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

Marie Bourjade^{1,2}, Charlotte Canteloup², Adrien Meguerditchian^{1,2}, Jacques Vauclair³ & Florence Gaunet¹

¹ Aix-Marseille Université, Centre National de la Recherche Scientifique (CNRS), Laboratoire de Psychologie Cognitive (UMR 7290), Marseille, France

² Station de Primatologie (UPS 846), Centre National de la Recherche Scientifique, Rousset, France

³ Research Centre in the Psychology of Cognition, Language and Emotion, Aix-Marseille Université, Aix-en-Provence, France

Corresponding author:

M. Bourjade, Laboratoire de Psychologie Cognitive (UMR 7290), Aix-Marseille Université, 3 place Victor Hugo, 13331 Marseille Cedex 3, France

E-mail addresses: marie.bourjade@univ-amu.fr, marie.bourjade@gmail.com

Telephone number: +033 4 42 99 24 59

Fax number: +0033 4 42 29 40 44

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

20

21 **Keywords:** Gaze alternation, Requesting gestures, Referential communication, Joint attention,
22 Intentionality, Nonhuman primates

23

24

25 In *Elsa's eyes* (1942) the poet Louis Aragon sees the world reflected in his wife Elsa's eyes and senses
26 the focus of her attention. This reference exemplifies that using another person's gaze is a hallmark
27 of human behaviour. The ability to infer attention direction from others' eye gaze is of tremendous
28 importance in infants' early development of communication skills (Bates et al. 1975; Franco and
29 Butterworth 1996; Camaioni 2004). Mutual gaze through direct eye contact with adults arises in
30 support of emotional engagement from two months onwards. Then, triadic gaze in reference to
31 objects, i.e. gaze alternation between the object and the recipient – also referred to as “joint
32 attention”, develops at the end of the child's first year (see Butterworth 2004 for a review). The
33 combination of pointing gestures with this joint attention engagement is taken as strong evidence of
34 intentional communication in infants (Bates et al. 1975; Desrochers et al. 1995; Butterworth 2004). It
35 has been posited that the human eye, particularly visible with a white sclera surrounding the iris, has
36 evolved special signal value to support such a form of communication, i.e. “the cooperative eye
37 hypothesis” (Kobayashi and Kohshima 2001; Tomasello et al. 2007). In contrast, whether the less
38 contrasted eye of nonhuman primates may hold signal value to conspecifics and may be an essential
39 component of their communication has been questioned by many authors (Emery 2000; Kobayashi
40 and Kohshima 2001; Tomasello et al. 2007).

41 Yet, there are accumulating clues as to the potential signal value of eye gaze in nonhuman
42 primates (Davidson et al. in press). In chimpanzees and orangutans for example, the direction of the
43 head is often incongruent with the direction of the eyes during on-going interactions (Kaplan and
44 Rogers 2002; Bethell et al. 2007). This suggests that eye gaze may have a specific function. The
45 saliency of eyes can also be increased by some species-typical gazing behaviour (i.e. sideways glances
46 in orang-utans, Kaplan and Rogers 2002) and by a large repertoire of facial expressions, which draw
47 attention to the eyes (Van Hoof, J. 1967; Redican and Rosenblum 1975) and have acquired specific
48 signal functions (e.g., Maestriperi 2005; Visalberghi et al. 2006). In a wide variety of primate species,
49 the eyes also convey mild threat signals via sustained stares at the addressees (Redican and
50 Rosenblum 1975). Mutual gaze occurs within mother-infant dyads to sustain mutual engagement,

51 albeit interchangeably with tactile stimulations (e.g. Japanese macaques: Ehardt and Blount 1984;
52 chimpanzees: Bard et al. 2005).

53 Eye gaze, and more generally gaze based on head direction has frequently been described in
54 great apes in the context of referential intentional communication (see Leavens and Hopkins 1999
55 for a review). For example, Bard (1990) reported that juvenile orangutans beg their mother for food
56 by looking back and forth between the mother's face and the food item. Other examples of apes
57 alternating gaze to referentially communicate about distal entities has been reported in captive
58 gorillas (e.g. Gomez 1994) and chimpanzees (e.g. Tomasello et al. 1985; Russell et al. 1997), but also
59 in wild chimpanzees (Hobaiter et al. 2013). In captivity, great apes are indeed inclined to use point-
60 like gestures to communicate with humans about objects, usually food items, and these gestures are
61 accompanied by gaze alternation (Tomasello et al. 1985; Leavens and Hopkins 1999; Pika 2008; Liebal
62 and Call 2012). Following the example of human infants, gaze alternation is considered to be a
63 standard indicator of intentional communication in non-human primates (Tomasello et al. 1994;
64 Leavens 2004), as well as in dogs (Gaunet and Deputte 2011; Marshall-Pescini et al. 2013). Leavens et
65 al. (1996; 1998; 2004; 2005) systematically measured the association between communicative signals
66 and gaze alternation by chimpanzees in food-requesting situations. The authors consistently found
67 that gaze alternation was exhibited significantly more often by individuals who attempted to
68 communicate about food using gestures or attention-getting vocalizations, than by those who did
69 not. In great apes, gaze alternation is therefore concomitant with intentional communication.

