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1 **Gestural communication in olive baboons (*Papio anubis*): repertoire and**
2 **intentionality**

3

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38 **Abstract**

39 Gesturing is a widespread phenomenon in the animal kingdom, as well as an important
40 facet of human language. As such, studying the communicative gestures of our close
41 phylogenetic relatives is essential to better understand its evolution. While recent studies have
42 shown that ape gestural communication shares some properties with human language, very little
43 is known about the properties of gestural communication in monkeys. The aims of this study
44 were to establish the first quantitative repertoire of gestural communication in a species of old-
45 world monkeys, the olive baboon *Papio anubis*, and to determine its properties in terms of
46 variability, flexibility and intentionality. Gestural communication was continuously recorded
47 on 47 captive olive baboons over one year. Their gestural repertoire was composed of 67 visual,
48 tactile, and audible gestures, that were used flexibly across different contexts, indicating means-
49 ends dissociation. We found that the use of gestures was variable across individuals and ages,
50 notably with repertoire size decreasing with age. Baboons used their gestures intentionally;
51 gesturers looked at the recipient, waited for a response, and took into account the attentional
52 state of their recipient. Particularly, they actively adjusted the modality of their gesture to the
53 recipient's visual attention, by using more visual gestures when the recipient was attending and
54 more tactile gestures when the recipient was not. Thus, the gestural communicative system of
55 olive baboons possesses properties which are similar to the ones of apes and to human language.
56 These intentional features of gestural communication, that may constitute a prerequisite of
57 language evolution, may have been present in the common ancestor of baboons and humans,
58 around 30-40 million years ago.

59

60 **Keywords:** Gesture, language, primate; intentionality, flexibility, sensory modality

61

62

63 **Introduction**

64 Gesturing is a widespread phenomenon in the animal kingdom, as well as an important
65 facet of human language. Indeed, before children start to speak, they produce a variety of
66 gestures, which paves the way of their spoken language development (Bates 1979; Carpenter
67 et al. 1998; Iverson and Goldin-Meadow 2005). Moreover, adults continue to use gestures to
68 accompany spoken and signed languages (McNeill 1985; Goldin-Meadow 2002, 2003). While
69 the evolutionary emergence of language is still equivocal, studying non-human primate gestures
70 is relevant to inform evolutionary models about the commonalities of forms, functions,
71 cognitive and neurobiological underpinnings of its gestural components. Communicative
72 gestures of our close phylogenetic relatives have been relatively little studied compared to
73 vocalisations. However, it is now well acknowledged that the researches on the gestural system
74 are of primary interest to reconstruct a coherent evolutionary scenario of language considered
75 as a multimodal communication system (Call and Tomasello 2007; Arbib et al. 2008; Waller et
76 al. 2013). Notably, there is increasing evidence that humans and apes share some intentional
77 communicative abilities likely to have evolved through gestural communication (Arbib et al.
78 2008; Liebal and Call 2012). However, it is not well-established that the gestural
79 communication of non-ape primates possesses similar properties; including the forms,
80 functions, flexibility and intentionality of gestures.

81 One of the main characteristics of human language is its incredible flexibility in
82 acquisition and usage. Recent studies have shown that gestures in apes are also used flexibly.
83 This flexibility is determined by the so-called ‘means-ends dissociation’. This criterion,
84 originating from developmental psychology through the investigation of communication in
85 human infants, is characterised by the flexible relation between forms and functions of
86 communicative signals, where different gestures can be used for the same goal and the same
87 gesture can be used for different goals (e.g. Call and Tomasello 2007; Pollick and de Waal

88 2007). In non-human primates, this is usually assessed by analysing the range of functional
89 contexts (such as play or agonistic) in which a gesture occurs, and the diversity of gestures
90 which occurs within a single context. A means-ends dissociation between gesture type and
91 context has been found in several species of apes, both in captive and wild populations
92 (chimpanzees, *Pan troglodytes*: Tomasello et al. 1994; Call and Tomasello 2007; Hobaiter and
93 Byrne 2011b; Roberts et al. 2012; bonobos, *Pan paniscus*: Pika et al. 2005b; Genty et al. 2015;
94 Graham et al. 2017; gorillas, *Gorilla gorilla*: Pika et al. 2003; Pika 2007; Genty et al. 2009;
95 orangutans, *Pongo pygmaeus*: Liebal et al. 2006; and siamangs, *Symphalangus Syndactylus*:
96 Liebal et al. 2004b). Apes are also able to learn new gestures taught by humans such as sign
97 language, often through extensive training including moulding of hands to form signs, but also
98 through no more extensive moulding of the signs than can be seen in human mothers of deaf
99 children (Patterson and Linden 1981; Fouts et al. 1989; Gardner et al. 1989; Miles 1990;
100 Tomasello and Camaioni 1997). Indeed, their gestural communicative system is also variable,
101 as all individuals do not produce the same set of gestures (e.g. Tomasello et al. 1994; Liebal et
102 al. 2004b; Pika et al. 2005b; Liebal et al. 2006). Individual repertoire size varies particularly
103 across age classes, with juveniles using a larger variety of gestures than adults (Tomasello et
104 al. 1994, 1997; Liebal et al. 2004b, 2006; Genty et al. 2009; Hobaiter and Byrne 2011a, b).
105 However, sex differences are scarcer and often limited to sexual context (e.g. Liebal et al.
106 2004b; Scott 2013).

