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Training experience in gestures affects the display of social gaze in baboons' communication with a human

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Abstract Gaze behaviour, notably the alternation of gaze between distal objects and social partners that accompanies primates' gestural communication is considered a standard indicator of intentionality. However, the developmental precursors of gaze behaviour in primates' communication are not well understood. Here, we capitalized on the training in gestures dispensed to olive baboons (*Papio anubis*) as a way of manipulating individual communicative experience with humans. We aimed to delineate the effects of such a training experience on gaze behaviour displayed by the monkeys in relation with gestural requests. Using a food-requesting paradigm, we compared subjects trained in requesting gestures (i.e. trained subjects) to naïve subjects (i.e. control subjects) for their occurrences of (1) gaze behaviour, (2) requesting gestures and (3) temporal combination of gaze alternation with gestures. We found that training did not affect the frequencies of looking at the human's face, looking at food or alternating gaze. Hence, social gaze behaviour occurs independently from the amount of communicative experience with humans. However, trained baboons—gesturing more than control subjects—exhibited most gaze alternation combined with gestures, whereas control baboons did not. By reinforcing the display of gaze alternation along with gestures, we suggest that training may have served to enhance the communicative function of hand gestures. Finally, this study brings the first quantitative report of monkeys producing requesting gestures without explicit training by humans (controls). These results may open a window on the developmental mechanisms (i.e. incidental learning vs. training) underpinning gestural intentional communication in primates.

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Introduction

In *Elsa's eyes* (1942), the poet Louis Aragon sees the world reflected in his wife Elsa's eyes and senses the focus of her attention. This reference exemplifies that using another person's gaze is a hallmark of human behaviour. The ability to infer attention direction from others' eye gaze is of tremendous importance in infants' early development of communication skills (Bates et al. 1975; Franco and Butterworth 1996; Camaioni 2004). Mutual gaze through direct eye contact with adults arises in support of emotional engagement from 2 months onwards. Then, triadic gaze in reference to objects, i.e. gaze alternation between the object and the recipient—also referred to as "joint attention", develops at the end of the child's first year (see

Butterworth 2004, for a review). The combination of pointing gestures with this joint attention engagement is taken as strong evidence of intentional communication in infants (Bates et al. 1975; Desrochers et al. 1995; Butterworth 2004). It has been posited that the human eye, particularly visible with a white sclera surrounding the iris, has evolved special signal value to support such a form of communication, i.e. "the cooperative eye hypothesis" (Kobayashi and Kohshima 2001; Tomasello et al. 2007). In contrast, whether the less contrasted eye of nonhuman primates may hold signal value to conspecifics and may be an essential component of their communication has been questioned by many authors (Emery 2000; Kobayashi and Kohshima 2001; Tomasello et al. 2007).

Yet, there are accumulating clues as to the potential signal value of eye gaze in nonhuman primates (Davidson et al. 2014). In chimpanzees and orangutans for example, the direction of the head is often incongruent with the direction of the eyes during on-going interactions (Kaplan and Rogers 2002; Bethell et al. 2007). This suggests that eye gaze may have a specific function. The saliency of eyes can also be increased by some species-typical gazing behaviour (i.e. sideway glances in orang-utans, Kaplan and Rogers 2002) and by a large repertoire of facial expressions, which draw attention to the eyes (Van Hoof 1967; Redican and Rosenblum 1975) and have acquired specific signal functions (e.g. Maestripieri 2005; Visalberghi et al. 2006). In a wide variety of primate species, the eyes also convey mild threat signals via sustained stares at the addressees (Redican and Rosenblum 1975). Mutual gaze occurs within mother–infant dyads to sustain mutual engagement, albeit interchangeably with tactile stimulations (e.g. Japanese macaques: Ehardt and Blount 1984; chimpanzees: Bard et al. 2005).

Eye gaze and more generally gaze based on head direction has frequently been described in great apes in the context of referential intentional communication (see Leavens and Hopkins 1999, for a review). For example, Bard (1990) reported that juvenile orangutans beg their mother for food by looking back and forth between the mother's face and the food item. Other examples of apes alternating gaze to referentially communicate about distal entities has been reported in captive gorillas (e.g. Gomez 1994) and chimpanzees (e.g. Tomasello et al. 1985; Russell et al. 1997), but also in wild chimpanzees (Hobaiter et al. 2013). In captivity, great apes are indeed inclined to use point-like gestures to communicate with humans about objects, usually food items, and these gestures are accompanied by gaze alternation (Tomasello et al. 1985; Leavens and Hopkins 1999; Pika 2008; Liebal and Call 2012). Following the example of human infants, gaze alternation is considered to be a standard indicator of intentional communication in nonhuman primates

(Tomasello et al. 1994; Leavens 2004), as well as in dogs (Gaunet and Deputte 2011; Marshall-Pescini et al. 2013). Leavens and Hopkins (1998), Leavens et al. (1996, 2004, 2005a, b) systematically measured the association between communicative signals and gaze alternation by chimpanzees in food-requesting situations. The authors consistently found that gaze alternation was exhibited significantly more often by individuals who attempted to communicate about food using gestures or attention-getting vocalizations, than by those who did not. In great apes, gaze alternation is therefore concomitant with intentional communication.