70 Intentional communication has been recently addressed in monkeys too. Contrarily to great
71 apes, monkeys undergo explicit training to acquire the use of requesting gestures, i.e. imperative
72 gestures used to communicate with humans about food. Like apes, monkeys are then capable of
73 using these gestural requests flexibly, with reference to the attentional state of the human (e.g. in
74 squirrel monkeys: Anderson et al. 2010; in capuchins: Hattori et al. 2010; in mangabeys: Maille et al.
75 2012; in baboons: Meunier et al. 2013; Bourjade et al. 2014), indicating that one criterion of their

76 intentional use is satisfied (Leavens 2004). These communicative exchanges are often accompanied
77 by gaze alternation between the food and the human's face, which is considered as supporting
78 evidence of their intentional nature (Mitchell and Anderson 1997; Kumashiro et al. 2002; Anderson
79 et al. 2007; Meunier et al. 2013; Bourjade et al. 2014). For example, we previously demonstrated
80 that olive baboons (*papio anubis*) were capable of tailoring both requesting gestures and auditory
81 signals to the state of the eyes (open vs. closed) of a human recipient, and that this intentional
82 gesturing was accompanied by gaze alternation between the food and the human's face (Bourjade et
83 al. 2014). Notably, baboons exhibited gaze alternation in reference to the visual attention of the
84 human. Several unsolved questions arose from this previous research. First, it appears unclear why
85 monkeys need training to communicate with humans, while apes do not. Yet, to our knowledge there
86 is no quantitative data so far about the display of gestural requests and of gaze behaviour by non-
87 trained captive monkeys. Second, it has not been clearly established whether and how such a
88 training experience may affect not only gesture production, but also the exhibition of social gaze and
89 their combination with gestures by trained monkeys.

90 Broadly speaking, the developmental precursors of gestures and social gaze in primates'
91 communication are not well understood (see Leavens and Bard 2011 for detailed review). In human
92 infants, the occurrence of pointing correlates with joint attention engagements (i.e., measured as
93 occurrences of gaze alternation) at various ages (e.g., Carpenter et al. 1998). The proportion of
94 pointing accompanied by social gaze is higher for declarative than imperative pointing (Cochet and
95 Vauclair 2010) and increases with age, suggesting that experience might play a significant role (Bates
96 et al. 1975; Franco and Butterworth 1996). Using a training procedure, Matthews et al. (2012)
97 showed that 9- to 11-months-old children trained to point did not produce more pointing but
98 exhibited more pointing associated with gaze alternation than control children. Also, the
99 appropriateness of adults' feedbacks to infants' pointing bids in naturally occurring interactions
100 positively affects gestures production and social gaze of 12- to 16-month old infants (Miller and
101 Lossia 2013; Miller and Gros-Louis 2013).

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

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

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

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

133

134 **Methods**

135

136 Subjects and housing conditions

137

138 Subjects were 20 olive baboons (*Papio anubis*) raised at the Primate Station of the Centre National
139 de la Recherche Scientifique (UPS 846, Rousset, France; Number of agreement for conducting
140 experiments on vertebrate animals: D13-087-7). Baboons, 11 males and 9 females ranging in age
141 from 6 to 16 years, were tested between August 2011 and March 2012 (Table 1). Two distinct groups
142 of subjects were involved. *Trained subjects* were 11 baboons (8 males and 3 females) that had been
143 trained to produce requesting gestures by an experimenter facing them, and next participated in a
144 study on intentional gesturing where the attentional state of the experimenter varied during testing
145 (Bourjade et al. 2014). *Control subjects* were 9 baboons (3 males and 6 females) that had not yet
146 been trained to request food from a human at the time of this study. After being used as controls in
147 the present study, five subjects (i.e., Sabine, Sestarde, Tulie, Ubu, Uranus) were later trained and
148 integrated into Bourjade et al. (2014)'s study. All subjects were mother-reared, except one (Rambo,
149 see Table 1), and lived in reproductive social groups comprising one adult male, two to five adult
150 females and their immature offspring. The baboons lived in 14-m² outdoor areas connected to 12-m²

151 indoor areas. The enclosures were enriched by wooden roosts and vertical structures of different
152 heights, both in the outdoor and indoor areas. Animals were fed by caretakers four times a day with
153 industrial monkey pellets, seeds, fresh vegetables and fruits and water *ad libitum*. There was no
154 other institutionalized interaction with humans out of food providing and medical interventions. All
155 procedures complied with the current French law and the current European directive (reference
156 86/609/CEE) relative to the protection of animals used for scientific purposes.

157

158 Apparatus

159

160 Prior to each test session, a concrete block (90 cm height) was placed inside the cage perpendicularly
161 to the mesh so that when subjects were seated on it, they could look at the experimenter's face and
162 gesture at about the height of a person. The mesh was equipped with a 10x60 cm opening. During
163 testing, a Plexiglas panel (80x35 cm) with two holes (10x15 cm) separated by 25 cm from centre to
164 centre was fixed over the opening so that baboons could pass their arms through each hole (Fig. 1).
165 This panel facilitated subsequent recording of baboons' gestures on video footages: baboons begged
166 through the holes in the presence of an experimenter standing 1 m in front of the cage. Two video
167 cameras were placed 2 m in front of the cage on both sides of the experimenter at an angle of 45° to
168 the subject's midline. All sessions were videotaped at a rate of 30 frames /s.