107 More importantly, there is increasing evidence that the production of gestures in apes
108 possesses the main criteria of intentionality, especially in terms of directing gestures toward
109 recipients, waiting for a response, and taking into account the attentional state of the recipient
110 (e.g. Call and Tomasello 2007; Byrne et al. 2017). Indeed, gestures are directed toward an
111 audience and the signaller waits briefly after gesturing to monitor the recipient for behavioural
112 response (i.e. response waiting; Tomasello et al. 1985, 1994; Call and Tomasello 2007).

113 Intentionality criteria have then notably been used as baseline conditions to select which type
114 of gesture to record or not when investigating the repertoire of gestural communication of apes
115 (e.g. Pika et al. 2003; Liebal et al. 2006; Hobaiter and Byrne 2011a; Roberts et al. 2014).
116 Furthermore, the signaller takes into account the attentional state of the recipient when
117 producing a gesture. This is the so-called ‘audience effect’, characterised by a sensitivity to the
118 presence/absence of a potential recipient and by the differential use of gestures as a function of
119 the attentional state of the recipient (Call and Tomasello 2007; Leavens et al. 2004a).
120 Particularly, gestures can vary in modality, and silent, visual gestures (i.e. gestures that create
121 no sound and no contact with the recipient) can only be effective if produced toward a recipient
122 that is visually attending, whereas tactile (i.e. gestures that create a contact with the recipient)
123 or audible gestures (i.e. gestures that create a sound while being performed) can potentially be
124 effective even if the recipient is not visually attending. For example, it has been shown
125 experimentally that chimpanzees are able to adapt their visual and auditory communicative
126 behaviours in accordance to the attentional and intentional status of a human observer when
127 begging for food (Hostetter et al. 2001; Povinelli et al. 2003; Leavens et al. 2004b; Poss et al.
128 2006; Leavens et al. 2010). However, individuals that have the opportunity to move in front of
129 the recipient before producing visually based gestures seem to favour this option (Liebal et al.
130 2004a, b). Observational studies of spontaneous communicative behaviours also indicated that
131 apes use more visual gestures when the recipient is already attending, and can, to some extent,
132 modify their use of tactile or audible gestures when the recipient is not attending (Tomasello et
133 al. 1994; Pika et al. 2003; Liebal et al. 2004b; Pika et al. 2005a, b ; Liebal et al. 2006; Genty et
134 al. 2009; Hobaiter and Byrne 2011a; but see also Tempelmann and Liebal 2012). Additionally,
135 in the absence of a response from the recipient, or when the response is apparently
136 unsatisfactory, apes either persist with using the same gesture, or elaborate by using another
137 gesture or signal until they are satisfied by the response (e.g., towards humans: Leavens et al.

138 2005; Cartmill and Byrne 2007; towards conspecifics: Liebal et al. 2004a; Hobaiter and Byrne
139 2011b; Roberts et al. 2013). Moreover, intentional communication may be more widespread in
140 the animal kingdom than originally thought, as suggested by recent evidence of intentional
141 production of gestures in fishes, birds, dogs and ungulates (Gaunet and Deputte 2011; Vail et
142 al. 2013; Malavasi and Huber 2016; Nawroth et al. 2016; Smith 2017; Townsend et al. 2017).
143 For example, horses (*Equus caballus*) were able to take into account the attentional state of the
144 human recipient when communicating about a desired out of reach reward (Malavasi and Huber
145 2016). These pieces of evidence indicate that intentional communication may have provided
146 adaptive benefits in the course of evolution.

147 In contrast with such an extended knowledge in apes, virtually nothing is known about
148 monkey gestural communication. Some studies have investigated the repertoire of gestures used
149 by several species of macaques, by looking notably at the effect of social structure on the type
150 of gestures performed and the context of use (Hinde and Rowell 1962; Maestriperi 1996, 1997,
151 1999, 2005; Hesler and Fischer 2007). Macaque species displaying higher levels of tolerance
152 and relaxed dominance might possess a wider range of communicative signals than less tolerant
153 species (e.g. Maestriperi 2005). In baboons, some gestural behaviours have been described in
154 olive baboons (*Papio anubis*, e.g., Smuts 2002) as well as in hamadryas baboons (*Papio*
155 *hamadryas*) within the ethogram provided by Kummer (1968). Some studies have also shown
156 that mandrills (*Mandrillus sphinx*) were able to spontaneously invent new gestures (Laidre
157 2008, 2011). However, compared to apes there is a real lack of systematic and comparable
158 studies on the gestural communication of monkeys. Notably, most studies showing that the
159 production of gestures by monkeys was intentional have been done in experimental settings
160 using trained gestures to request food toward humans (e.g. Hattori et al. 2010; Maille et al.
161 2012; Meunier et al. 2013; Bourjade et al. 2014; Canteloup et al. 2014, 2015; but see also Gupta
162 and Sinha 2016). For example, when begging for food, olive baboons gestured more often when

163 the experimenter could see them and adjusted their visual and auditory gestures to the visual
164 attention of the human recipient (Bourjade et al. 2014). This raises the question of whether these
165 skills have been learned during the experiments or whether monkeys possess a preexisting
166 ability to discriminate recipients' attention. Consequently, it remains unclear which types of
167 intra-specific gestures are used by monkeys, and whether they possess the same advanced
168 properties as ape gestures (Pika et al. 2005a).