Intentional communication has been recently addressed in monkeys too. Contrarily to great apes, monkeys undergo explicit training to acquire the use of requesting gestures, i.e. imperative gestures used to communicate with humans about food. Like apes, monkeys are then capable of using these gestural requests flexibly, with reference to the attentional state of the human (e.g. in squirrel monkeys: Anderson et al. 2010; in capuchins: Hattori et al. 2010; in mangabeys: Maille et al. 2012; in baboons: Meunier et al. 2013; Bourjade et al. 2014), indicating that one criterion of their intentional use is satisfied (Leavens 2004). These communicative exchanges are often accompanied by gaze alternation between the food and the human's face, which is considered as supporting evidence of their intentional nature (Mitchell and Anderson 1997; Kumashiro et al. 2002; Anderson et al. 2007; Meunier et al. 2013; Bourjade et al. 2014). For example, we previously demonstrated that olive baboons (*papio anubis*) were capable of tailoring both requesting gestures and auditory signals to the state of the eyes (open vs. closed) of a human recipient, and that this intentional gesturing was accompanied by gaze alternation between the food and the human's face (Bourjade et al. 2014). Notably, baboons exhibited gaze alternation in reference to the visual attention of the human. Several unsolved questions arose from this previous research. First, it appears unclear why monkeys need training to communicate with humans, while apes do not. Yet, to our knowledge, there is no quantitative data so far about the display of gestural requests and of gaze behaviour by nontrained captive monkeys. Second, it has not been clearly established whether and how such a training experience may affect not only gesture production, but also the exhibition of social gaze and their combination with gestures by trained monkeys.

Broadly speaking, the developmental precursors of gestures and social gaze in primates' communication are not well understood (see Leavens and Bard 2011, for detailed review). In human infants, the occurrence of pointing correlates with joint attention engagements (i.e. measured as occurrences of gaze alternation) at various ages (e.g. Carpenter et al. 1998). The proportion of

pointing accompanied by social gaze is higher for declarative than imperative pointing (Cochet and Vauclair 2010) and increases with age, suggesting that experience might play a significant role (Bates et al. 1975; Franco and Butterworth 1996). Using a training procedure, Matthews et al. (2012) showed that 9- to 11-months-old children trained to point did not produce more pointing but exhibited more pointing associated with gaze alternation than control children. Also, the appropriateness of adults' feedbacks to infants' pointing bids in naturally occurring interactions positively affects gestures production and social gaze of 12- to 16-month-old infants (Miller and Lossia 2013; Miller and Gros-Louis 2013).

In line with the pattern observed in human infants, the proportion of chimpanzees' pointing addressed to humans and associated with gaze alternation increases with apes' ages (Tomasello et al. 1985; Russell et al. 1997; Leavens and Hopkins 1998). This suggests that in chimpanzees too, the combination of social gaze with gestures develops through communicative experiences. In this respect, Bard et al. (2014) provided recent comprehensive evidence that postnatal engagement experiences with humans affected joint attention skills of captive chimpanzees. Thus, recent research suggests that gestures and social gaze may have intertwined and experience-dependent development in human and chimpanzee infants, while no comparable knowledge exists for monkeys yet.

Here, we addressed this question in captive olive baboons (*P. anubis*). The training in gestures dispensed to the monkeys appeared to be a dramatic opportunity to manipulate individual communicative experience with humans. Using a food-requesting paradigm, we compared gaze and gestural behaviour of individual baboons between 11 trained subjects (trained subjects hereafter) that participated in Bourjade et al. (2014) and 9 naïve subjects (control subjects hereafter) that had not been trained for requesting food from a human at the time of the study. We measured how this differential training experience later affected (1) the exhibition of gaze behaviour (i.e. gaze at the human's face, gaze at food and gaze alternation), (2) the sheer occurrence of requesting gestures, and (3) the temporal combination of gaze alternation with gestures.

One hypothesis derived from our previous results (Bourjade et al. 2014) is that baboons may incidentally learn to alternate gaze during the training in requesting gestures. Indeed, the training is usually performed by a responsive human facing and looking at the monkeys who systematically reinforces their requesting gestures with food rewards. In contrast to this explicit training, incidental learning of concurrent social gazes (whatsoever the primary motives of their display) might occur owing to gesture systematic reinforcement. Therefore, if training

experience is responsible for the display of gaze behaviour by baboons in front of a human, only trained subjects should exhibit gaze behaviour in the food-requesting situation. Alternatively, if gaze behaviour displayed by baboons in this situation predated the experience of being trained to gesture by a human, then both groups should exhibit gaze behaviour in the food-requesting situation. Additionally, if the amount of experience with humans is likely to affect baboons' joint attention skills like chimpanzees' ones, then trained subjects should exhibit higher abilities in combining gaze alternation with gestures than control subjects.