169

170 Training procedure

171

172 Only trained subjects learnt to beg through one of the holes of the Plexiglas panel to request the
173 food reward held in the experimenter's hand. The training was performed by an experimenter

174 standing in front of the cage, looking at the focal subject and holding a raisin in open palm out in
175 front of the subject. The training consisted of progressively increasing the distance to the subject,
176 while anticipating its grasping attempts. Ten training trials were presented to the monkeys per
177 training session. Training sessions were performed at various distances from the cage according to a
178 three-step procedure. In the first step, the raisin was kept within the reach of the subject who
179 extended one arm to grasp it in the experimenter's hand. In the second step, the distance increased
180 up to the limit of being out-of-reach and the experimenter anticipated the attempts of the subject to
181 reach the food in giving the subject the raisin each time the subject initiated an arm extension out of
182 the cage. In the third step, the experimenter stood out of the subject's arm reach and kept on giving
183 the subject the raisin immediately after each initiation of arm extension. Each subject moved on to
184 the next step when it consistently extended one (or two) arm(s) towards the raisin over the 10
185 training trials performed at a given distance. When subjects refused to extend an arm, training trials
186 were immediately resumed at the distance corresponding to the previous step.

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

194

195 Testing procedure

196

197 Both trained and control subjects were presented with exactly the same test condition; during test
198 trials, the experimenter stood 1 m in front of the cage holding a piece of banana in one hand, facing
199 and looking at the subject. This condition corresponds to the “Eyes open” condition of Bourjade et al.
200 (2014). Note that the experimenter did not stare at the baboons but looked alternately to the eyes
201 and the upper part of the nose so as to avoid possible fear reactions. Each test trial lasted 30
202 seconds, after which the experimenter gave the subject the piece of banana regardless of its
203 behaviour during the trial. All subjects received a total of four test trials. For trained subjects, test
204 trials (of the “Open eyes” condition considered in this study) had been presented once in either first,
205 second, third or fourth positions of the four test trials dispensed per session and per day (see
206 Bourjade et al. 2014). Two “motivation” trials had also been given to trained subjects between each
207 test trial in order to renew their motivation and to refresh the training in gestures. These motivation
208 trials were performed the same way as test trials except that the piece of food was given in response
209 to the first gestural request (i.e., as in third-step training sessions). For control subjects, the four test
210 trials were not spread over different days so as to avoid learning in the course of the experiment due
211 to spacing effect of training trials (e.g., Sisti et al. 2007). Control baboons were not either exposed to
212 “motivation” trials and the next test trial took place once they had eaten the reward. The four test
213 trials were therefore presented in a row. As the timing of test trials inevitably differed between the
214 two groups, we checked it had no impact on baboons’ behaviour by comparing the occurrences of all
215 behaviour types between the first and last test trials of each group (one-sample permutation tests: p
216 > 0.05 for all behaviour types considered; see Online Resources 1) and by designing statistical models
217 with the number of the test trial as a fixed effect for each dependent variable (see *Time models*,
218 Online Resources 2 & 3, and the results section below).

219

220 Data scoring and reliability

221

222 Two different types of behaviour were observed and scored on the videos for further analysis. First,
223 *requesting gestures* consisted of extending one or two arm(s) with fingers and hand(s) being in line
224 with the arm(s). A first main observer (Coder 1, BR) coded all occurrences of requesting gestures at
225 the normal speed of 30 frames/s using VLC media player. A requesting gesture set out when the wrist
226 crossed the mesh and ended with the partial or complete withdrawal of the arm. A new occurrence
227 was scored whenever the subject's wrist was brought back inside the cage. Second, *gaze behaviour*
228 took the form of (i) gazing at the experimenter's face, (ii) gazing at the food and (iii) gaze alternation
229 between the experimenter's face and the food. A gaze was defined as a visual fixation terminated by
230 blinking or directing the eyes to a new location (Kaplan and Rogers 2002). We considered gaze
231 alternation bouts as any series of two consecutive gazes minimum alternating between the
232 experimenter's face and the piece of banana, without blinking or directing the eyes to another
233 location. Before coding gaze behaviour, all videos were slightly transformed in the software
234 Avidemux 2.5 (32-bit) using the following procedure. A crop filter was first applied to zoom in and
235 centre the face of the subject on the screen. The brightness was then adjusted so as to distinguish
236 the eyes that could be in the shade of the baboon's prominent eyebrows. Another main coder (Coder
237 2, CC) coded all occurrences of each gaze behaviour type frame by frame (one frame = 0.033 s).
238 Reliability was assessed using Cohen's Kappa, k , in which the observed agreement between two
239 observers is corrected for the agreement by chance alone (Martin and Bateson 2007). Amongst the
240 total number of test trials, 65 (25%) were randomly assigned to three novel coder (Coder 3, BF;
241 Coder 4, CP; Coder 5, MA) who were blind to the hypotheses of the current paper. Coder 3 (40 trials)
242 and Coder 5 (25 trials) recoded requesting gestures. Coder 4 (40 trials) and Coder 5 (25 trials)
243 recoded gaze behaviour. Reliability was assessed between the output of Coder 1 and the additive
244 outputs of Coders 3 and 5 for the number of requesting gestures (Cohen's $k = 0.78$), and between the
245 output of Coder 2 and the additive outputs of Coders 4 and 5 for the number of occurrences of gaze
246 behaviour (Cohen's $k = 0.77$). The duration of gaze behaviour (with gazes at the experimenter's face

247 and at food pooled together) was also compared between Coder 2 and Coder 4 (40 trials) using a
248 Pearson's correlation, which was highly significant (Pearson's $r = 0.89$, $t = 64.00$, $p < 0.001$).