169 It is worth noting that the gestural communication of both baboons and chimpanzees
170 involve cerebral areas located in the left hemisphere which appear similar to the areas involved
171 in human language (Meguerditchian et al. 2011a; Meguerditchian and Vauclair 2014; Marie et
172 al. 2018). Recent studies further showed that olive baboons, like apes and humans (e.g. Knecht
173 et al. 2000; Hopkins et al. 2012; Meguerditchian et al. 2012, 2013), were mostly right-handed
174 for gesturing (i.e., the ground slapping gesture: slapping of the hand on the ground), and those
175 hand preferences were very consistent over time and across populations (Meguerditchian and
176 Vauclair 2006; Meguerditchian et al. 2011b; Molesti et al. 2016). Baboons seem to share
177 interesting neurobiological underpinnings with chimpanzees and humans, and therefore rise as
178 an excellent model to investigate the communicative and socio-cognitive precursors of
179 language (e.g. Fagot et al. 2018).

180 Therefore, the present study investigated whether the abilities shown by olive baboons
181 expanded beyond the experimental context and applied to intra-specific communicative
182 interactions. Using a methodology closely modelled after ape studies, we established the first
183 naturalistic repertoire of gestural communication in olive baboons, based on observations of
184 three groups of captive baboons. Then, we examined the flexibility, variability, and
185 intentionality of gesture use in order to determine if an old-world monkey species would possess
186 similar communicative properties to human and non-human apes. By providing the first
187 quantitative description of monkey gestures, this study will help further document baboon

188 communication as well as the evolution of complex communication and sociality within the
189 primate lineage.

190

191 **Method**

192 *Subjects*

193 This study was conducted on three social groups of captive-born olive baboons (*Papio*
194 *anubis*) living at the Station de Primatologie of the Centre National de la Recherche Scientifique
195 (CNRS, UPS 846, Rousset, France). In total, 47 subjects were systematically observed in this
196 study: 13 males and 34 females; 4 infants (0-1 year), 9 juveniles (1-4 years), 7 subadults (4-7
197 years), and 27 adults (from 7 years). The subjects were aged from 0 to 25 years old, and were
198 housed in large cages or parks from 15 to 650 m². They received monkey pellets twice per day,
199 as well as fresh fruits, vegetables and grains. Water was available ad libitum. The groups 1, 2
200 and 3, were respectively composed of 32, 6 and 9 individuals.

201

202 *Procedure*

203 Data were collected during one year, from October 2015 to October 2016. A
204 communicative gesture was defined as a movement of the body or part of the body, directed to
205 a specific partner or audience. This definition thus included actions of the whole body, of parts
206 of the body (e.g. limb, head), and facial expressions (i.e. movements of parts of the face). A
207 gesture could be directed to a partner via eye gaze, body orientation or physical contact (e.g.
208 Liebal et al. 2004b). In contrast with ape studies (e.g. Liebal et al. 2006; Hobaiter and Byrne
209 2011a), the methodological approach was to record any behaviour corresponding to this
210 definition without screening gestures a priori with intentionality criteria. Instead, we tested

211 every single criterion of intentionality on our gestural data set, leaving the case for non-
212 intentional communicative gestures open throughout.

213 Focal animal sampling was used (Altmann 1974) to observe each subject for a total of 5
214 h. For this, each focal monkey was randomly selected and followed for 60 sessions of 5 min. In
215 total, 80% of the focal sessions were collected in live using a voice recorder, and 20% of the
216 focal sessions were videotaped using a digital video camera (SANYO Xacti ®) recording at
217 30fps (1920 x 1080 Full-SQH). The data were then transferred to Excel spreadsheets while
218 listening to the records and scanning the videos (see details of data collection in Online
219 Resource 1). If the focal subject moved outside the vision range for more than 1 min, the record
220 was deleted, and the session was started again once the subject became available. Each monkey
221 was observed only once per day, and the focal sessions were balanced between the morning and
222 afternoon periods and spread over seasons. All gestures produced by the focal monkey were
223 recorded to extract the following information:

224 1. The ID of the recipient

225 2. The type of gesture produced (see details in Online Resource 1)

226 3. The orientation of the signaller (Liebal et al. 2004b): (a) ‘looking’ was defined as the signaller
227 having its eyes and/or face directed toward the recipient, (b) ‘not looking’ was defined as the
228 signaller having its head turned away from the recipient with no eye contact.

229 4. Response waiting (Hobaiter and Byrne 2011a): (a) ‘response waiting’ was recorded when
230 the signaller maintained its related recipient-directed posture beyond the end of the gesture
231 and/or some visual contact with the recipient, (b) ‘no response waiting’ was recorded otherwise.

232 5. The recipient attention (Liebal et al. 2004b): (a) ‘attending’ was defined as the recipient
233 having its eyes and/or face directed toward the signaller, (b) ‘not attending’ was defined as the

234 recipient having its head turned away from the signaller or having its attention distracted by
235 another individual or event in its environment.