Methods

Subjects and housing conditions

Subjects were 20 olive baboons (*P. anubis*) raised at the Primate Station of the Centre National de la Recherche Scientifique (UPS 846, Rousset, France; number of agreement for conducting experiments on vertebrate animals: D13-087-7). Baboons, 11 males and 9 females ranging in age from 6 to 16 years, were tested between August 2011 and March 2012 (Table 1). Two distinct groups of subjects were involved. *Trained subjects* were 11 baboons (8 males and 3 females) that had been trained to produce requesting gestures by an experimenter facing them, and next participated in a study on intentional gesturing where the attentional state of the experimenter varied during testing (Bourjade et al. 2014). *Control subjects* were nine baboons (three males and six females) that had not yet been trained to request food from a human at the time of this study. After being used as controls in the present study, five subjects (i.e. Sabine, Sestarde, Tulie, Ubu and Uranus) were later trained and integrated into Bourjade et al. (2014)'s study. All subjects were mother-reared, except one (Rambo, see Table 1), and lived in reproductive social groups comprising one adult male, two to five adult females and their immature offspring. The baboons lived in 14-m² outdoor areas connected to 12-m² indoor areas. The enclosures were enriched by wooden roosts and vertical structures of different heights, both in the outdoor and in the indoor areas. Animals were fed by caretakers four times a day with industrial monkey pellets, seeds, fresh vegetables and fruits and water ad libitum. There was no other institutionalized interaction with humans out of food providing and medical interventions. All procedures complied with the current French law and the current European directive (reference 86/609/CEE) relative to the protection of animals used for scientific purposes.

Table 1 Individuals' characteristics, gestural and gaze alternation behaviour over the four test trials

Group	Ind	Sex	Age	Total number of GA (n)	Probability of GA/s	Total number of gestures (n)	Total time spent gesturing (s)	Theoretical number of GA with gestures	Probability of GA with gestures at chance level	Total number of GA with gestures (n)	p values of binomial tests
Trained	Anelka	Male	6	21	0.18	17	38	6.65	0.32	16	<0.001
Trained	Katy	Female	16	20	0.17	17	38	6.33	0.32	17	<0.001
Trained	Marius	Male	14	10	0.08	24	53	4.42	0.44	9	0.007
Trained	Momo	Male	14	20	0.17	22	59	9.83	0.49	16	0.006
Trained	Oscar	Male	13	18	0.15	25	53	7.95	0.44	17	<0.001
Trained	Perfide	Female	12	40	0.33	33	73	24.33	0.61	27	<0.001
Trained	Prise	Female	12	33	0.28	35	70	19.25	0.58	28	0.001
Trained	Raimu	Male	11	30	0.25	38	80	20.00	0.67	28	0.001
Trained	Rambo	Male	11	11	0.09	10	20	1.83	0.17	4	0.101
Trained	Rodolphe	Male	11	35	0.29	35	73	21.29	0.61	29	0.008
Trained	Toti	Male	9	23	0.19	28	62	11.88	0.52	17	0.038
	Trained			261[a]	0.20[b]	284[a]	619[a]	122.39[c]	0.47[d]	208[a]	<0.001
Control	Sabine	Female	10	33	0.28	0	0	0.00	0.00	0	–
Control	Sandra	Female	10	17	0.14	1	3	0.43	0.03	1	0.404
Control	Sestarde	Female	10	17	0.14	1	5	0.71	0.04	0	1.000
Control	Tulie	Female	8	28	0.23	12	24	5.60	0.20	9	0.152
Control	Tulipe	Female	9	37	0.31	7	15	4.63	0.13	7	0.322
Control	Ubu	Male	8	38	0.32	2	4	1.27	0.03	2	0.316
Control	Uranus	Male	8	35	0.29	0	0	0.00	0.00	0	–
Control	Vueï	Female	7	20	0.17	0	0	0.00	0.00	0	–
Control	Zampano	Male	8	22	0.18	0	0	0.00	0.00	0	–
	Control			247[a]	0.23[b]	23[a]	51[a]	11.66[c]	0.05[d]	19[a]	0.057

GA Gaze alternation bouts

[a] Sum of occurrences of all individuals over the four trials

[b] Sum of GA at group level divided by 120 s, multiplied by the number of individuals in the group

[c] Probability of GA/s at group level multiplied by the total time spent gesturing at group level

[d] Theoretical number of GA with gestures at group level divided by the sum of GA at group level

Apparatus

Prior to each test session, a concrete block (90 cm height) was placed inside the cage perpendicularly to the mesh so that when subjects were seated on it, they could look at the experimenter's face and gesture at about the height of a person. The mesh was equipped with a 10 × 60 cm opening. During testing, a Plexiglas panel (80 × 35 cm) with two holes (10 × 15 cm) separated by 25 cm from centre to centre was fixed over the opening so that baboons could pass their arms through each hole (Fig. 1). This panel facilitated subsequent recording of baboons' gestures on video footages: baboons begged through the holes in the presence of 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.

