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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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*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).

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.

Keywords

audience attention, gestural communication, intentionality, language, nonhuman primate

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 non-vocal 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 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.

<H1>Methods

<H2>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.

<H2>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 10x60 cm opening through which the baboons could freely pass their arms. During testing, a Plexiglas panel of 80x35 cm with two 10x15 cm holes separated by 25 cm from centre to centre was fixed to the mesh over the opening (see Supplementary Videos S1–S4). This panel was devised to facilitate subsequent recording of baboons' gestures on video footage. Baboons were hence allowed to beg through the holes towards an experimenter standing 1 m in front of the cage. Two video cameras were placed 2 m in front of the cage on both sides of the experimenter at an angle of 45° to the subject's midline. All sessions were videotaped at a rate of 30 frames/s.

<H2>*Test Procedure*

All subjects were previously trained to beg through one of the holes of the Plexiglas panel to request the food reward held in the experimenter's hand (see the Appendix for the full procedure). Baboons were then tested for their requesting behaviour in four conditions. In the control condition, the condition Out, the experimenter deposited a piece of banana (4 cm long throughout the study) on the ground, 1 m in front of the cage, and left the test area (see Supplementary Video S1). In the other three conditions, the test conditions, the experimenter stood 1 m in front of the cage holding a piece of banana in one hand always in sight of the subject: (1) Eyes open: the experimenter faced and looked at the subject (see Supplementary Video S2); (2) Eyes closed: the experimenter faced the subject but kept her eyes closed (see Supplementary Video S3); (3) Back turned: the experimenter was oriented away from the subject but held the food behind her back (see Supplementary Video S4). Note that the experimenter did not stare at the baboons in the Eyes open condition but rather looked alternately to the eyes and the upper part of the nose so as to avoid possible fear reactions. Each test session comprised four 30 s experimental trials alternated with eight motivation trials in which the experimenter offered the subject the food as soon as it requested it. At the end of each 30 s experimental trial, the experimenter gave the subject the piece of banana regardless of its behaviour during the trial. Each baboon received four test sessions (one per day), each experimental condition being presented once per session. The order of exposure to the four conditions was counterbalanced between subjects and sessions; four distinct random orders of conditions were presented to four groups of four subjects using a Latin square procedure so as to control for possible habituation to the procedure (see full details in Appendix Table A2).

<H2>Data Scoring and Reliability

Two different types of manual gestures were observed during the study and scored on the videos for further analysis. Begging gestures were visual gestures consisting of extending one or two arm(s) with fingers and hand(s) being in line with the arm(s) (Fig. 1). Attention-getting gestures were auditory-based gestures consisting of banging the Plexiglas panel. Visual orienting behaviour that took the form of gaze alternation bouts between the experimenter's face and the food was also recorded. A first main observer coded all occurrences of begging gestures and attention-getting behaviours at 30 frames/s using a VLC media player. A begging gesture started when the wrist crossed the mesh and ended with the partial or complete withdrawal of the arm. A new occurrence was scored whenever the subject brought its arm back, with the elbow being inside the cage, and extended it again. A new occurrence of attention-getting gesture was scored each time the subject banged the Plexiglas panel producing distinct sounds. A second main observer coded all occurrences of visual orienting behaviour frame by frame using Avidemux 2.5 (32-bit). Gaze alternation bouts were recorded based on the conservative number of four consecutive looks alternating between the experimenter's face and the piece of banana. For reliability purposes, 15% of the video material was randomly assigned to two novel observers who were naïve to the experiment. This resulted in a total of 40 experimental trials, each of 30 s, in 10 different test sessions. One novel observer coded the begging and attention-getting gestures while the other coded gaze alternation bouts. Reliability was assessed within pairs of main and novel observers and was high for both gestures (Cohen's k = 0.82) and gaze alternation bouts (Cohen's k = 0.76).

<H2>Statistical analysis

We used an approach of multimodel inference to determine which cues to attention most affected the responses of the subjects (Burnham & Anderson, 2004). We processed the numbers of begging gestures, attention-getting gestures and gaze alternation bouts produced by the 16 subjects over all test sessions across experimental conditions. Missing data occurred for one subject (Tulie) in the last test session and were considered as such in the models. We followed a three-step procedure: (1) we fitted several models varying the nature of cues to attention as fixed effects (Table 1); (2) we selected the models that best fitted the observed data; and (3) we performed tests of significance on the retained models.