236 6. Behavioural context, as judged qualitatively by the available pre- and post- information that
237 accompanied the signaller's gesture (Schneider et al. 2012): (a) parental care (behaviours
238 involving the care of a mother toward her infant), (b) agonistic (aggressive behaviours such as
239 chasing, biting or threatening), (c) submissive (submissive behaviours such as fleeing, usually
240 following an aggressive behaviour received), (d) play (play behaviours such as play-wrestle
241 and rough-and-tumble play), (e) sexual (behaviours accompanying mating interaction), (f) allo-
242 grooming (a monkey grooms a partner, i.e. goes through the fur of another monkey with its
243 fingers, removing dirt and/or parasites), (g) affiliative (friendly approaches toward other
244 individuals such as greeting, excluding allo-grooming), and (h) other (i.e. gesture that could not
245 be categorised in a particular context).

246 7. Combination (Liebal et al. 2004b, 2006): gestures were either produced in isolation and
247 recorded as 'single' or simultaneously with others and recorded as 'combined'.

248

249 *Data analysis*

250 A total of 2820 focal sessions were collected (i.e. 235h of focal observation),
251 corresponding to 60 sessions (i.e. 5h) for each of the 47 subjects. Following the data collection,
252 a total of 2256 audio sessions were transcribed (i.e. 80% of the sessions) and 564 videos were
253 coded (i.e. 20% of the sessions) to extract all the information on the gestures produced by the
254 subjects. In order to assess the reliability of the behavioural sampling, 75% of the videos (i.e.
255 15% of the total focal sessions) were coded by a second observer blind to the hypotheses of the
256 study. Consistency between observers was excellent (Cohen's Kappa, $k = 0.94$ for gesture type,
257 $k = 0.90$ for the orientation of the signaller, and $k = 0.89$ for response waiting; see Online

258 Resource 1 for details). According to their intrinsic structure, each gesture was classified (e.g.
259 Pika et al. 2003) as either visual, audible, or tactile. While all gestures had a visual component,
260 a gesture was classified as audible if it generated some sound while being performed, as tactile
261 if it included physical contact with the recipient, or as visual in all other cases. All gestures that
262 were observed at least two times were included in the repertoire and in the analyses. All gestures
263 were treated as independent gestures in the analyses.

264

265 Flexibility

266 Flexibility refers to the so-called ‘mean-end dissociation’ between gesture form and
267 function. It was assessed by counting the number of different gesture types used within the same
268 context and the number of contexts in which one gesture type was used (Pika et al. 2005; Liebal
269 et al. 2006; Call and Tomasello 2007; Genty et al. 2009). We analysed whether the proportions
270 of gesture types used in several contexts or in only one context differed statistically from a
271 uniform distribution using a Binomial test. For this, the proportions observed in our dataset
272 were compared to a theoretical uniform distribution where the proportion of gestures used in
273 several contexts was equal to the proportion of gestures used in one context.

274

275 Variability

276 We ran a series of analyses to investigate whether gestural communication was variable
277 across individuals, ages and sexes. Particularly, we investigated whether the repertoire size, the
278 rate of production of gestures and the use of the modalities were variable. First, we calculated
279 the repertoire size of each individual (i.e. the number of different gesture types that the
280 individual produced at least once). As it followed a normal distribution, we compared repertoire
281 sizes across age classes using a One-way ANOVA, and across sex classes using a T-test. Then,

282 for each individual, we calculated the rate of gesture production (i.e. the number of gestures
283 produced per hour). This variable was not normally distributed and the rates across age classes
284 and between sexes were compared using a Kruskal-Wallis and a Mann-Whitney U test
285 respectively. Finally, we investigated whether the modalities of the gestures used were affected
286 by the age or sex of the individuals, using GLMMs with a Poisson distribution and a log link
287 function (see Online Resource 2, Table S1). The number of gestures produced was the
288 dependent variable whereas the type of modality (i.e. audible, tactile, or visual), age class (i.e.
289 infant, juvenile, subadult, or adult), and sex (i.e. male or female) were the categorical test
290 variables.

291

292 Intentionality

293 To assess whether the gestural communication of olive baboons was intentional, we
294 investigated three indicators of intentionality: the orientation of the signaller while producing
295 the gesture, whether the signaller waited for a response from the recipient, and the attentional
296 state of the recipient. Each indicator of intentionality was investigated separately on the total
297 gestural output. Also, percentages of gestures on which these criteria were observed are
298 reported for each single gesture type in Table 1.

299 First, we ran GLMMs with a Poisson distribution and a log link function to assess whether
300 subjects produced more gestures (a) when looking at the recipient than when not looking, (b)
301 when waiting for a response of the recipient than when not waiting, and (c) when the recipient
302 was attending than when the recipient was not attending (see Online Resource 2, Table S2).
303 The number of gestures produced was the dependent variable, and the variables orientation (i.e.
304 looking vs. not looking), response waiting (i.e. waiting vs. not waiting), and attention (i.e.
305 attending vs. not attending) were the categorical test variables entered in each corresponding

306 model. Sex (i.e. male or female) and age class (i.e. infant, juvenile, subadult, or adult) were the
307 categorical control variables.

308 Second, we evaluated the effect of age on intentionality. For this, for each individual we
309 calculated the percentage of gestures produced when they looked at the recipient, when they
310 waited for a response of the recipient, and when the recipient was attending, and we compared
311 the percentages across age classes using Kruskal-Wallis tests.