249

250 Statistics

251 We used an approach of multimodel inference to determine which factors most affected subjects'
252 gestural and gaze behaviour (Burnham and Anderson 2004). We processed the number of requesting
253 gestures, the number and duration of gaze at the human's face, the number and duration of gaze at
254 the food, and the number of gaze alternation bouts produced by the 20 subjects over all the four test
255 trials. We followed a three-step procedure (detailed in Online Resource 2): (1) we fitted several
256 models with either the main factor (training: *Main model*) or the confounding factors (subjects' sex:
257 *Sex model*; test trials: *Time model*), or the interaction between the two (subjects' sex x training:
258 *Interaction model*) as fixed effects; (2) we selected the model that best fitted the observed data for
259 each behavioural variable; and (3) we performed tests of significance on the retained models using
260 chi-square tests of the log-likelihood ratios (Brown and Prescott 2006). We fitted generalized linear
261 mixed models on each behavioural dependent variable with a *Poisson family* adapted to count data
262 and a *log link function* (Brown and Prescott 2006). Pseudoreplication caused by repeated
263 observations of the same individual was taken into consideration by adding the individual as a
264 random effect. Best fitting models were selected on the basis of the lowest AICc (i.e., Akaike
265 information criterion corrected), which applies a second-order correction adapted to small samples
266 (Burnham and Anderson 2004).

267 For studying the combination of gaze alternation with gestures, we determined the duration
268 that each subject spent gesturing over the 120 s of test trials and calculated the theoretical
269 probability of observing one gaze alternation exhibited during one gesture at chance level (Table 1).
270 Theoretical probabilities were calculated by multiplying the time spent gesturing (in seconds) by the
271 probability of observing an occurrence of gaze alternation per second and divided by the observed

272 total number of gaze alternation bouts. We then performed binomial tests on the proportion of gaze
273 alternation bouts exhibited during a gesture for each individual and at group level. Spearman
274 correlations coefficients were applied to the number of requesting gestures and the number of gaze
275 alternation bouts for each group. All tests were two-tailed and were performed with R 3.1.0 software
276 (<http://cran.r-project.org>) with level of significance set at 0.050.

277

278 **Results**

279

280 Gestural behaviour

281

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

290

291 Frequency of gaze behaviour

292

293 None of the factors tested explained significant variance in the number of looks at the human's face,
294 the number of looks at food and the number of gaze alternation bouts. The model that best fitted to
295 the number of looks at the human's face did not significantly differ from the null model (*Sex model*:
296 AIC = 153.6, see Online Resource 3; chi-square tests for the log-likelihood ratios, best fitting model –
297 null model, $p = 0.098$). As for the number of looks at food (Null model: AIC = 134.6) and the number
298 of gaze alternation bouts (Null model: AIC = 98.72), none of the models designed with either training
299 (trained vs. control groups), subject's sex, and test trial, better fitted to the observed data than the
300 null model. There was therefore no significant effect of the training on the number of looks at the
301 human's face and at food (Fig.3a), and on the number of gaze alternation bouts recorded in trained
302 subjects (mean number \pm SEM = 23.73 ± 2.92), and in control subjects (mean number \pm SEM = 27.44
303 ± 2.87 ; Fig. 4).

304

305 Duration of gaze behaviour

306

307 The time spent looking at the human's face was best approximated by the model that had the
308 training and the test trial as fixed effects (*Time model*: AIC = 415, see Online Resource 3; chi-square
309 tests for the log-likelihood ratios, best fitting model – null model, $p < 0.001$). However, neither the
310 effect of the training (Wald test -all test sessions, $z = -0.25$, $p = 0.801$), and of test trial (Wald tests -
311 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: $z = -$
312 0.92 , $p = 0.356$), nor the interaction between the two (Wald tests –between groups, trial 1 – trial 2: z
313 $= -1.35$, $p = 0.176$; trial 1-trial 3: $z = 0.12$, $p = 0.902$; trial 1 – trial 4: $z = 0.77$, $p = 0.443$) reached
314 significance (Fig. 3b).

315 Likewise, the time spent looking at food was best approximated by the model that had the
316 training and the test trial as fixed effects (*Time model*: AIC = 380.3, see Online Resource 3; chi-square

317 tests for the log-likelihood ratios, best fitting model – null model, $p < 0.001$). The training affected
318 the time spent looking at food, with trained baboons looking longer at food than control baboons
319 (Wald test –all test trials: $z = 3.20$, $p = 0.001$; Fig. 3b). Neither the test trial (Wald tests -both groups,
320 trial 1 – trial 2: $z = 1.45$, $p = 0.148$; trial 1- trial 3: $z = 0.23$, $p = 0.822$; trial 1 – trial 4: $z = -0.08$, $p =$
321 0.940), nor the interaction between training and test trial (Wald tests –between groups, trial 1 – trial
322 2: $z = -0.27$, $p = 0.785$; trial 1-trial 3: $z = -1.11$, $p = 0.266$; trial 1 – trial 4: $z = -0.10$, $p = 0.917$) affected
323 the duration of looks at food.