<H3>Model fitting

As the frequency distribution of all dependent variables was not normal, we selected a Poisson family with a log link function adapted to count data for fitting generalized linear mixed models with ‘condition’ as fixed effect (i.e. Main Models). Pseudoreplication caused by repeated observations of the same individual was taken into consideration by adding the individual as a random effect. Second, we examined the possible variation of behavioural responses over time (habituation) by fitting models with the interaction between ‘condition’ and ‘block’ of test sessions as fixed effects and ‘individual’ and ‘block’ as random effects (i.e. Time Models). The first two test sessions were pooled as block 1 and the last two test sessions as block 2. Third, we tested which postural cues to attention had the strongest effect on dependent variables by performing nested models of the parameter ‘condition’ (i.e. Nested Models). This procedure allowed us to weight the relative influence of the different cues to attention (e.g. state of the eyes, body orientation) ‘nested’ in the parameter ‘condition’, and advantageously replace traditional post hoc comparisons. To test whether the effect of the state of the eyes could be stronger than the effect of head and body orientation, we pooled the Eyes closed and Back turned conditions into condition Cannot see to compare with condition Can see (i.e. Eyes open). To test whether the effect of head and body orientation could be stronger than the effect of the state of the eyes, we pooled the Eyes open and Eyes closed conditions into condition Front to compare with condition Back (i.e. Back turned).

<H3>Model selection

For each dependent variable we proceeded to select the best fitting models on the basis of the lowest AICc (i.e. Akaike information criterion corrected, Table 1), which applies a second-order correction adapted to small samples (Burnham & Anderson, 2004).

<H3>Test of significance

We used chi-square tests of the log-likelihood ratios to test whether the retained models fitted the observed data significantly better than a hypothetical null model in which no fixed effect had been implemented (Brown & Prescott, 2006). All tests were two tailed and were performed with R 2.10.1 software (http://cran.r-project.org) with level of significance set at 0.050.

<H1>Results

<H2>Recognition of Recipient's Visual Attention

The baboons adjusted their begging behaviour to the visual attentional state of the experimenter (Fig. 2). The experimental condition most affected the number of begging gestures (Table 1, Main Model). Baboons gestured more when the experimenter had her eyes open than in the other three conditions, Eyes closed (Wald test: $z = -2.28$, $P = 0.023$), Back turned (Wald test: $z = -9.30$, $P < 0.001$) and Out (Wald test: $z = -11.64$, $P < 0.001$). Body orientation by itself (Table 1, Front/Back Model) and the state of the experimenter's eyes alone (Table 1, Can see/Cannot see Model) were not better predictors of subjects' responses than experimental conditions mixing both cues (Table 1), suggesting that both played a role in the understanding of attentional state by baboons. In a transfer test performed by novel experimenters so as to exclude possible conditioned responses driven by the sight of the main experimenter, baboons showed very similar responses (see the Appendix and Fig. A1).

The baboons displayed significantly more gaze alternation bouts (Table 1, Main Model: Fig. 3) when the experimenter had her eyes open than when her eyes were closed (Wald test: $z = -2.13$, $P = 0.033$) or when her back was turned (Wald test: $z = -6.41$, $P < 0.001$). Body orientation by itself (Table 1, Front/Back model) and the state of the experimenter's eyes alone (Table 1, Can see/Cannot see model) were not better predictors of subjects' responses than experimental conditions mixing both cues (Table 1) suggesting that both played a role in the understanding of attentional state by baboons.

<H2>Attraction of Recipient's Visual Attention

Of the 16 subjects, 14 displayed attention-getting gestures, i.e. auditory-based gestures consisting of banging the apparatus. Banging was more frequent when the experimenter was present than when she was absent (Wald test: $z = -4.22$, $P < 0.001$), and when the experimenter could not see the subject than when she could (Wald test: $z = 0.029$, $P = 0.029$), during the first two test sessions only (Table 1, Can See/Cannot See Nested Model). Restricting our analysis to these two sessions in which no habituation to the procedure was likely to occur, we found that baboons performed more banging when the experimenter could not see them than when she could (one-sample permutation test: $t = 2.09$, $P = 0.021$; Fig. 4). Body orientation of the experimenter either alone (Table 1, Front/Back Model) or in combination with the state of her eyes (Table 1, Main Model) were not better predictors of the subjects' banging than being seen or not by the experimenter (Table 1).