312 Finally, we further examined the effect of the recipient's visual attention on the gesture
313 modality used by the signaller. For this, we investigated whether baboons actively adjusted their
314 gesture modality to the recipient's attention, using the method described by Hobaiter and Byrne
315 (2011a). Thus, we calculated the variation in the choice of audible, tactile, and visual gestures,
316 according to whether the recipient was attending or not attending. First, for each individual we
317 calculated the proportions of all gestures produced that involved audible, tactile or visual
318 gestures. Then, we divided this individual's dataset in two subsets depending on whether the
319 recipient was attending or not attending, and we recalculated the proportions of each modality
320 for each subset. Finally, we calculated the percentage of variation, which corresponded to the
321 variation in the use of each modality according to the attentional state of the recipient, based on
322 the formula $(\beta/\alpha - 1) \times 100$, where for example α represented the proportion of visual gestures
323 produced in the overall corpus, while β represented the proportion of visual gestures produced
324 when the recipient was attending. These percentages of variation, which could be positive or
325 negative, indicated active adjustment of the modality to the attention of the recipient. We
326 analysed whether the choice of different modalities varied according to the attentional state of
327 the recipient with a Friedman test. As we could not disentangle the link between attention and
328 modality when several gestures of different modalities were produced at the same time, these
329 analyses were run only on single gestures.

330

331 All tests were two-tailed, and the level of significance was set at 0.05. We used parametric
332 statistics when the data followed a normal distribution and used non-parametric statistics
333 otherwise. GLMMs were run in Stata v12.1 (Stata Corp, 2011), while all the other tests were
334 run in IBM SPSS v21 (IBM Corp, 2012). For the GLMMs, we used a statistical model selection
335 approach to determine which models best fitted our data (see details in Online Resource 2). We
336 followed a three-steps procedure: (1) we fitted several models with the test and/or control
337 variables as fixed effects; (2) we selected the models that best fitted the observed data on the
338 basis of the lowest AICc (i.e. Akaike information criterion corrected, Burnham and Anderson
339 2004; Symonds and Moussalli, 2011); and (3) we performed tests of significance on the retained
340 models using Chi-square tests of the log-likelihood ratios (Brown and Prescott 2006). For each
341 GLMM, the ID of the subject as well as the ID of the group were entered as random factors
342 (Pinheiro and Bates 2000; Rabe-Hesketh and Skrondal 2008). Only results of the retained
343 models are presented in the results section below. Further information is available in Online
344 Resource 2. Note that supplementary analyses were conducted to evaluate the potential effect
345 of using two distinct methods of data collection on some of the results presented hereafter. We
346 obtained exact same results on (i) the complete data set, (ii) the subset of data collected on
347 videos, and (iii) the subset of data from live coding, indicating that our results are not impacted
348 by data collection methods (see Online Resource 2, Table S4).

349

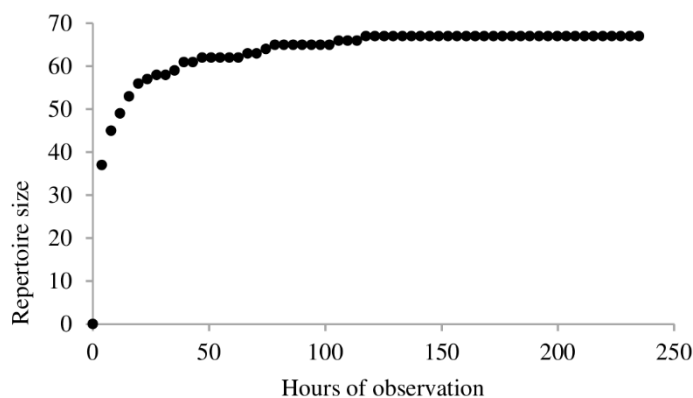
350 **Results**

351 *Repertoire*

352 In total, 8855 occurrences of gesture were recorded. This allowed us to establish the first
353 repertoire of gestural communication in olive baboons with a list of 67 gestures produced,
354 which included facial expressions, manual gestures, and bodily gestures (Table 1). Among all
355 these gestures, 4 were audible gestures, 24 were tactile gestures, and 39 were visual gestures.

356 Examining the cumulative number of new gestures recorded for all subjects indicated that our
357 observation time was sufficient to reach the repertoire size of olive baboons, as an asymptote
358 was reached at 117.5 hours of observation (i.e. 30 sessions of 5 min, so 2.5 hours, for each of
359 the 47 subjects; Figure 1). It can be noted that we described most of the gestures based on action
360 (Table 1). The gestures ‘presentation’, ‘lip-smack’ and ‘give ground’ were observed the most
361 often (i.e. more than 600 occurrences), whereas the gestures ‘headstand’, ‘invite young’ and
362 ‘kiss’ were observed the least often (i.e. up to 5 occurrences). There were two idiosyncratic
363 gestures (i.e. gestures that are exclusively produced by one individual): ‘hand own genitals’
364 was produced only by a subadult female, and ‘elephant’ was produced only by a juvenile male.
365 The gestures ‘headstand’ and ‘roll’ were used by less than 5% of the subjects. While the gestures
366 ‘groom present’, ‘give ground’, ‘grooming intention’ and ‘lip smack’ were used by more than
367 94% of the subjects, the gesture ‘hand-body touch’ was used by all subjects. Each subject
368 produced around 188 gestures (mean \pm SE = 188.4 \pm 11.2). Among the 8855 gestures recorded,
369 6549 (74%) were performed as single gesture and 2306 (26%) were combined with another
370 gesture at the same time.

371



372

373 **Figure 1:** Cumulative record of olive baboons’ gestural repertoire. The cumulative number of
374 new gestures recorded (i.e. repertoire size) is plotted against the number of hours of
375 observations of all baboons. Asymptote was reached after 117.5 hours of observation.