324

325 Combination of gaze alternation with gesture

326

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

338

339 **Discussion**

340

341 To our knowledge, these results are the first quantitative report on the effects of differential training
342 experience on monkeys' communicative behaviour in food-requesting situations. Unexpectedly,
343 control baboons produced a few requesting gestures by their own -though in average 10 times fewer
344 than trained subjects. If training in gestures expectedly influenced gestural production, it did not
345 affect baboons' gaze behaviour frequencies. This contradicts our hypothesis that gaze alternation
346 may have been incidentally learnt by baboons during the training. However, the training in gestures
347 led to a specific pattern of gaze alternation in relation to gestural requests; trained baboons
348 exhibited gaze alternation combined with their gestures above chance level. These findings shed light
349 on the manner that particular experience can shape monkeys' socio-cognitive skills.

350 The display of food-requesting gestures has been well documented in captive great apes who
351 had been trained in some kind of communication with humans (e.g. human sign language, pointing
352 to the keys of a keyboard) and later on, started to use them flexibly in a variety of contexts (see
353 Tomasello and Call 1997; Pika 2008 for reviews). Likewise, monkeys' requesting gestures have been
354 recently described when explicit training was performed by humans in specific contexts (Anderson et
355 al. 2010; Hattori et al. 2010; Maille et al. 2012; Meunier et al. 2013; Bourjade et al. 2014), whereas
356 reports of naturally occurring gestural requests remain anecdotic (Hess et al. 1993; Kumashiro et al.
357 2002; Meguerditchian and Vauclair 2009). Here, we report the case of five olive baboons that
358 gestured towards the human, while none of them had been explicitly trained to do that. Four of the
359 five subjects were female baboons and only one was housed with an adult male (Toti) that had been
360 trained to request food. It is thus unlikely that these females socially learnt to request food by
361 observing others doing so. This raises the question of the various forms of learning that can be
362 derived from experience. Note that we have called *incidental* learning in this study the possibility
363 that baboons associate a behaviour B (gaze) to a behaviour A (gesture) that was systematically
364 reinforced. It is *incidental* because reinforcement of the behaviour B would have not been systematic

365 as for behaviour A, though reinforcement could have occurred frequently enough for an association
366 to be formed. In this respect, different forms of incidental learning might occur out of experimental
367 contexts thanks to the daily exposure of baboons to their caretakers. Such other forms of incidental
368 learning with humans may have led to differential gestural behaviour in control baboons, and trained
369 baboons as well. Importantly, further investigation is needed to tease apart the role of experience, of
370 individual intrinsic factors (e.g., dominance rank, sex, or genetically predisposed skills) and of their
371 interplay in monkeys' propensity to communicate with humans. Note however that without training,
372 roughly half of control baboons gestured, a proportion that equals that of institutionalized
373 chimpanzees that do point (Leavens and Bard 2011). Although chimpanzees' pointing may be more
374 sophisticated regarding spatial reference to the target and manual dexterity than baboons'
375 requesting gestures -and therefore that these two behaviours might differ substantially- this suggests
376 that both gestures might share common developmental mechanisms. Ontogenetic ritualization is a
377 candidate mechanism for the development of these gestures by chimpanzees and baboons through
378 multiple interactions with human partners (e.g., Tomasello and Call 1997).

379 Consequently, it may be hypothesized that the different abilities of chimpanzees and
380 baboons to communicate with humans about food mostly rely on differential experience with
381 interacting humans. This offers substantial support to the fact that trained baboons differ
382 quantitatively rather than qualitatively from control baboons regarding this competence. To some
383 extent, these observations support previous findings about the effects of intensive exposure to
384 humans on cognitive abilities, i.e. so-called enculturation (Call and Tomasello 1996; Tomasello and
385 Call 1997). In several studies, human-reared or language-trained apes outperformed their standard-
386 reared captive counterparts in social cognition experiments (e.g. Call and Tomasello 1994; Lyn et al.
387 2010; Russell et al. 2011; Bard et al. 2014). It appeared to be also the case for one Japanese macaque
388 that pointed towards food, but also towards a TV screen while watching a movie with a human
389 (Kumashiro et al. 2002). Similarly, our data suggest that postnatal experience can affect later
390 cognitive outcomes such as the production of requesting gestures by monkeys (see Leavens and Bard

391 2011 for a review). Indeed, monkeys' gestures that mostly result from explicit training by humans are
392 then sensitive to the presence and visual attention of an audience and are associated with
393 behavioural indicators of intentionality such as gaze alternation (Kumashiro et al. 2002; Anderson et
394 al. 2010; Meunier et al. 2013; Bourjade et al. 2014).

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

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

442 behaviour might reveal either the expectation of securing inaccessible food by the baboons, or a way
443 of acting upon this expectation, or both. However, more research is needed to draw any conclusion
444 about the signal value of gaze alternation. Indeed, if gaze alternation was driven by non-
445 communicative motives, it would still stand as a social cue possibly perceived and used by others to
446 infer the target (i.e., reference) of the emitter's attention.

