

Do bonobos say NO by shaking their head?

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Electronic supplementary material: Video material is provided

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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 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*

25 ***Introduction***

26 The *head shake* gesture (i.e., moving the head horizontally from side to side) is
27 regularly used as a communicative signal in humans. Although head shaking can fulfil
28 several communicative functions, e.g., as a feedback signal during conversation (see
29 Cassell, 2000; McClave, 2000), it has been generally associated with an explicit or implicit
30 negative connotation in many parts of the world (Darwin, 1872; Morris, 1994; Kendon,
31 2002; cf., Darwin, 1872; Cassell, 2000, for cultural variations to this norm).

32 Head gestures have also been described in the African great apes, but not in
33 orangutans (e.g., van Lawick-Goodall, 1968; van Hooff, 1973; Becker, 1984; Tomasello et
34 al., 1997; Pika et al., 2003, 2005; Liebal et al., 2006; Tanner et al., 2006; Cartmill, 2008;
35 Genty et al., 2009). More specifically, three main forms of head gestures have been
36 identified: *bows* (moving the torso and the head back and forth), *nods* (moving the head
37 vertically up and down) and *shakes* (moving the head horizontally from side to side).
38 Except for two isolated reports of chimpanzees signalling ‘no’ through head shaking
39 (Kortlandt, 1962; de Waal, 1982), head shakes in African great apes have been mainly
40 associated with an affiliative function, for instance, in the context of play (e.g., bonobos:
41 Pika, 2007; chimpanzees: van Hooff, 1973; gorillas: Tanner et al., 2006).

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

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49 **Methods**

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51 The reported observations were made during data collection for a research project
52 that focused on gestural acquisition in non-human great apes (Schneider, in preparation).
53 We videotaped 25 great ape infants during their first 20 months of life: six bonobos (*Pan*
54 *paniscus*), eight chimpanzees (*Pan troglodytes*), three gorillas (*Gorilla gorilla*), and eight
55 orangutans (*Pongo pygmaeus*). The ape infants – housed in six European zoological parks
56 – were observed at different time periods, based on their age and their accessibility for
57 filming, between July 2001 and August 2008.

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

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

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73 **Results**

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

80 Of the 49 head shakes observed in bonobos, 13 occurred while trying to inhibit or
81 terminate a particular non-social behaviour of the recipient through active manipulation
82 (e.g., pulling back an infant that is running away). These 13 'preventive' instances
83 occurred during seven bouts of interactions and were primarily observed in mother-infant
84 dyads, with the mother and infant adopting the sender and recipient role, respectively (see
85 Table 1 for additional information). However, in one instance an adult male showed a head
86 shake after the infant reached for the male's food and in another instance a mother
87 employed head shaking after an adult female took food from her. We recorded the
88 preventive signals in three behavioural contexts: affiliation, ingestion, and access (see
89 Liebal et al., 2006 for context definitions).

90 The signals were performed by four individuals living in three different captive
91 groups (the two communicators from Dierenpark Planckendael belonged to the same
92 group). The mother-offspring dyad formed by Ulindi and Luiza produced a total of 16 head
93 shakes by the mother (ten preventive). Yala produced eight head shakes (one preventive)
94 towards her offspring Kivu, while Kidogo and Djanoa only produced a single head shake in
95 their dyad (which was preventive in both cases). In three of the seven interactions, one
96 head shake occurred; in three interactions two head shakes were performed, and in one

97 interaction four head shakes were displayed. No other head gestures in bonobos or
98 chimpanzees were used with this preventive function. To illustrate the use of the
99 preventive head shakes, here we provide a description of two of the observed episodes
100 (video recordings of these examples are available as electronic supplementary material).

101 **Example 1**

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

113 **Example 2**

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

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121 *Discussion*

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

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

143 Nevertheless, additional research is required. Single-case observations of head
144 shaking with a negative connotation have been reported in chimpanzees (Kortlandt, 1962;

145 de Waal, 1982). Future research using a more systematic, cross-species approach could
146 clarify whether our observed inter-species differences were due to small sample sizes or
147 observation times. Furthermore, more detailed studies are needed to establish the
148 functional role of all forms of head gestures (e.g., shake, nod, bow) for each species.

149 Current research on gestural communication in great apes has shown that the use of
150 the head as a communication device is more prevalent in African apes compared to
151 orangutans and other primates (Becker, 1984; Liebal et al., 2006; Cartmill, 2008).
152 Although some monkeys possess well-defined head gestures (e.g., head flagging in gray-
153 cheeked mangabeys; Wallis, 1983), they appear more stereotyped and less diverse than
154 those observed in African great apes. Calling attention to the preventive communicative
155 function of a previously described gesture contributes to expand the variety of motives
156 underlying gestural use in the great apes. Until now, most great ape gestures, not just head
157 gestures, have been interpreted as invitations to engage in various activities or as
158 announcements of impending behaviour (Call & Tomasello, 2007). It is true that some
159 intention movements can inform recipients about the actor's intent to prevent some activity.
160 For instance a dominant animal can take a step in the direction of an object to inform others
161 about its intent to claim it, and thus preventing others from taking it. However, this is quite
162 different from the head shaking gesture which, by itself, does not indicate any particular
163 action. If the use of preventive head shaking is confirmed in genus *Pan*, this would raise a
164 further, more speculative, evolutionary question: Do these gestures reflect a primitive
165 precursor of the human head shake that denotes negation? This is an intriguing possibility
166 but additional data along the lines indicated above will be needed to be able to provide an
167 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.

<i>Location</i>	<i>Sender-recipient dyad</i>	<i>Number of head shakes per interaction bout</i>	<i>Context</i>
		2	Affiliation ^a
Leipzig Zoo	Mother → Offspring <i>Ulindi</i> <i>Luiza</i>	2	Affiliation
		2	Access ^b
		4	Ingestion
Dierenpark Planckendael	Adult male → Infant <i>Kidogo</i> <i>Habari</i>	1	Ingestion
	Mother → Adult Female <i>Djanao</i> <i>Hortense</i>	1	Ingestion
Berlin Zoo	Mother → Offspring <i>Yala</i> <i>Kivu</i>	1	Affiliation

268 ^aSee *Example 1* in text. ^bSee *Example 2* in text.