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Olive baboons, *Papio anubis*, adjust their visual and auditory intentional gestures to the visual attention of others

Marie Bourjade [a,b,*], Adrien Meguerditchian [b,c], Audrey Maille [d], Florence Gaunet [c], Jacques Vauclair [a]

[a] Research Centre in the Psychology of Cognition, Language and Emotion, PsyCLE, Aix-Marseille University, Aix-en-Provence, France
[b] Centre National de la Recherche Scientifique, Station de Primatologie UPS 846, Rousset, France
[c] Laboratoire de Psychologie Cognitive, Aix-Marseille University, Marseille, France
[d] UMR 6552 Ethos 'Ethologie Animale et Humaine', Université de Rennes 1 – CNRS, Station Biologique, Paimpont, France

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Although nonhuman primates' gestural communication is often considered to be a likely precursor of human language, the intentional properties in this communicative system have not yet been entirely elucidated. In particular, little is known about the intentional nature of monkeys' gestural signalling and related social understanding. We investigated whether olive baboons can (1) adjust their requesting gestures to the visual attention of the experimenter with special emphasis on the state of the eyes (open versus closed), and (2) flexibly tailor visual and auditory-based gestures to elaborate their communication as a function of whether or not the experimenter can see them. Using a food-requesting paradigm, we found monkeys able to favour either visual or auditory-based requesting gestures to match the experimenter's visual attention. Crucially, when the human was not visually attending, they silenced visual gestures to some extent but performed more attention-getting gestures. This is, to our knowledge, the first report of monkeys elaborating attention-getting signals to compensate for communication breakdown. Gestural communication was also supported by gaze alternation between the experimenter's face and the food, especially when the human was visually attending. These findings offer evidence that olive baboons understand the state of the eyes in others' visual attention and use requesting gestures intentionally. They emphasize that Old World monkeys shift to acoustic communication when the recipient is not visually attending. In contrast to that of human infants and great apes, this acoustic communication is purely gestural, not vocal.

Intentional communication is collaborative in essence since it requires mutual attention from both parties in the interaction (Tomasello, Carpenter, Call, Behne, & Moll, 2005). When producing gestural requests such as pointing gestures, the sender should be able to perceive the visual attention of the recipient (Butterworth, 2004). In human infants, taking a partner's attentional state into account when gesturing is seen only from around 15 months of age (Bates, Camaioni, & Volterra, 1975; Franco & Butterworth, 1996; Leavens & Hopkins, 1999). The best evidence of an understanding of attention in children is the coordination with others' attention to external targets, also called 'joint attention' (Butterworth, 2004; Scaife & Bruner, 1975). This ability is considered critical for the development of both language and the ability to attribute mental states to others (Camaioni, Perucchini, Bellagamba, & Colonnesi, 2004; Reddy, 2004).

Nonhuman primates do communicate with gestures too. A communicative gesture has recently been defined as 'any nonvocal bodily action directed to a recipient that is mechanically ineffective and represents a meaning, beyond itself, that is in part manifested by others of the social group' (Scott & Pika, 2012, p. 158; but see Perlman, Tanner, & King, 2012 for an alternative view of mechanical effectiveness). Great apes and cercopithecines produce these communicative signals, and so far research has mostly emphasized their use, function and language-like properties (Pika & Liebal, 2012). Indeed, this gestural system of communication is often considered to be the most likely precursor of human language (Corballis, 2003; Pollick & de Waal, 2007; Vauclair, 2004) owing to shared similarities such as the flexible and voluntary use of gestures (Liebal & Call, 2012; Meguerditchian, Cochet, & Vauclair, 2011), or the brain specialization for gesturing (Corballis, 2003; Hopkins & Vauclair, 2012). However, whether nonhuman primates gesture with the genuine intent to modify their recipient's

* Correspondence and present address: M. Bourjade, Laboratoire de Psychologie Cognitive, Aix-Marseille University, 3 place Victor Hugo, 13331 Marseille Cedex 3, France.
E-mail addresses: marie.bourjade@univ-amu.fr, marie.bourjade@gmail.com (M. Bourjade).

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behaviour, attention or knowledge has not yet been entirely elucidated (Gómez, 2007). Although there is solid evidence that great apes are sensitive to their partner's attentional state when gesturing, little is known about the intentional nature of monkeys' gestural signalling and related social understanding (Call & Tomasello, 2007; Scott & Pika, 2012). Specifically, for both great apes and monkeys it is not clear whether the relevant cues to attention of the recipient are the eyes or more general indicators such as head and body orientation (Emery, 2000; Povinelli & Eddy, 1996; Povinelli, Eddy, Hobson, & Tomasello, 1996; but see Kaminski, Call, & Tomasello, 2004).