376

377 **Table 1:** Detailed repertoire of communicative gestures by olive baboons. For each gesture, is
378 given its description, modality, the total number of occurrences recorded, the number of
379 subjects who produced it, the group and context in which the gesture was recorded, the number
380 of subjects of each sex and age class who produced the gesture, the percentage of occurrences
381 where the subject was looking at the recipient, waiting for a response from the recipient, and
382 the percentage of occurrences where the recipient was attending. Sex: F = Female, M = Male;
383 Age class: I = Infant, J = Juvenile, S = Subadult, A = Adult.

384 ¹ In > 10% of the occurrences, the observer could not distinguish between several recipients

385 ² In > 10% of the occurrences the information was not available

Gesture	Description	Modality	Occurrence	Subject	Group	Context	Sex	Age	% Looking	% Response waiting	% Attending
Air bite	The monkey performs a biting movement in the air. There is no contact with the recipient.	Visual	75	24	1, 2, 3	Affiliative, agonistic, other, play, sexual	13 F, 11 M	2 I, 8 J, 4 S, 10 A	100	100	96
Back and forth look	The monkey looks alternately between two recipients, by turning its head in an exaggerated way between the recipients (usually between an opponent and a potential ally). The eyes are wide open.	Visual	36	15	1, 2	Affiliative, agonistic, play	12 F, 3 M	0 I, 3 J, 4 S, 8 A	100	100	94
Bared teeth	The mouth is half opened, and the lips and lip corners are retracted so that the teeth are exposed in a white band.	Visual	74	25	1, 2, 3	Affiliative, agonistic, grooming, play, submissive	21 F, 4 M	4 I, 6 J, 2 S, 13 A	96	97	99
Bend	In an exaggerated movement, the monkey bends its upper body downward, close to the ground, to place its face in front of the recipient's face, usually an infant.	Visual	19	7	2, 3	Affiliative, parental care, submissive	4 F, 3 M	0 I, 2 J, 0 S, 5 A	100	100	53
Bite	The monkey bites the recipient.	Tactile	19	13	1, 2, 3	Agonistic	10 F, 3 M	1 I, 5 J, 3 S, 4 A	100	100	89
Biting threat	The mouth is wide open, showing the teeth.	Visual	463	41	1, 2, 3	Affiliative, agonistic, parental care, play, sexual, submissive	28 F, 13 M	4 I, 9 J, 6 S, 22 A	100	100	97
Body contact	The monkey approaches the recipient so close that parts of its body touch the recipient's body. There is no other interaction between the individuals (e.g. no grooming, embracing, or physical contact during fighting).	Tactile	162	37	1, 2, 3	Affiliative, other	27 F, 10 M	4 I, 7 J, 6 S, 20 A	15	5	29
Body-body rubbing	The monkey gently rubs its body against the body of the recipient.	Tactile	10	10	1, 2, 3	Affiliative, play	6 F, 4 M	0 I, 2 J, 1 S, 7 A	80	40	40
Charge	The monkey charges the recipient over a short distance.	Visual	153	35	1, 2, 3	Agonistic, other, play, sexual	23 F, 12 M	3 I, 9 J, 3 S, 20 A	100	100	98
Chase	The monkey chases the recipient at high speed.	Visual	91	28	1, 2, 3	Affiliative, agonistic, play, sexual	19 F, 9 M	2 I, 9 J, 3 S, 14 A	100	100	100
Crouch	The monkey presses its belly on the ground, and hides its arms, legs and head under its body.	Visual	7	6	1	Affiliative, agonistic, submissive	5 F, 1 M	0 I, 2 J, 1 S, 3 A	100	100	100
Display	The monkey vigorously shakes its body up and down, jumps on site. It can be similar than object shake, but without making sound.	Visual	45	14	1, 2, 3	Affiliative, agonistic, other, play	7 F, 7 M	4 I, 6 J, 1 S, 3 A	100	100	97 ²
Elephant	The juvenile holds the upper part of its arm between its teeth and shakes the rest of its arm up and down, which looks like the trunk of an elephant (idiosyncratic gesture).	Visual	16	1	2	Affiliative, play	0 F, 1 M	0 I, 1 J, 0 S, 0 A	100	100	81