<H2>*Adjustment of Gestures to Recipient's Visual Attention*

Considering the first two test sessions, we investigated whether subjects favoured visual requests (food-begging gestures) over auditory-based gestures (banging) when the experimenter could see them compared to when she could not. Gesture types produced by the baboons were affected by the possibility of being seen by the experimenter (Fisher's exact probability test: $P < 0.001$). Baboons made more visual requests when the experimenter could see them than when she could not. Conversely, they banged more when the experimenter could not see them than when she could (Fig. 5).

<H1>Discussion

Three novel findings resulted from this study. First, baboons tailored communicative signals from different modalities as a function of a human's visual attention based on the state of the eyes. Second, gestures were accompanied by gaze alternation between the human's face and the food. Third, monkeys spontaneously elaborated attention-getting signals when there was a communication breakdown. Until now, this latter ability was considered as a feature unique to communication of humans and great apes. Collectively, these findings provide solid evidence that baboons understand the state of the eyes in others' visual attention and use requesting gestures intentionally.

The primate brain contains neurons that are selectively responsive to eye direction, head orientation and body orientation, possibly as part of a hierarchical process for determining the direction of another's attention (see Emery, 2000 for a review). In baboons, the eye region is the primary focus of attention during processing of both humans' and conspecifics' faces (Martin-Malivel, Mangini, Fagot, & Biederman, 2006) and is essential for face recognition (Kyes & Candland, 1987). Monkeys also distinguish directed from averted gazes from both a conspecific and a human (Keating & Keating, 1982) and they follow the gaze direction of other individuals (Tomasello, Call, & Hare, 1998), sometimes relying on eye gaze direction only (e.g. in rhesus macaques, *Macaca mulatta*: Lorincz, Baker, & Perrett, 2000; in baboons: Vick, Bovet, & Anderson, 2001). Furthermore, monkeys use humans' state of the eyes as a cue to adjust behaviour in competitive situations (e.g. Flombaum & Santos, 2005; Vick & Anderson, 2003). It is therefore puzzling that sensitivity to others' state of the eyes has hardly ever been evidenced in a communicative context, except in a few studies (Hattori et al., 2010; Hostetter et al., 2007;). Here, we found that baboons performed virtually no gestural behaviour when the human was absent, but produced most visual gestures when the human was facing them with her eyes open. This suggests that their requesting behaviour was not merely driven by the sight of the food. Instead, it appears to be genuine communication motivated by the presence of the human partner. Moreover, while the information provided by the head and body orientation may be sufficient for interpreting direction of attention in quadrupedal species (Emery, 2000), this study shows that baboons also use open eyes as a cue when it is available in a communicative context.

In one study very similar to ours, Kaminski et al. (2004) pointed out a hierarchical use of cues to attention by chimpanzees. The apes responded primarily to body orientation and secondarily to face orientation only when the experimenter’s body was oriented towards them. The present study did not allow us to distinguish between the possibly hierarchical contribution of head and body cues. However, the baboons responded more with visual signals to the Eyes closed than the Back turned conditions, and neither body orientation by itself nor the state of the experimenter’s eyes was a better predictor of the subjects’ begging for food than the Eyes open condition which mixed both cues. This suggests that not only the state of the eyes but also body and head orientation were relevant cues to others’ visual attention for olive baboons. However, it remains possible that baboons respond to the state of the eyes only when the human’s body is oriented towards them.