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

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

467

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469

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474

475 **References**

- 476 Anderson J, Kuwahata H, Fujita K (2007) Gaze alternation during “pointing” by squirrel monkeys
477 (*Saimiri sciureus*)? *Anim Cogn* 10:267–271. doi: 10.1007/s10071-006-0065-0
- 478 Anderson JR, Kuroshima H, Hattori Y, Fujita K (2010) Flexibility in the use of requesting gestures in
479 squirrel monkeys (*Saimiri sciureus*). *Am J Primatol* 72:707–714. doi: 10.1002/ajp.20827
- 480 Aragon L (1942) *Les yeux d’Elsa*, Editions de la Braconnière. Coll. des Cahiers du Rhône, Paris
- 481 Bard K, Bakeman R, Boysen S, Leavens D (2014) Emotional engagements predict and enhance social
482 cognition in young chimpanzees. *Dev. Sci.* doi: 10.1111/desc.12145
- 483 Bard KA (1990) “Social tool use” by free-ranging orangutans: A Piagetian and developmental
484 perspective on the manipulation of an animate object. In: Parker ST, Gibson KR (eds)
485 *Language and intelligence in monkeys and apes: Comparative developmental perspectives.*
486 Cambridge University Press, Cambridge, pp 356–378
- 487 Bard KA, Myowa-Yamakoshi M, Tomonaga M, et al. (2005) Group differences in the mutual gaze of
488 chimpanzees (*Pan troglodytes*). *Dev Psychol* 41:616–624. doi: 10.1037/0012-1649.41.4.616
- 489 Bates E, Camaioni L, Volterra V (1975) The acquisition of performatives prior to speech. *Merrill-*
490 *Palmer Q* 21:205–226
- 491 Bethell EJ, Vick S-J, Bard KA (2007) Measurement of eye-gaze in chimpanzees (*Pan troglodytes*). *Am J*
492 *Primatol* 69:562–575. doi: 10.1002/ajp.20376
- 493 Bourjade M, Meguerditchian A, Maille A, et al. (2014) Olive baboons, *Papio anubis*, adjust their visual
494 and auditory intentional gestures to the visual attention of others. *Anim Behav* 87:121–128.
495 doi: 10.1016/j.anbehav.2013.10.019

- 496 Bräuer J, Call J, Tomasello M (2006) Are apes really inequity averse? *Proc R Soc B Biol Sci* 273:3123–
497 3128. doi: 10.1098/rspb.2006.3693
- 498 Brown H, Prescott R (2006) *Applied Mixed Models in Medicine*. John Wiley & Sons, Chichester
- 499 Burnham KP, Anderson DR (2004) Multimodel inference: Understanding AIC and BIC in model
500 selection. *Sociol Methods Res* 33:261–304. doi: 10.1177/0049124104268644
- 501 Butterworth G (2004) Joint Visual attention in infancy. In: Bremner G, Fogel A (eds) *Blackwell
502 Handbook of Infant Development*. Blackwell Publishing Ltd, pp 213–240
- 503 Call J, Tomasello M (1996) The effect of humans on the cognitive development of apes. In: Russon
504 AE, Bard KA, Parker ST (eds) *Reaching into thought: The minds of the great apes*. Cambridge
505 University Press, Cambridge, pp 371–403
- 506 Call J, Tomasello M (1994) Production and comprehension of referential pointing by orangutans
507 (*Pongo pygmaeus*). *J Comp Psychol* 108:307–317. doi: 10.1037/0735-7036.108.4.307
- 508 Camaioni L (2004) Early Language. In: Bremner G, Fogel A (eds) *Blackwell handbook of infant
509 development*, Blackwell Publishing Ltd, pp 404–426
- 510 Carpenter M, Nagell K, Tomasello M, et al. (1998) Social cognition, joint attention, and
511 communicative competence from 9 to 15 months of age. *Monogr Soc Res Child Dev* 63:i. doi:
512 10.2307/1166214
- 513 Cochet H, Vauclair J (2010) Pointing gestures produced by toddlers from 15 to 30 months: Different
514 functions, hand shapes and laterality patterns. *Infant Behav Dev* 33:431–441. doi:
515 10.1016/j.infbeh.2010.04.009
- 516 Davidson GL, Butler S, Fernández-Juricic E, et al. (in press) Gaze sensitivity: function and mechanisms
517 from sensory and cognitive perspectives. *Anim Behav*. doi: 10.1016/j.anbehav.2013.10.024
- 518 Desrochers S, Morissette P, Ricard M (1995) Two perspectives on pointing in infancy. In: Moore C,
519 Dunham PJ (eds) *Joint attention: Its origins and role in development*. Lawrence Erlbaum
520 Associates Inc, Hillsdale, pp 85–101
- 521 Dufour V, Pelé M, Sterck EHM, Thierry B (2007) Chimpanzee (*Pan troglodytes*) anticipation of food
522 return: Coping with waiting time in an exchange task. *J Comp Psychol* 121:145–155. doi:
523 10.1037/0735-7036.121.2.145
- 524 Ehardt CL, Blount BG (1984) Mother-infant visual interaction in Japanese macaques. *Dev Psychobiol*
525 17:391–405. doi: 10.1002/dev.420170406
- 526 Emery NJ (2000) The eyes have it: the neuroethology, function and evolution of social gaze. *Neurosci
527 Biobehav Rev* 24:581–604. doi: 10.1016/S0149-7634(00)00025-7
- 528 Franco F, Butterworth G (1996) Pointing and social awareness: declaring and requesting in the
529 second year. *J Child Lang* 23:307–336. doi: 10.1017/S0305000900008813
- 530 Gaunet F, Deputte BL (2011) Functionally referential and intentional communication in the domestic
531 dog: effects of spatial and social contexts. *Anim Cogn* 14:849–860. doi: 10.1007/s10071-011-
532 0418-1