Table 1 continued

Gesture	Description	Modality	Occurrence	Subject	Group	Context	Sex	Age	% Looking	% Response waiting	% Attending
Embrace	The monkey wraps its arms and/or legs around the body of the recipient.	Tactile	72	25	1, 2, 3	Affiliative, parental care, play	16 F, 9 M	4 I, 9 J, 1 S, 11 A	99	93	90
Eyebrow raising	The eyes are wide open and the eyebrows are raised, making the paler skin above the eyelids visible.	Visual	477	42	1, 2, 3	Affiliative, agonistic, play, submissive	30 F, 12 M	2 I, 9 J, 4 S, 27 A	100	100	86 ²
Flee	The monkey flees at high speed, away from the recipient.	Visual	139	33	1, 2, 3	Affiliative, agonistic, play, submissive	24 F, 9 M	3 I, 9 J, 6 S, 15 A	99	99	96
Freeze	The arms are spread forward on the ground, the head is placed backward, and the body is lowered backward.	Visual	51	23	1, 2, 3	Affiliative, agonistic, play, submissive	18 F, 5 M	0 I, 7 J, 5 S, 11 A	100	98	72
Give ground	The monkey moves away from the recipient, but not at high speed. This is in response of a behaviour or an approach made by the recipient.	Visual	939	44	1, 2, 3	Affiliative, agonistic, grooming, other, play, sexual, submissive	34 F, 10 M	4 I, 9 J, 7 S, 24 A	93	78	86
Grab	The monkey grabs the recipient, without pushing or pulling.	Tactile	207	32	1, 2, 3	Affiliative, agonistic, grooming, other, parental care, play	22 F, 10 M	4 I, 9 J, 4 S, 15 A	93	92	78
Greeting	The monkey is placed side by side with the recipient, top to tail, its head turned toward the hindquarter of the recipient.	Visual	35	16	1, 3	Affiliative, agonistic	14 F, 2 M	0 I, 1 J, 1 S, 14 A	100	100	100
Groom present	The monkey presents a body part to be groomed to the recipient, by positioning this body part in front of the recipient.	Visual	457	44	1, 2, 3	Affiliative, grooming, sexual, submissive	32 F, 12 M	3 I, 9 J, 7 S, 25 A	21	99	98
Grooming initiation	The monkey starts to groom the recipient, that is, goes through the fur of the recipient with its fingers, removing dirt and/or parasites.	Tactile	482	46	1, 2, 3	Affiliative, agonistic, grooming, parental care, sexual, submissive	33 F, 13 M	3 I, 9 J, 7 S, 27 A	95	13	48
Ground rubbing	The monkey rubs the ground or another support with the palm of its hand(s).	Visual	60	15	1, 2, 3	Agonistic, other, play	9 F, 6 M	1 I, 4 J, 1 S, 9 A	93	92	90 ²
Ground slapping	The monkey slaps the ground or another support with the palm of its hand(s).	Audible	127	17	1, 2, 3	Affiliative, agonistic, play, submissive	11 F, 6 M	1 I, 3 J, 2 S, 11 A	99	99	74 ²
Hand-body touch	The monkey touches with its hand(s) the body of the recipient.	Tactile	464	47	1, 2, 3	Affiliative, agonistic, grooming, other, parental care, play, sexual	34 F, 13 M	4 I, 9 J, 7 S, 27 A	95	94	77
Hand-genitals touch	The monkey touches with its hand(s) the genital area of the recipient.	Tactile	51	29	1, 2, 3	Affiliative, play, sexual	19 F, 10 M	2 I, 5 J, 6 S, 16 A	100	96	80
Hand-hand touch	The monkey touches the hand(s) of the recipient with its hand(s).	Tactile	51	11	1, 2, 3	Affiliative, agonistic, play	7 F, 4 M	2 I, 3 J, 1 S, 5 A	84	84	88

Table 1 continued

Gesture	Description	Modality	Occurrence	Subject	Group	Context	Sex	Age	% Looking	% Response waiting	% Attending
Hand-own genitals	The female inserts her fingers inside her genitals (idiosyncratic gesture).	Visual	42	1	1	Affiliative, submissive	1 F, 0 M	0 I, 0 J, 1 S, 0 A	100	98	97 ²
Head bob	The monkey moves its head up and down vertically.	Visual	11	11	1, 2, 3	Agonistic, play	7 F, 4 M	1 I, 2 J, 2 S, 6 A	100	100	70
Head push	The monkey pushes the recipient with its head in a brief movement.	Tactile	19	12	1, 2, 3	Affiliative, other	8 F, 4 M	0 I, 1 J, 1 S, 10 A	95	95	42
Head shake	The monkey shakes its head from side to side.	Visual	36	18	1, 2, 3	Affiliative, agonistic, play, sexual, submissive	13 F, 5 M	0 I, 3 J, 1 S, 14 A	100	100	91
Head-body rubbing	The monkey gently rubs its head against the body of the recipient.	Tactile	21	15	1, 2, 3	Affiliative, play	8 F, 7 M	1 I, 5 J, 2 S, 7 A	95	95	71
Headstand	The monkey does a headstand, i.e. stands on its own head.	Visual	2	2	2, 3	Play	1 F, 1 M	2 I, 0 J, 0 S, 0 A	100 ¹	100 ¹	0 ¹
Invite young	The monkey lowers its hindquarter and presents it to an infant or juvenile, as an invitation to climb.	Visual	4	3	1, 2, 3	Affiliative	3 F, 0 M	0 I, 0 J, 0 S, 3 A	100	100	100
Jump on	The monkey bounces on the back of the recipient.	Tactile	42	9	1, 2, 3	Affiliative, agonistic, other, play	5 F, 4 M	3 I, 6 J, 0 S, 0 A	71	55	52
Kick	The monkey kicks the recipient with its foot/feet.	Tactile	20	7	1, 3	Affiliative, grooming, play	4 F, 3 M	2 I, 5 J, 0 S, 0 A	55	55	70
Kiss	The monkey firmly presses its mouth on the mouth of the recipient, usually an infant or juvenile.	Tactile	5	4	1, 3	Affiliative	2 F, 2 M	0 I, 1 J, 0 S, 3 A	100	100	100
Lift	The eyebrows and scalp are lifted up and down, rhythmically.	Visual	132	36	1, 2, 3	Affiliative, agonistic, play, sexual	28 F, 8 M	2 I, 5 J, 6 S, 23 A	99	99	81 ²
Lip smack	The monkey opens and closes its lips rapidly, with the lips covering its teeth and the tongue sticking out.	Audible	753	46	1, 2, 3	Affiliative, agonistic, grooming, other, parental care, play, sexual, submissive	34 F, 12 M	3 I, 9 J, 7 S, 27 A	100	97	87
Lunge	The monkey makes a sudden intense forward movement toward the recipient. Only the upper body is moved.	Visual	99	33	1, 2, 3	Agonistic, other, play, sexual, submissive	23 F, 10 M	3 I, 8 J, 4 S, 18 A	100	100	94
Make room	The monkey moves only a part of its body away from the recipient.	Visual	158	40	1, 2, 3	Affiliative, other, play, submissive	32 F, 8 M	4 I, 8 J, 6 S, 22 A	93	85	93
Mating initiation	The male starts to mount the female by clasping its feet around her upper legs while holding her hips with its hands, and starts intromission as well as pelvic thrusts.	Tactile	51	12	1, 2, 3	Sexual	0 F, 12 M	0 I, 6 J, 1 S, 5 A	84	41	67