If our findings seem contradictory to certain previous studies in which food was deposited on a platform (e.g. Kaminski et al., 2004; Povinelli & Eddy, 1996), they do corroborate the findings from other studies in which food was held in the experimenter’s hand (e.g. Hattori et al. 2010; Hostetter et al. 2007).This slight methodological difference may therefore deserve further discussion. As previously stressed for great apes, body orientation, but not face orientation, may convey information about the experimenter’s physical ability to give food rather than information about her ability to perceive a visual signal (Kaminski et al., 2004; Tempelmann et al., 2011). We suggest that holding food in the hands may increase and keep constant the disposition of the human to give food regardless of body orientation. Under such circumstances, it is possible that subjects process more subtle cues to attention such as the open versus closed state of the experimenter's eyes when begging for food. In a similar experiment, capuchin monkeys, *Cebus apella*, successfully adjusted their requesting gestures to the attentional state of a human holding food in one hand, but failed to adjust their requesting gestures to the attentional state of a human when gestures had to be directed at food deposited on a table (Hattori et al., 2010). While both gestures are communicative, pointing towards food on a table appears to be a rather difficult task for monkeys (e.g. Hattori et al., 2010). More research is hence needed to understand whether pointing towards an external target and begging from an experimenter require differential cognitive means for attracting the partner's attention.

Wild baboons have been reported to use visual orienting behaviour to attract a partner's visual attention. For instance, they solicit help in conflicts by looking alternately to an opponent and a solicited helper (Packer, 1977). Here, we report evidence of gaze alternation supporting gestural communication that was tuned to the visual attention of the recipient. Gaze alternation has long been considered as a cornerstone of the development of intentional communication in human infants (Bates et al., 1975; Camaioni et al., 2004; Franco & Butterworth, 1996). In line with a previous study (Meunier et al., 2012), our baboons displayed visual orienting behaviour that was related not only to the locations of the social partner and the object of interest, but also to the state of the eyes of the experimenter. This suggests that baboons understand others' visual attention as a prerequisite for coordinating their own attention with that of others towards an external target. This is reminiscent of children developing joint visual attention (Butterworth, 2004).

However, the fact that the state of the eyes is not always used as a cue by nonhuman primates to infer attention direction (e.g. Kaminski et al., 2004; Maille et al., 2012; Povinelli & Eddy, 1996), or when it is used it does not necessarily supplant head and body cues (e.g.

this study), has led some to contrast simple learning of cues to attention with actual understanding of visual attention (Gómez, 1998; Povinelli & Eddy, 1996). In this respect, it is likely that, owing to explicit training, baboons discriminated cues to the Eyes open condition as cues that increased the likelihood of getting the reward. However, neither visual orientating nor attention-getting behaviour was explicitly trained in the present study, yet it was flexibly adjusted to the visual attention of the experimenter. Baboons produced more visual gestures and visual orienting behaviours, but fewer attention-getting gestures when the experimenter could see them than when she could not. Whether baboons had implicitly learned these cues to attention during training or through prior experience, which may result in implicit knowledge of others' visual attention, is not possible to disentangle here. Whatever the operating process, it most probably led to an increased understanding of the conditions under which their communicative signals can be effective.

The use of acoustic communication (i.e. including vocalizations, nonvoiced sounds or bimodal communication such as visual/auditory-based gestures) as a means of attracting the attention of an otherwise inattentive partner has been reported in chimpanzees (Hopkins, Taglialatela, & Leavens, 2007; Hostetter et al. 2007; Leavens et al. 2004), although not found in all studies (Tempelmann et al., 2011; Theall & Povinelli, 1999). To our knowledge, our results are the first report of monkeys producing gestures as a means of elaborating communication that failed to elicit the desired outcome. We thus propose that baboons possess flexible communicative means that they can use with the same intent, although the present study did not systematically manipulate the expected outcome of the communicative exchange (but see Leavens et al., 2005). In contrast to a previous study that found baboons banged the cage as a result of frustration (Meunier et al., 2012), the behavioural pattern observed here does not result from thwarted communicative bids only, as evidenced by differential responses as a function of condition (owing to the fact that all experimental trials lasted for only 30 s and were systematically rewarded). Baboons produced more auditory-based gestures but fewer visual gestures when the experimenter could not see them, suggesting they might have used auditory communication as a substitute for visual communication to capture the attention of the experimenter.

