittig, et al., 2016a; Lonsdorf, Anderson, et al., 2014; Murray et al., 2014). Moreover, infants of multiparous mothers might have more social opportunities and interactions than infants of primiparous mothers (Fröhlich, Wittig, et al., 2016b; van Lawick-Goodall, 1967), especially if the latter immigrated relatively recently and only rarely associated with others. Finally, the substantial intersite variation reported for chimpanzee behaviour in the wild (Boesch et al., 2002) highlights the need to account for within-species variability in studies of communicative development.

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