Training procedure

Only trained subjects learnt to beg through one of the holes of the Plexiglas panel to request the food reward held in the experimenter's hand. The training was performed by an experimenter standing in front of the cage, looking at the focal subject and holding a raisin in open palm out in front of the subject. The training consisted of progressively increasing the distance to the subject, while anticipating its grasping attempts. Ten training trials were presented to the monkeys per training session. Training sessions were performed at various distances from the cage according to a three-step procedure. 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 attempts of the subject to reach the food in giving the subject the raisin each time the
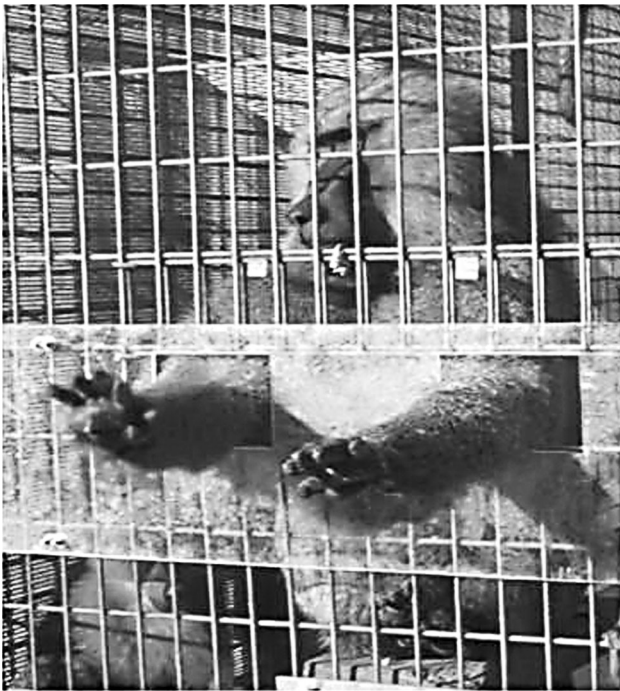
Fig. 1 Apparatus used in the food-requesting paradigm

subject initiated an arm extension out of the cage. In the third step, the experimenter stood out of the subject's arm reach and kept on giving the subject the raisin immediately after each initiation of arm extension. Each subject moved on to the next step when it consistently extended one (or two) arm(s) towards the raisin over the ten training trials performed at a given distance. When subjects refused to extend an arm, training trials were immediately resumed at the distance corresponding to the previous step.

From the third step, in order to specify requesting gestures from rough arm extensions, we considered as "valid" only the gestures for which (1) the subject did not try to grasp the raisin by rotating its shoulder so as to go further through the wire mesh, and (2) the subject's fingers were extended in line with the hand and the arm. Subjects had to reach the criterion of 80 % of valid gestures across three consecutive third-step training sessions administered once a day. Trained baboons needed in average 12 ± 1 training sessions spread over 22.3 ± 3.5 days to reach the criterion.

Testing procedure

Both trained and control subjects were presented with exactly the same test condition; during test trials, the experimenter stood 1 m in front of the cage holding a piece of banana in one hand, facing and looking at the subject. This condition corresponds to the "Eyes open" condition of Bourjade et al. (2014). Note that the experimenter did not stare at the baboons but looked alternately to the eyes

and the upper part of the nose so as to avoid possible fear reactions. Each test trial lasted 30 s, after which the experimenter gave the subject the piece of banana regardless of its behaviour during the trial. All subjects received a total of four test trials. For trained subjects, test trials (of the "Eyes open" condition considered in this study) had been presented once in either first, second, third or fourth positions of the four test trials dispensed per session and per day (see Bourjade et al. 2014). Two "motivation" trials had also been given to trained subjects between each test trial in order to renew their motivation and to refresh the training in gestures. These motivation trials were performed the same way as test trials except that the piece of food was given in response to the first gestural request (i.e. as in third-step training sessions). For control subjects, the four test trials were not spread over different days so as to avoid learning in the course of the experiment due to spacing effect of training trials (e.g. Sisti et al. 2007). Control baboons were not either exposed to "motivation" trials and the next test trial took place once they had eaten the reward. The four test trials were therefore presented in a raw. As the timing of test trials inevitably differed between the two groups, we checked it had no impact on baboons' behaviour by comparing the occurrences of all behaviour types between the first and last test trials of each group (one-sample permutation tests: $p > 0.05$ for all behaviour types considered; see Online Resources 1) and by designing statistical models with the number of the test trial as a fixed effect for each dependent variable (see *Time models*, Online Resources 2 and 3, and the results section below).

Data scoring and reliability

Two different types of behaviour were observed and scored on the videos for further analysis. First, *requesting gestures* consisted of extending one or two arm(s) with fingers and hand(s) being in line with the arm(s). A first main observer (Coder 1, BR) coded all occurrences of requesting gestures at the normal speed of 30 frames/s using VLC media player. A requesting gesture set out 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's wrist was brought back inside the cage. Second, *gaze behaviour* took the form of (1) gazing at the experimenter's face, (2) gazing at the food and (3) gaze alternation between the experimenter's face and the food. A gaze was defined as a visual fixation terminated by blinking or directing the eyes to a new location (Kaplan and Rogers 2002). We considered gaze alternation bouts as any series of two consecutive gazes minimum alternating between the experimenter's face and the piece of banana, without blinking or directing the eyes to another location.