This study brings critical insight to the interplay between intentional communication and social understanding through the primate lineage. Human infants (Liszkowski, Albrecht, Carpenter, & Tomasello, 2008) and chimpanzees (Hopkins et al., 2007; Hostetter et al., 2007; Leavens et al., 2004) are known to use vocalizations as a means of recruiting their partner's attention. Here, we emphasize that Old World monkeys are also capable of shifting to acoustic communication when the recipient is not visually attending. In contrast to human infants and chimpanzees, this acoustic communication is purely gestural, not vocal. This finding questions the evolutionary emergence of vocal intentional communication in the primate lineage. Intentional acoustic communication might have been 'scaffolded' onto the special intent to attract others' attention (see Falk, 2004), initially through gestural communication in Old World monkeys and progressively through both gestural and vocal communication in great apes, before turning out predominantly vocal in early humans. Future research may address this topical question of whether acoustic intentional communication might have appeared in evolution concomitantly to the understanding of another's attention.

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Supplementary Material

Supplementary material is available, in the online version of this article, at doi

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Appendix

Training of the subjects

All subjects took part in training trials. The procedure comprised three steps in which the experimenter stood in front of the cage of the focal subject holding a raisin in her open palm in front of the subject, while progressively increasing the distance to the cage. In the first step, the raisin was kept within the reach of the subject who extended one arm to grasp it in the experimenter's hand. In the second step, the distance increased up to the limit of being out of reach and the experimenter anticipated the attempt of the subject to reach the food in giving the subject the raisin each time the subject initiated an arm extension out of the cage. In the third step, the experimenter stood out of the subject's arm reach and went on giving the subject the raisin immediately after each initiation of arm extension. For the arm extensions being considered as begging gestures, we set postural criteria ensuring that manual actions were no longer mechanically effective: (1) the subject had not to try to grasp the raisin by rotating its shoulder so as to go further through the wire mesh; (2) the subject's fingers had to be extended in line with the hand and the arm. Subjects had to reach the criterion of 80% of valid gestures across three consecutive 10-trials sessions administered once a day.

Replication with novel experimenters

Two extra test sessions were performed with novel experimenters so as to exclude possible conditioned responses driven by the sight of the main experimenter. Baboons were presented once to a novel woman and once to a novel man in a 2 by 2 design relying on the experimenter's novelty (main experimenter versus novel experimenters first) and experimenter's sex (novel woman versus novel man first). Experimental procedure and data analysis were similar to those for the main experiment.

Baboons showed similar behavioural trends when they were tested with novel experimenters over two test sessions (see Appendix Fig. A1). They adjusted their begging behaviour to the visual attentional state of the experimenter (Main Model: AIC = 156.4; chi-square tests for the log-likelihood ratios: Main Model – Null Model: $P < 0.001$). Baboons produced significantly more gestures in the Eyes open than in the Back turned (Wald test: $z = -4.20$, $P < 0.001$) and Out (Wald test: $z = -6.47$, $P < 0.001$) conditions, but not in the Eyes closed condition (Wald test: $z = -1.14$, $P = 0.253$).

Body orientation by itself (Front/Back Model: AIC = 155.7) may consequently be a better predictor of subjects' responses than experimental conditions mixing both cues, although the two models did not differ significantly (chi-square tests for the log-likelihood ratios: Main Model – Front/Back Model: $P = 0.251$). However, the state of the experimenter's eyes was not an accurate predictor of the subjects' responses (Can see/Cannot see Model: AIC = 164.5; chi-square tests for the log-likelihood ratios: Main Model – Can see/Cannot see Model: $P < 0.010$).

These findings support the proposal that baboons' gestural communication is driven not by the sight of the food reward alone nor by the sight of the main experimenter who could have been associated with the delivery of the reward. We propose that baboons' begging gestures should be interpreted as genuine communicative attempts motivated by the presence of a partner whose cooperation is required to get the reward. Further testing is, however, needed to find out whether baboons processed well-known and novel faces differently and whether such differential treatment may explain why they did not rely on the state of the novel experimenter's eyes to adjust their communicative behaviour in this experiment.

