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NEWS AND PERSPECTIVES

Do bonobos say NO by shaking their head?

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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 negatively connoted head-shaking behavior 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., 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 (see 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 1969; 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 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 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 nonhuman great apes (Schneider 2010). 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

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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' behavior using focal animal sampling and scored all communicative behavior 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 nonfocal animals were also recorded whenever she was near the infant and therefore in the view of the camera. Overall, we obtained 190 h of focal animal observations (bonobos = 69 h, chimpanzees = 79 h, gorillas = 16 h, orangutans = 26 h). We used a standardized and validated ethogram to score the communicative signals (see Liebal et al. 2006 for definitions and criteria of communicative behavior). Three forms of head gestures, as mentioned and defined in the "Introduction" (bow, nod, and shake), were identified. Additionally, we scored the following behavioral 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 behavioral contexts: play and affiliation. Of the 49 head shakes observed in bonobos, 13 occurred while trying to inhibit or terminate a particular nonsocial behavior 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 1 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 (nonpreventive) head shakes were used to initiate or to maintain behavior 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 we were unable to code the observed context were characterized as unknown.

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 eight 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 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, 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 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 toward 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 infant's 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.

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

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

[a] See "Example 1" in text

[b] See "Example 2" in text

shakes in bonobos accompanying an active effort to terminate or prevent the recipient from engaging in a particular behavior. 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 interindividual tolerance and diffused hierarchical structures (Paoli et al. 2006; Hare et al. 2007). For example, according to the "emotional reactivity hypothesis" (Hare and Tomasello 2005), bonobos differ from other apes in their social-problem-solving strategies because their emotional temperament affords more cooperative behavior. In relation to this, Maestripieri (1999) proposed that species living in egalitarian–individualized 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 (Kortlandt 1969; de Waal 1982). Future research using a more systematic, cross-species approach could clarify whether our 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, 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; 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 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 behavior (Call and 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, 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.

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