Before coding gaze behaviour, all videos were slightly transformed in the software Avidemux 2.5 (32-bit) using the following procedure. A crop filter was first applied to zoom in and centre the face of the subject on the screen. The brightness was then adjusted so as to distinguish the eyes that could be in the shade of the baboon's prominent eyebrows. Another main coder (Coder 2, CC) coded all occurrences of each gaze behaviour type frame by frame (one frame = 0.033 s). Reliability was assessed using Cohen's Kappa, k, in which the observed agreement between two observers is corrected for the agreement by chance alone (Martin and Bateson 2007). Amongst the total number of test trials, 65 (25 %) were randomly assigned to three novel coder (Coder 3, BF; Coder 4, CP; Coder 5, MA) who were blind to the hypotheses of the current paper. Coder 3 (40 trials) and Coder 5 (25 trials) recoded requesting gestures. Coder 4 (40 trials) and Coder 5 (25 trials) recoded gaze behaviour. Reliability was assessed between the output of Coder 1 and the additive outputs of Coders 3 and 5 for the number of requesting gestures (Cohen's $k = 0.78$), and between the output of Coder 2 and the additive outputs of Coders 4 and 5 for the number of occurrences of gaze behaviour (Cohen's $k = 0.77$). The duration of gaze behaviour (with gazes at the experimenter's face and at food pooled together) was also compared between Coder 2 and Coder 4 (40 trials) using a Pearson's correlation, which was highly significant (Pearson's $r = 0.89$, $t = 64.00$, $p < 0.001$).

Statistics

We used an approach of multimodel inference to determine which factors most affected subjects' gestural and gaze behaviour (Burnham and Anderson 2004). We processed the number of requesting gestures, the number and duration of gaze at the human's face, the number and duration of gaze at the food, and the number of gaze alternation bouts produced by the 20 subjects over all the four test trials. We followed a three-step procedure (detailed in Online Resource 2): (1) we fitted several models with either the main factor (training: *Main model*) or the confounding factors (subjects' sex: *Sex model*; test trials: *Time model*), or the interaction between the two (subjects' sex × training: *Interaction model*) as fixed effects; (2) we selected the model that best fitted the observed data for each behavioural variable; and (3) we performed tests of significance on the retained models using Chi-square tests of the log-likelihood ratios (Brown and Prescott 2006). We fitted generalized linear mixed models on each behavioural dependent variable with a *Poisson family* adapted to count data and a *log link function* (Brown and Prescott 2006). Pseudoreplication caused by repeated observations of the same individual was taken into consideration by adding the

individual as a random effect. Best fitting models were selected on the basis of the lowest AICc (i.e. Akaike information criterion corrected), which applies a second-order correction adapted to small samples (Burnham and Anderson 2004).

For studying the combination of gaze alternation with gestures, we determined the duration that each subject spent gesturing over the 120 s of test trials and calculated the theoretical probability of observing one gaze alternation exhibited during one gesture at chance level (Table 1). Theoretical probabilities were calculated by multiplying the time spent gesturing (in seconds) by the probability of observing an occurrence of gaze alternation per second and divided by the observed total number of gaze alternation bouts. We then performed binomial tests on the proportion of gaze alternation bouts exhibited during a gesture for each individual and at group level. Spearman correlations coefficients were applied to the number of requesting gestures and the number of gaze alternation bouts for each group. All tests were two-tailed and were performed with R 3.1.0 software (http://cran.r-project.org) with level of significance set at 0.050.

Results

Gestural behaviour

The training (trained group vs. control group) was the main factor explaining the variance of the number of requesting gestures (best fitting model: AIC = 110.2, see Online Resources 3; Chi-square tests for the log-likelihood ratios, best fitting model–null model, $p < 0.001$). Baboons trained to request food by a human produced up to ten times more requesting gestures than control subjects (Wald test: $z = 6.94$, $p < 0.001$). Importantly, of the nine control subjects, five individuals did produce some requesting gestures (Fig. 2): one male (Ubu) produced 2 requests, and four females produced 1 (Sestarde), 1 (Sandra), 7 (Tulipe) and 12 (Tulie) requesting gestures, respectively (Table 1). The remaining four control subjects did not gesture.

Frequency of gaze behaviour

None of the factors tested explained significant variance in the number of looks at the human's face, the number of looks at food and the number of gaze alternation bouts. The model that best fitted to the number of looks at the human's face did not significantly differ from the null model (*Sex model*: AIC = 153.6, see Online Resource 3; Chi-square tests for the log-likelihood ratios, best fitting model–null model, $p = 0.098$). As for the number of looks at food (null model: AIC = 134.6) and the number of gaze
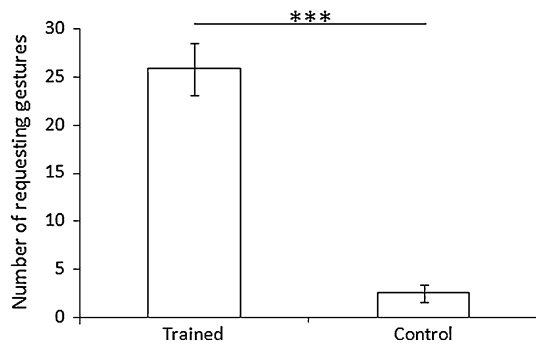
Fig. 2 Mean number (±SEM) of requesting gestures by trained and control baboons. Wald test, ***$p < 0.001$

alternation bouts (null model: AIC = 98.72), none of the models designed with either training (trained vs. control groups), subject's sex, and test trial, better fitted to the observed data than the null model. There was therefore no significant effect of the training on the number of looks at the human's face and at food (Fig. 3a), and on the number of gaze alternation bouts recorded in trained subjects (mean number ± SEM = 23.73 ± 2.92), and in control subjects (mean number ± SEM = 27.44 ± 2.87; Fig. 4).