Table 1. Summary of the models fitted for each dependent variable

Model name	Fixed effect	Random effect	AICc	ΔAICc	Significance
Dependent variable: number of begging gestures					
Null Model	None	Individual	812.10	510.11	***
Main Model	**Condition**	**Individual**	**301.99**	**0.00**	/
Time Model	Block, condition, block:condition	Individual:block	308.70	6.71	NS
Front/back Nested Model	Condition	Individual	305.19	3.20	*
Can see/cannot see Nested Model	Condition	Individual	356.19	54.20	***
Dependent variable: number of gaze alternation bouts					
Null Model	None	Individual	281.70	45.21	***
Main Model	**Condition**	**Individual**	**236.49**	**0.00**	/

Time Model	Block, condition, block:condition	Individual:block	246.40	9.91	NS
Front/back Nested Model	Condition	Individual	239.09	2.60	*
Can see/cannot see Nested Model	Condition	Individual	258.19	21.70	***
Dependent variable: number of attention-getting gestures					
Null Model	None	Individual:block	409.80	123.00	***
Main Model	Condition	Individual	297.89	11.09	***
Time Model	Block, condition, block:condition	Individual:block	290.20	3.40	NS
Front/back Nested Model	Condition, block, condition:block	Individual:block	289.40	2.60	***
Can see/cannot see Nested Model	**Condition, block, condition:block**	**Individual:block**	**286.80**	**0.00**	/

Interactions between two effects are represented by colons. Bold characters indicate the retained model for each dependent variable. AICc: Akaike information criterion with second-order correction; ΔAICc: difference between the AIC of model *i* and the AIC of the retained model. Chi-square tests for the log-likelihood ratios: *$P < 0.05$, ***$P < 0.001$.

Table A1. Subjects who participated in the study

Name	Sex	Age	Rearing history	Place of birth
Anelka	Male	6	Mother reared	Captivity
Katy	Female	16	Mother reared	Captivity
Marius	Male	14	Mother reared	Captivity
Momo	Male	14	Mother reared	Captivity
Oscar	Male	13	Mother reared	Captivity
Perfide	Female	12	Mother reared	Captivity
Prise	Female	12	Mother reared	Captivity
Raimu	Male	11	Mother reared	Captivity
Rambo	Male	11	Nursery	Captivity
Rodolphe	Male	11	Mother reared	Captivity
Sabine	Female	10	Mother reared	Captivity
Sestarde	Female	10	Mother reared	Captivity
Toti	Male	9	Mother reared	Captivity
Tulie	Female	9	Mother reared	Captivity
Ubu	Male	8	Mother reared	Captivity
Uranus	Male	8	Mother reared	Captivity

Table A2. Orders of exposure to experimental conditions

Subjects' group	First session	Second session	Third session	Fourth session
Group 1	Random order 1	Random order 2	Random order 3	Random order 4
Group 2	Random order 2	Random order 3	Random order 4	Random order 1
Group 3	Random order 3	Random order 4	Random order 1	Random order 2
Group 4	Random order 4	Random order 1	Random order 2	Random order 3

Random order 1: Eyes Open, Out, Eyes Closed, Back Turned; random order 2: Eyes Closed, Eyes Open, Out, Back Turned; random order 3: Eyes Closed, Out, Back Turned, Eyes Open; random order 4: Back Turned, Eyes Closed, Eyes Open, Out.

Figure captions

Figure 1. Begging gestures: (a) unimanual with the right hand and (b) bimanual.

Figure 2. Mean rate/min ± SEM of begging gestures for each experimental condition (*N* = 16 subjects).

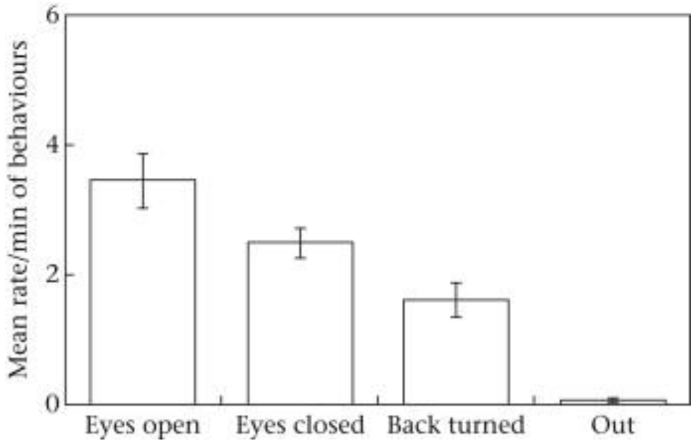

Figure 3. Mean rate/min ± SEM of gaze alternation bouts for each experimental condition (*N* = 16 subjects).