Deictic gestures that refer to external targets are used by nonhuman primates to perform requests (Gómez, 2005; Pika, 2008). To be considered as intentional, they must fulfil several criteria used for prelinguistic children's pointing (Bates et al., 1975; Leavens, 2004): (1) the gesture is goal-oriented and the signal persists or is completed with other signals until the desired outcome is reached; (2) the gesture is adjusted in accordance to the attentional state of the audience, whose attention can be regained by the use of additional attention-getting behaviours; and (3) the gesture is supported by visual orienting behaviours alternating between the recipient and the distal object of interest (gaze alternation). Evidence is accumulating that great apes use visual gestures only if the recipient is visually attending (e.g. bonobos, *Pan paniscus*: Pika, Liebal, Call, & Tomasello, 2005; orang-utans, *Pongo pygmaeus*: Liebal, Pika, & Tomasello, 2006; gorillas, *Gorilla gorilla*: Genty, Breuer, Hobaiter, & Byrne, 2009; chimpanzees, *Pan troglodytes*: Hobaiter & Byrne, 2011) and persist with (e.g. Genty & Byrne, 2010; Liebal, Call, & Tomasello, 2004) or elaborate (Cartmill & Byrne, 2007; Leavens, Russell, & Hopkins, 2005) their gestures until they achieve a certain goal. However, attempts to determine which cues to attention are used by apes and monkeys to adjust their communication have led to mixed results. While it is often not possible to characterize the state of the eyes of individuals in naturalistic settings (e.g. Emery, 2000; Genty et al., 2009), experimental studies have further demonstrated that nonhuman primates generally use body orientation (e.g. great apes: Hostetter, Cantero, & Hopkins, 2001; Kaminski et al., 2004; Povinelli et al., 1996; monkeys: Hattori, Kuroshima, & Fujita, 2010; Meunier, Prieur, & Vauclair, 2012) or face orientation (e.g. great apes: Tempelmann, Kaminski, & Liebal, 2011; monkeys: Maille, Engelhart, Bourjade, & Blois-Heulin, 2012) as an indicator of a human's attention, although they may sometimes use face orientation only when the human's body is oriented towards them (e.g. chimpanzees: Kaminski et al., 2004). However, there is little evidence that nonhuman primates adjust their signals to the open and directed state of the recipient's eyes (but see Hattori et al., 2010; Hostetter, Russell, Freeman, & Hopkins, 2007). Instead, many studies have failed to demonstrate that subjects tailor their gestural signals as a function of the state of the experimenter's eyes (Kaminski et al., 2004; Povinelli et al., 1996; Theall & Povinelli, 1999). Although chimpanzees have been reported to move into someone's visual field before starting to gesture rather than using auditory or tactile signals to regain attention (Liebal, Call, Tomasello, & Pika, 2004), two studies showed that chimpanzees favoured the modality of communication that best fitted the experimenter's visual attention (Leavens, Hostetter, Wesley, & Hopkins, 2004), using auditory signals specifically when the experimenter could not see them (Hostetter et al., 2007). While this may constitute the best evidence so far that great apes can finely tune their gestures to the level of attention of the recipient, there is no such evidence for monkeys, to which this stringent paradigm remains to be applied.

We addressed this question in olive baboons using a food-requesting paradigm. Baboons use two distal threat gestures in their natural communication, i.e. 'slapping ground' and 'rubbing ground' (Estes, 1991; Kummer, 1968), usually performed towards an obviously attending partner (Meguerditchian & Vauclair, 2006; Meguerditchian et al., 2011). They are further known to rely on the use of gaze cues by conspecifics for soliciting help in conflicts (Packer, 1977) and for deceptive communication (Whiten & Byrne, 1988). In experimental settings baboons gestured more towards a human facing them than one oriented away (Meunier et al., 2012), but no study has disambiguated which cues to attention they relied on.

We manipulated the experimenter's visual attention by varying the orientation of the experimenter's whole body, including head (front/back), and the state of her eyes (open/closed). We then addressed whether baboons (1) adjust their requesting gestures to the visual attention of the experimenter with special emphasis on the state of her eyes, and (2) flexibly tailor visual and auditory signals to elaborate their communication as a function of whether or not the experimenter can see them. If baboons are able to use the state of the eyes as a cue to visual attention, they should produce more requests when the experimenter's eyes are open than when they are closed. If they not only use the state of the eyes as a cue to attention, but also understand the role of open eyes as an attentional state that is specific to their visual behaviour, baboons should tailor their gestural communication to the visual attention of the experimenter, and therefore produce more auditory-based gestures than visual gestures when the experimenter cannot see them compared to when she can. However, if baboons rely on more general cues to attention such as body orientation, they should produce more requests when the experimenter is facing them than when the experimenter is oriented away.

METHODS

Subjects

The experiments took place in the Primate Station of the Centre National de la Recherche Scientifique (UPS 846, Rousset, France; Agreement number for conducting experiments on vertebrate animals: D13-087-7). Sixteen baboons, 10 males and six females, ranging in age from 6 to 16 years were tested between August 2011 and March 2012 (see Appendix Table A1). All subjects lived in reproductive social groups comprising one adult male, two to five adult females and their immature offspring (up to 2 years old). Groups had free access to 14 m^2 outdoor areas connected to 12 m^2 indoor areas. The enclosures were enriched by wooden platforms and vertical structures of different heights, in both the outdoor and indoor areas. All monkeys were fed four times a day with industrial monkey pellets, seed mixture, fresh vegetables and fruits. Water was available ad libitum and subjects were never deprived of food or water during testing. Subjects were tested in their outdoor area, and only females were partly isolated from dominant individuals (which were kept inside) during testing. The experimental procedure complied with the current French laws and the European directive 86/609/CEE. According to Article 3 (definitions) of the current European directive, this experiment does not qualify as an experimental procedure and therefore does not require institutional ethics approval.

Apparatus

Prior to each test session, we placed inside the cage a concrete block perpendicularly to the mesh, at about 90 cm from the ground so that subjects could gesture at about the height of a person. The mesh was equipped with a 10 × 60 cm opening through which the baboons could freely pass their arms. During testing, a Plexiglas panel of 80 × 35 cm with two 10 × 15 cm holes separated by 25 cm from centre to centre was fixed to the mesh over the opening (see