Duration of gaze behaviour

The time spent looking at the human's face was best approximated by the model that had the training and the test trial as fixed effects (*Time model*: AIC = 415, see Online Resource 3; Chi-square tests for the log-likelihood ratios, best fitting model–null model, $p < 0.001$). However, neither the effect of the training (Wald test—all test sessions, $z = -0.25$, $p = 0.801$), and of test trial (Wald tests—both groups, trial 1–trial 2: $z = 1.82$, $p = 0.069$; trial 1–trial 3: $z = 0.02$, $p = 0.986$; trial 1–trial 4: $z = -0.92$, $p = 0.356$), nor the interaction between the two (Wald tests—between groups, trial 1–trial 2: $z = -1.35$, $p = 0.176$; trial 1–trial 3: $z = 0.12$, $p = 0.902$; trial 1–trial 4: $z = 0.77$, $p = 0.443$) reached significance (Fig. 3b).

Likewise, the time spent looking at food was best approximated by the model that had the training and the test trial as fixed effects (*Time model*: AIC = 380.3, see Online Resource 3; Chi-square tests for the log-likelihood ratios, best fitting model–null model, $p < 0.001$). The training affected the time spent looking at food, with trained baboons looking longer at food than control baboons (Wald test—all test trials: $z = 3.20$, $p = 0.001$; Fig. 3b). Neither the test trial (Wald tests—both groups, trial 1–trial 2: $z = 1.45$, $p = 0.148$; trial 1–trial 3: $z = 0.23$, $p = 0.822$; trial 1–trial 4: $z = -0.08$, $p = 0.940$), nor the interaction between training and test trial (Wald tests—between groups, trial 1–trial 2: $z = -0.27$, $p = 0.785$; trial 1–trial 3: $z = -1.11$, $p = 0.266$;
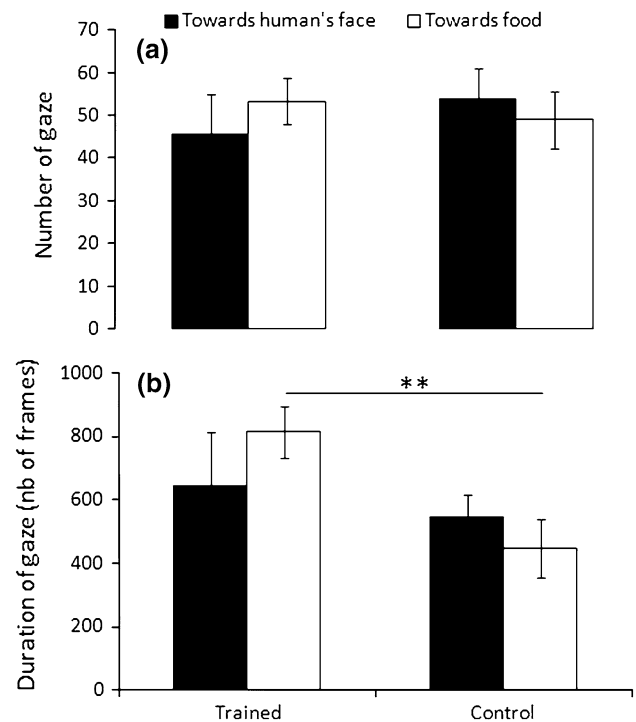

Fig. 3 Gaze behaviour towards the human's face and the food by trained and control baboons; **a** mean number (±SEM) of looks, **b** mean duration (±SEM) of looks expressed in number of frames; Wald test, **$p < 0.01$

trial 1–trial 4: $z = -0.10$, $p = 0.917$) affected the duration of looks at food.

Combination of gaze alternation with gesture

Trained subjects exhibited significantly more gaze alternation bouts with gesture than expected at chance level (Binomial test, $p < 0.001$; Fig. 4). This significant combination of gaze alternation with gestures was found in 10 out of the 11 trained subjects (Table 1). Although there was a tendency for the five control subjects to display gaze alternation in combination with gestures, the observed number of gaze alternation bouts exhibited with gestures did not significantly differ from chance (Binomial test, $p = 0.057$). None of the five control subjects producing gestures displayed combination of gaze alternation with gestures significantly above chance, possibly due to low statistical power (Table 1). Additionally, there was a positive correlation between the number of gaze alternation bouts and the number of gestures produced by trained subjects (Spearman correlation coefficient, rs = 0.72, $p = 0.015$). No such relationship was found in control subjects (Spearman correlation coefficient, rs = 0.24, $p = 0.531$) (Fig. 5).
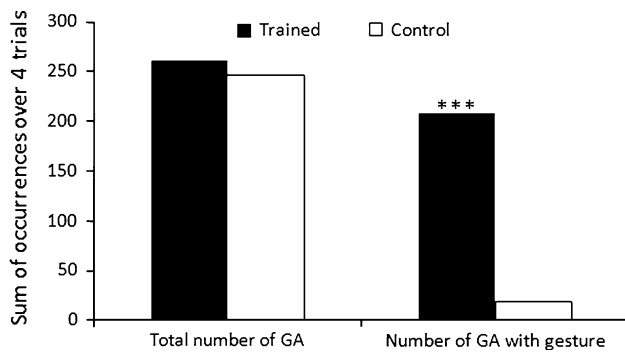
Fig. 4 Gaze alternation bouts (GA) in trained and control baboons; Binomial test, ***$p < 0.001$
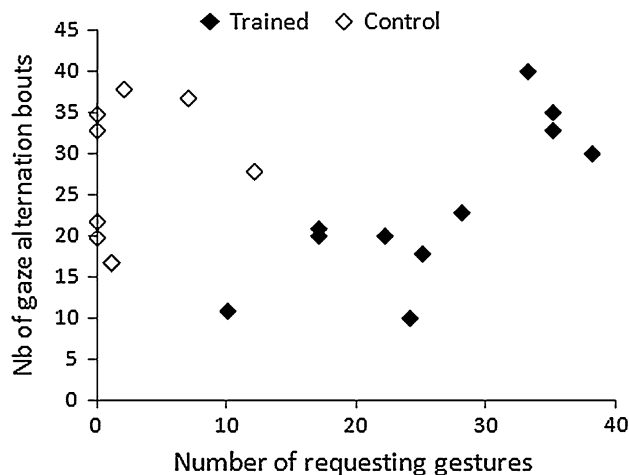

