Running head: Do bonobos say NO by shaking their head?

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Title: Do bonobos say NO by shaking their head?

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Electronic supplementary material: Video material is provided

Abstract Head shaking gestures are commonly used by African great apes to solicit activities such as play. Here, we report observations of head shaking in four bonobos apparently aimed at preventing the recipient from doing something. This may reflect a primitive precursor of the negative connoted head shaking behaviour in humans. Further investigations are needed to clarify the preventive function of head shakes and their evolutionary role in the evolution of negation in humans.

Keywords Communication; Gestures; Head shaking; *Pan paniscus*

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., as a feedback signal during conversation (see Cassell, 2000; McClave, 2000), it has been generally associated with an explicit or implicit negative connotation in many parts of the world (Darwin, 1872; Morris, 1994; Kendon, 2002; cf., Darwin, 1872; Cassell, 2000, for cultural variations to this norm).

Head gestures have also been described in the African great apes, but not in orangutans (e.g., van Lawick-Goodall, 1968; van Hooff, 1973; Becker, 1984; Tomasello et al., 1997; Pika et al., 2003, 2005; Liebal et al., 2006; Tanner et al., 2006; Cartmill, 2008; Genty et al., 2009). 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 (Kortlandt, 1962; de Waal, 1982), 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 we report the first observations of head shakes in bonobos 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 present study provides a quantitative estimate of the prevalence and diversity of head gestures across all four ape species and presents a detailed description of observed episodes of 'preventive' head shaking in bonobos.

Methods

The reported observations were made during data collection for a research project that focused on gestural acquisition in non-human great apes (Schneider, in preparation). We 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.

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

We used a standardised and validated ethogram to score the communicative signals (see Liebal et al., 2006 for definitions and criteria of communicative behaviour). Three forms of head gestures, as mentioned and defined in the introduction (bow, nod and shake), were identified. Additionally, we scored the following behavioural contexts in which the gestures occurred: access, affiliation, agonism, grooming, ingestion, play, locomotion, sexual and submission (see Liebal et al., 2006 for definitions).

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 is running away). These 13 'preventive' instances occurred during seven bouts of interactions and were primarily observed in mother-infant dyads, with the mother and infant adopting the sender and recipient role, respectively (see Table 1 for additional information). However, 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. We recorded the preventive signals in three behavioural contexts: affiliation, ingestion, and access (see Liebal et al., 2006 for context definitions).

The 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 (ten preventive). Yala produced eight head shakes (one preventive) towards her offspring Kivu, while Kidogo and Djanoa only produced a single head shake in their dyad (which was preventive in both cases). In three of the seven interactions, one head shake occurred; in three interactions two head shakes were performed, and in one

interaction four 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, here we provide a description of two of the observed episodes (video recordings of these examples are available as electronic supplementary material).

Example 1

The mother and her female offspring were sitting next to each other on the ground. The offspring started crawling away towards 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 a while 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 towards 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 a while, 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 towards the piece of leek.

Discussion

To date African great apes have been observed to display head shakes mainly for initiating or resuming interactions such as play. Here, we 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 we observed head gestures in both chimpanzees and bonobos, only the latter employed head shakes (cf., van Hooff, 1973; Tomasello et al., 1997; Liebal et al., 2004). 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 (Paoli et al., 2006; Hare et al., 2007). 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 who 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 (Kortlandt, 1962;

de Waal, 1982). Future research using a more systematic, cross-species approach could clarify whether our observed inter-species 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, 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 to orangutans and other primates (Becker, 1984; Liebal et al., 2006; Cartmill, 2008). 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 the 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, 2007). 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, and 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 be able to provide an informed answer.

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266 ***Tables***

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Table 1 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

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