- 533 Gomez JC (1994) The emergence of intentional communication as a problem-solving strategy in the
534 gorilla. In: Parker ST, Gibson KR (eds) *Language and intelligence in monkeys and apes:*
535 *Comparative developmental perspectives*, 2nd edn. Cambridge University Press, Cambridge,
536 pp333-355
- 537 Hattori Y, Kuroshima H, Fujita K (2010) Tufted capuchin monkeys (*Cebus apella*) show understanding
538 of human attentional states when requesting food held by a human. *Anim Cogn* 13:87–92.
539 doi: 10.1007/s10071-009-0248-6
- 540 Hess J, Novak MA, Povinelli DJ (1993) “Natural pointing” in a rhesus monkey, but no evidence of
541 empathy. *Anim Behav* 46:1023–1025
- 542 Hobaiter C, Leavens DA, Byrne RW (2013) Deictic gesturing in wild chimpanzees, (*Pan troglodytes*)?
543 Some possible cases. *J Comp Psychol* No Pagination Specified. doi: 10.1037/a0033757
- 544 Kaplan G, Rogers LJ (2002) Patterns of Gazing in Orangutans (*Pongo pygmaeus*). *Int J Primatol*
545 23:501–526. doi: 10.1023/A:1014913532057
- 546 Kobayashi H, Kohshima S (2001) Unique morphology of the human eye and its adaptive meaning:
547 comparative studies on external morphology of the primate eye. *J Hum Evol* 40:419–435. doi:
548 10.1006/jhev.2001.0468
- 549 Kumashiro M, Ishibashi H, Itakura S, Iriki A (2002) Bidirectional communication between a Japanese
550 monkey and a human through eye gaze and pointing. *Cah Psychol Cogn Psychol Cogn* 21:3–
551 32.
- 552 Leavens DA (2004) Manual deixis in apes and humans. *Interact Stud* 5:387–408. doi:
553 10.1075/is.5.3.05lea
- 554 Leavens DA, Bard KA (2011) Environmental influences on joint attention in great apes: Implications
555 for human cognition. *J Cogn Educ Psychol* 10:9–31. doi: 10.1891/1945-8959.10.1.9
- 556 Leavens DA, Hopkins WD (1999) The whole-hand point: The structure and function of pointing from a
557 comparative perspective. *J Comp Psychol* 113:417–425. doi: 10.1037/0735-7036.113.4.417
- 558 Leavens DA, Hopkins WD (1998) Intentional communication by chimpanzees: A cross-sectional study
559 of the use of referential gestures. *Dev Psychol* 34:813–822. doi: 10.1037/0012-1649.34.5.813
- 560 Leavens DA, Hopkins WD, Bard KA (1996) Indexical and referential pointing in chimpanzees (*Pan*
561 *troglodytes*). *J Comp Psychol* 110:346–353. doi: 10.1037/0735-7036.110.4.346
- 562 Leavens DA, Hostetter AB, Wesley MJ, Hopkins WD (2004) Tactical use of unimodal and bimodal
563 communication by chimpanzees, *Pan troglodytes*. *Anim Behav* 67:467–476. doi:
564 10.1016/j.anbehav.2003.04.007
- 565 Leavens DA, Russell JL, Hopkins WD (2005) Intentionality as measured in the persistence and
566 elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Dev* 76:291–306. doi:
567 10.1111/j.1467-8624.2005.00845.x
- 568 Leavens DA, Hopkins WD, Bard KA (2005) Understanding the point of chimpanzee pointing:
569 epigenesis and ecological validity. *Curr Dir Psychol Sci* 14:185–189. doi: 10.1111/j.0963-
570 7214.2005.00361.x

- 571 Liebal K, Call J (2012) The origins of non-human primates' manual gestures. *Philos Trans R Soc B Biol*
572 *Sci* 367:118–128. doi: 10.1098/rstb.2011.0044
- 573 Lock A (2004) Preverbal communication. In: Bremner G, Fogel A (eds) *Blackwell handbook of infant*
574 *development*. Blackwell Publishing Ltd, pp 379–403
- 575 Lyn H, Russell JL, Hopkins WD (2010) The impact of environment on the comprehension of
576 declarative communication in apes. *Psychol Sci* 21:360–365. doi:
577 10.1177/0956797610362218
- 578 Maestripieri D (2005) Gestural communication in three species of macaques (*Macaca mulatta*, *M.*
579 *nemestrina*, *M. arctoides*): Use of signals in relation to dominance and social context. *Gesture*
580 5:57–73. doi: 10.1075/gest.5.1.06mae
- 581 Maille A, Engelhart L, Bourjade M, Blois-Heulin C (2012) To beg, or not to beg? That is the question:
582 mangabeys modify their production of requesting gestures in response to human's
583 attentional states. *PLoS ONE* 7:e41197. doi: 10.1371/journal.pone.0041197
- 584 Marshall-Pescini S, Colombo E, Passalacqua C, et al. (2013) Gaze alternation in dogs and toddlers in
585 an unsolvable task: evidence of an audience effect. *Anim Cogn* 16:933–943. doi:
586 10.1007/s10071-013-0627-x
- 587 Martin P, Bateson P (2007) *Measuring behaviour: An introductory guide*. Cambridge University Press
- 588 Matthews D, Behne T, Lieven E, Tomasello M (2012) Origins of the human pointing gesture: a training
589 study. *Dev Sci* 15:817–829. doi: 10.1111/j.1467-7687.2012.01181.x
- 590 Meguerditchian A, Vauclair J (2009) Contrast of hand preferences between communicative gestures
591 and non-communicative actions in baboons: Implications for the origins of hemispheric
592 specialization for language. *Brain Lang* 108:167–174. doi: 10.1016/j.bandl.2008.10.004
- 593 Meunier H, Prieur J, Vauclair J (2013) Olive baboons communicate intentionally by pointing. *Anim*
594 *Cogn* 16:155–163. doi: 10.1007/s10071-012-0558-y
- 595 Miller JL, Gros-Louis J (2013) Socially guided attention influences infants' communicative behavior.
596 *Infant Behav Dev* 36:627–634. doi: 10.1016/j.infbeh.2013.06.010
- 597 Miller JL, Lossia AK (2013) Prelinguistic infants' communicative system: Role of caregiver social
598 feedback. *First Lang* 33:524–544.
- 599 Mitchell RW, Anderson JR (1997) Pointing, withholding information, and deception in capuchin
600 monkeys (*Cebus apella*). *J Comp Psychol* 111:351–361. doi: 10.1037/0735-7036.111.4.351
- 601 Packer C (1977) Reciprocal altruism in *Papio anubis*. *Nature* 265:441–443. doi: 10.1038/265441a0
- 602 Pika S (2008) Gestures of apes and pre-linguistic human children: Similar or different? *First Lang*
603 28:116–140. doi: 10.1177/0142723707080966
- 604 Redican WK, Rosenblum LA (1975) *Facial expressions in nonhuman primates*. Stanford Research
605 Institute
- 606 Russell CL, Bard KA, Adamson LB (1997) Social referencing by young chimpanzees (*Pan troglodytes*). *J*
607 *Comp Psychol* 111:185–193. doi: 10.1037/0735-7036.111.2.185