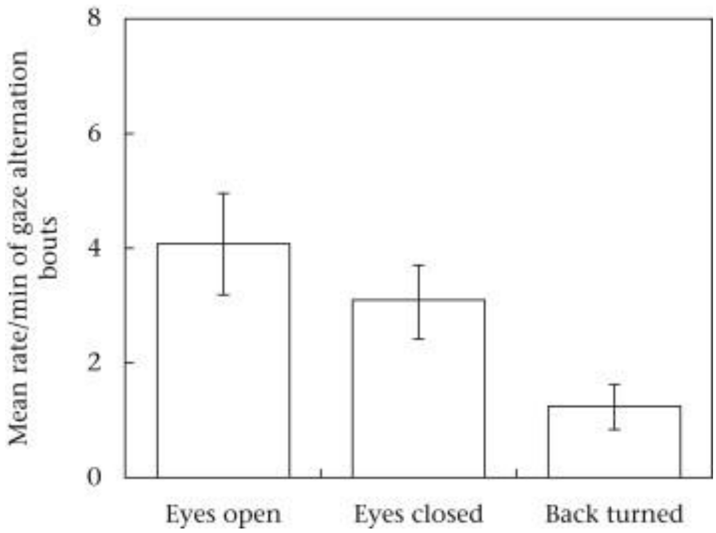

Figure 4. Mean rate/min ± SEM of attention-getting gestures depending on experimenter's visual attention during session block 1 (*N* = 16 subjects). One-sample permutation test: $*P < 0.05$.

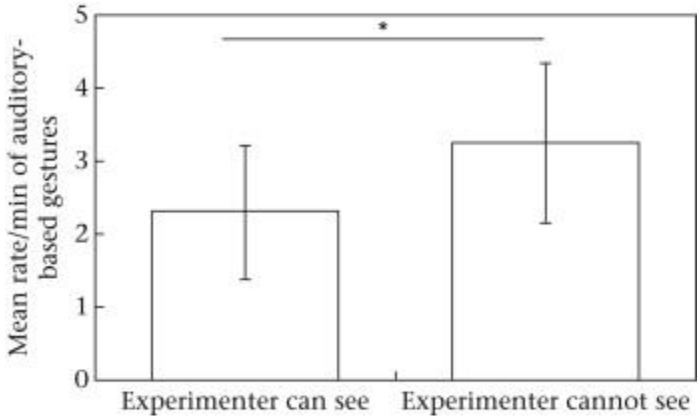

Figure 5. Percentages of visual and auditory-based gestures depending on experimenter's visual attention during session block 1 (N = 16 subjects). Fisher's exact probability test: ***P < 0.001.

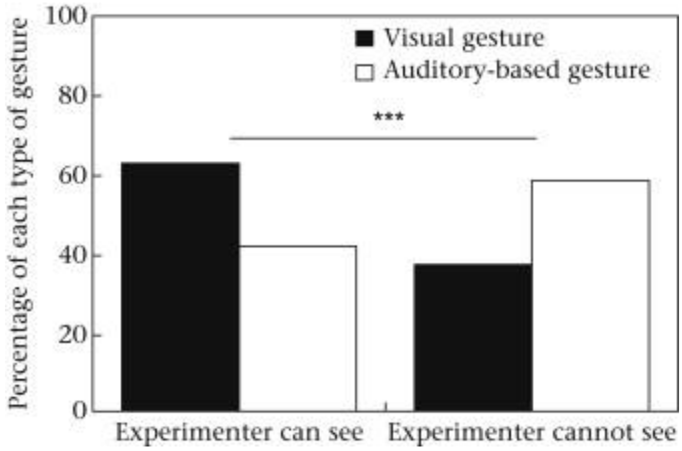

Figure A1. Mean rate/min ± SEM of begging gestures towards novel experimenters for each experimental condition (N=15 subjects).