Fig. 5 Number of gaze alternation bouts as a function of the number of gestures, *filled diamond* trained subjects, *open diamond* control subjects

Discussion

To our knowledge, these results are the first quantitative report on the effects of differential training experience on monkeys' communicative behaviour in food-requesting situations. Unexpectedly, control baboons produced a few requesting gestures by their own—though in average ten times fewer than trained subjects. If training in gestures expectedly influenced gestural production, it did not affect baboons' gaze behaviour frequencies. This contradicts our hypothesis that gaze alternation may have been incidentally learnt by baboons during the training. However, the training in gestures led to a specific pattern of gaze alternation in relation to gestural requests; trained baboons exhibited gaze alternation combined with their gestures above chance level. These findings shed light on the manner that particular experience can shape monkeys' socio-cognitive skills.

The display of food-requesting gestures has been well documented in captive great apes who had been trained in

some kind of communication with humans (e.g. human sign language, pointing to the keys of a keyboard) and later on, started to use them flexibly in a variety of contexts (see Tomasello and Call 1997; Pika 2008, for reviews). Like-wise, monkeys' requesting gestures have been recently described when explicit training was performed by humans in specific contexts (Anderson et al. 2010; Hattori et al. 2010; Maille et al. 2012; Meunier et al. 2013; Bourjade et al. 2014), whereas reports of naturally occurring gestural requests remain anecdotic (Hess et al. 1993; Kumashiro et al. 2002; Meguerditchian and Vauclair 2009). Here, we report the case of five olive baboons that gestured towards the human, while none of them had been explicitly trained to do that. Four of the five subjects were female baboons and only one was housed with an adult male (Toti) that had been trained to request food. It is thus unlikely that these females socially learnt to request food by observing others doing so. This raises the question of the various forms of learning that can be derived from experience. Note that we have called *incidental* learning in this study the possibility that baboons associate a behaviour B (gaze) to a behaviour A (gesture) that was systematically reinforced. It is *incidental* because reinforcement of the behaviour B would have not been systematic as for behaviour A, though reinforcement could have occurred frequently enough for an association to be formed. In this respect, different forms of incidental learning might occur out of experimental contexts thanks to the daily exposure of baboons to their caretakers. Such other forms of incidental learning with humans may have led to differential gestural behaviour in control baboons, and trained baboons as well. Importantly, further investigation is needed to tease apart the role of experience, of individual intrinsic factors (e.g. dominance rank, sex, or genetically predisposed skills) and of their interplay in monkeys' propensity to communicate with humans. Note, however, that without training, roughly half of control baboons gestured, a proportion that equals that of institutionalized chimpanzees that do point (Leavens and Bard 2011). Although chimpanzees' pointing may be more sophisticated regarding spatial reference to the target and manual dexterity than baboons' requesting gestures—and therefore that these two behaviours might differ substantially—this suggests that both gestures might share common developmental mechanisms. Ontogenetic ritualization is a candidate mechanism for the development of these gestures by chimpanzees and baboons through multiple interactions with human partners (e.g. Tomasello and Call 1997).

Consequently, it may be hypothesized that the different abilities of chimpanzees and baboons to communicate with humans about food mostly rely on differential experience with interacting humans. This offers substantial support to the fact that trained baboons differ quantitatively rather

than qualitatively from control baboons regarding this competence. To some extent, these observations support previous findings about the effects of intensive exposure to humans on cognitive abilities, i.e. the so-called enculturation (Call and Tomasello 1996; Tomasello and Call 1997). In several studies, human-reared or language-trained apes outperformed their standard-reared captive counterparts in social cognition experiments (e.g. Call and Tomasello 1994; Lyn et al. 2010; Russell et al. 2011; Bard et al. 2014). It appeared to be also the case for one Japanese macaque that pointed towards food, but also towards a TV screen while watching a movie with a human (Kumashiro et al. 2002). Similarly, our data suggest that postnatal experience can affect later cognitive outcomes such as the production of requesting gestures by monkeys (see Leavens and Bard 2011 for a review). Indeed, monkeys' gestures that mostly result from explicit training by humans are then sensitive to the presence and visual attention of an audience and are associated with behavioural indicators of intentionality such as gaze alternation (Kumashiro et al. 2002; Anderson et al. 2010; Meunier et al. 2013; Bourjade et al. 2014).