- 608 Russell JL, Lyn H, Schaeffer JA, Hopkins WD (2011) The role of socio-communicative rearing
609 environments in the development of social and physical cognition in apes. *Dev Sci* 14:1459–
610 1470. doi: 10.1111/j.1467-7687.2011.01090.x
- 611 Sisti HM, Glass AL, Shors TJ (2007) Neurogenesis and the spacing effect: Learning over time enhances
612 memory and the survival of new neurons. *Learn Mem* 14:368–375. doi: 10.1101/lm.488707
- 613 Tomasello M, Call J (1997) *Primate Cognition*. Oxford University Press
- 614 Tomasello M, Call J, Nagell K, et al. (1994) The learning and use of gestural signals by young
615 chimpanzees: A trans-generational study. *Primates* 35:137–154. doi: 10.1007/BF02382050
- 616 Tomasello M, George BL, Kruger AC, et al. (1985) The development of gestural communication in
617 young chimpanzees. *J Hum Evol* 14:175–186. doi: 10.1016/S0047-2484(85)80005-1
- 618 Tomasello M, Hare B, Lehmann H, Call J (2007) Reliance on head versus eyes in the gaze following of
619 great apes and human infants: the cooperative eye hypothesis. *J Hum Evol* 52:314–320. doi:
620 10.1016/j.jhevol.2006.10.001
- 621 Van Hoof, J. (1967) The facial displays of catarrhine monkeys and apes. In: Morris, D (ed) *Primate*
622 *Ethology*. Weiden-feld & Nicholson, London, pp 7–68
- 623 Visalberghi E, Valenzano DR, Preuschoft S (2006) Facial Displays in *Cebus apella*. *Int J Primatol*
624 27:1689–1707. doi: 10.1007/s10764-006-9084-6
- 625 Watanabe M, Cromwell HC, Tremblay L, et al. (2001) Behavioral reactions reflecting differential
626 reward expectations in monkeys. *Exp Brain Res* 140:511–518. doi: 10.1007/s002210100856
- 627 Whiten A, Byrne RW (1988) Tactical deception in primates. *Behav Brain Sci* 11:233–244. doi:
628 10.1017/S0140525X00049682
- 629

630 Table 1. Individuals' characteristics, gestural and gaze alternation behaviour over the four test trials. GA: gaze alternation bouts.

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
		<i>Trained</i>		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	—
		<i>Control</i>		247 ^(a)	0.23 ^(b)	23 ^(a)	51 ^(a)	11.66 ^(c)	0.05 ^(d)	19 ^(a)	0.057

631

632 ^(a) Sum of occurrences of all individuals over the four trials

- 633 (b) Sum of GA at group level divided by 120 s, multiplied the number of individuals in the group.
- 634 (c) Probability of GA/s at group level multiplied by the total time spent gesturing at group level.
- 635 (d) Theoretical number of GA with gestures at group level divided by the sum of GA at group level.
- 636

637 Figure captions

638

639 **Fig.1** Apparatus used in the food-requesting paradigm

640

641 **Fig.2** Mean number (\pm SEM) of requesting gestures by trained and control baboons. Wald test, *** p

642 < 0.001

643

644 **Fig.3** Gaze behaviour towards the human's face and the food by trained and control baboons; (a)

645 mean number (\pm SEM) of looks, (b) mean duration (\pm SEM) of looks expressed in number of frames;

646 Wald test, ** $p < 0.01$

647

648 **Fig.4** Gaze alternation bouts (GA) in trained and control baboons; Binomial test, *** $p < 0.001$

649

650 **Fig.5** Number of gaze alternation bouts as a function of the number of gestures, (a) trained subjects,

651 (b) control subjects