We were specifically concerned with the acquisition of gaze behaviour in monkeys' communication. Our results suggest that social gaze behaviour occurs independently from the amount of communicative experience with humans. Indeed, training experience did not affect the frequencies of looking at the human's face, looking at food and alternating gaze, although the time spent looking at food increased. During training, baboons could have formed associations between the experimental setup and the specific outcome of obtaining food rewards (Watanabe et al. 2001). This might explain why trained subjects spent longer time looking at food than control subjects, which had not been exposed to the same possibility of obtaining food rewards. The duration of looks may hence reveal differential attentional biases related to the strength of the subject's food expectations (e.g. Watanabe et al. 2001; Bräuer et al. 2006; Dufour et al. 2007). Interestingly, the training also led to a specific pattern of gaze alternation in relation to gestural requests. Trained baboons exhibited gaze alternation combined with gestures above chance level, whereas control baboons did not. This suggests that the temporal combination of gaze alternation with gestures results from learning processes that operated during the training. Moreover, the occurrence of gestures correlates with the incidence of gaze alternation in trained baboons, but not in controls. The training had thus purposely systematized the use of requesting gestures, with the shaping of gaze behaviour patterns as a by-product, perhaps by enhancing the communicative function of hand gestures. In sum, the combination of gaze alternation with gestures in baboons relies on a particular learning operated during the

training, which may be intertwined with the development of hand gestures, although the development of these skills as experience progresses remains an essential question that needs further investigation.

The function of gaze alternation remains nevertheless equivocal. Following the literature on intentional gestural communication, gaze alternation may serve monitoring functions of the communicative exchanges (e.g. Bates et al. 1975; Butterworth 2004; Camaioni 2004; Leavens 2004). Trained baboons may have checked whether (1) the partner was attentive and/or, (2) their gestures were efficient. However, it is unlikely that gaze alternation by control baboons served as a means to monitor their gestural signals because such signals were virtually absent for many of them (i.e. zero or one requesting gestures). It remains possible that baboons monitored the human's gaze direction by virtue of an associative learning between gaze directed at them and food delivery. Such an association might have been incidentally learnt (in the two groups) during repetitive exposure to food provision by human caretakers and reinforced by training experience. Under this hypothesis, gaze alternation would result from an attentional conflict between the reflexive attraction for food and the voluntary attention paid to the human's face. However, owing to explicit training, we expected this association between human's directed gaze and food delivery to be stronger in trained than in control baboons. The reason why control baboons displayed as much gaze alternation as trained baboons is therefore not straightforward under this hypothesis. Lastly, gaze alternation may serve communicative functions. For instance, it naturally occurs during intraspecific conflict interactions where a threatened baboon uses quick glances between its aggressor and a potential helper to request help during the conflict (Packer 1977; Whiten and Byrne 1988). In this context, gaze alternation might be used to recruit assistance from the helper, in reference to the opponent. One could argue that similar function was achieved here. Gaze alternation would primarily serve social recruitment, referentially (see Leavens and Hopkins 1999; Lock 2004), and thus play an essential role in intentional visual communication. Both control and trained baboons would be likely to display gaze alternation to recruit the assistance of the human in reference to inaccessible food. Furthermore, gaze alternation clumped together with gestures in trained baboons might reflect that these behaviours stem from the same motive; that is acting upon the human to secure inaccessible food (i.e. The Referential Problem Space, Leavens 2005). In sum, the resulting pattern of gaze behaviour might reveal either the expectation of securing inaccessible food by the baboons, or a way of acting upon this expectation, or both. However, more research is needed to draw any conclusion about the signal value of gaze alternation. Indeed, if gaze

alternation was driven by noncommunicative motives, it would still stand as a social cue possibly perceived and used by others to infer the target (i.e. reference) of the emitter's attention.

By comparing baboons trained to gestures with baboons not trained to do so, this study enabled to delineate the effects of training in gestures on monkeys' communicative behaviour in a food-requesting situation. Whatever the function of gaze alternation, its display is clearly affected by previous experience in gestural communication with humans. This is important knowledge for the field of human and nonhuman primates' gestural communication. Although our study is not purely developmental, the communicative skills obtained in trained baboons after roughly 3 weeks of intensive experience with humans are reminiscent to human infants' communicative features in several ways. Note for instance that the incidence of gestures and gaze alternation correlates in developing children (e.g. Carpenter et al. 1998) as in baboons (this study) and that children trained to point exhibit more pointing associated with gaze alternation than control children (Matthews et al. 2010), like baboons in this study. It may be argued that the systematic reinforcement performed in explicit training mimics in some ways the reinforcements operated by highly responsive adults in free interactions with infants, as these two factors predict the display of social gaze in 9- to 11-month-old human infants (Matthews et al. 2010).

This study stresses that differential reinforcements, like differential degree of communicative experience, may therefore partly underpin the huge interindividual differences observed in primates developing joint attention skills (Leavens and Bard 2011 for a discussion on the onset of these behaviours), within species, but also between two different species like chimpanzees and baboons. In consequence, we suggest that monkeys may be valuable model species to open a window on the developmental mechanisms underpinning primates' gestural intentional communication.

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