Table 1 continued

Gesture	Description	Modality	Occurrence	Subject	Group	Context	Sex	Age	% Looking	% Response waiting	% Attending
Mock bite	The monkey gently grips the recipient with its teeth, without roughness.	Tactile	410	40	1, 2, 3	Affiliative, agonistic, grooming, other, parental care, play, sexual, submissive	27 F, 13 M	4 I, 9 J, 4 S, 23 A	96	96	86
Mount	The monkey grabs the hindquarter of the recipient with its hands and mount the recipient, without sexual behaviour. Pelvic thrusts can be observed.	Tactile	86	28	1, 2, 3	Affiliative, agonistic, play, sexual	17 F, 11 M	1 I, 9 J, 4 S, 14 A	93	84	87
Mouth-body touch	The monkey approaches its face to the body of the recipient and touches it with its mouth.	Tactile	29	16	1, 2, 3	Affiliative, parental care	12 F, 4 M	1 I, 2 J, 3 S, 10 A	100	93	72
Mouth-genitals touch	The monkey approaches its face to the genital area of the recipient and touches it with its mouth.	Tactile	66	30	1, 2, 3	Affiliative, agonistic, grooming, other, parental care, play, sexual	19 F, 11 M	1 I, 8 J, 4 S, 17 A	98	89	80
Mouth-mouth touch	The monkey approaches its face so close to the face of the recipient, that its mouth gently touches the mouth of the recipient.	Tactile	45	29	1, 2, 3	Affiliative, parental care, play	22 F, 7 M	4 I, 6 J, 5 S, 14 A	100	87	93
Object shake	The monkey vigorously shakes a support or fixed object with its hands, legs, or full body, making sound.	Audible	108	20	1, 2, 3	Affiliative, agonistic, other, play	9 F, 11 M	0 I, 8 J, 3 S, 9 A	94 ¹	90 ¹	90 ¹
Open mouth	The mouth is opened, and the lips cover the teeth. The eyes are wide open.	Visual	60	15	1, 2, 3	Affiliative, agonistic, play	12 F, 3 M	1 I, 3 J, 2 S, 9 A	100	100	91 ²
Peer	The monkey is close to the recipient and intensely looks it in the eyes. The head is lowered and placed forward.	Visual	164	37	1, 2, 3	Affiliative, agonistic, grooming, other, parental care, play, sexual, submissive	30 F, 7 M	1 I, 7 J, 6 S, 23 A	100	99	59
Pelvic thrusts	The monkey does pelvic thrusts, by moving its bottom forward and backward. This was recorded outside of Mount and Mating intention.	Visual	9	3	1	Affiliative	3 F, 0 M	0 I, 1 J, 0 S, 2 A	100	100	78
Pirouette	The monkey spins around, by a twirling movement of whole body.	Visual	13	5	1, 2, 3	Play	1 F, 4 M	1 I, 4 J, 0 S, 0 A	100	85	77
Presentation	The monkey presents its hindquarters to the recipient. The tail is often raised or moved to the side. Sometimes the monkey grabs the hair of its hindquarter or legs.	Visual	624	42	1, 2, 3	Affiliative, agonistic, grooming, play, sexual, submissive	34 F, 8 M	3 I, 9 J, 7 S, 23 A	97	97	81
Pull	The monkey grabs hold of a recipient's body part and pulls it.	Tactile	115	23	1, 2, 3	Affiliative, agonistic, grooming, parental care, play	16 F, 7 M	3 I, 9 J, 2 S, 9 A	93	95	47
Pursed lips	The monkey protrudes its lips together ahead, forming a round shape. The teeth are not visible.	Visual	48	12	1, 3	Affiliative, other, sexual, submissive	12 F, 0 M	0 I, 1 J, 5 S, 6 A	87 ¹	82 ¹	97 ¹

Table 1 continued

Gesture	Description	Modality	Occurrence	Subject	Group	Context	Sex	Age	% Looking	% Response waiting	% Attending
Push	The monkey pushes the recipient with its hand(s).	Tactile	113	27	1, 2, 3	Affiliative, agonistic, grooming, other, parental care, play, sexual	16 F, 11 M	1 I, 6 J, 4 S, 16 A	92	97	40
Roll	The monkey does a forward or backward roll.	Visual	8	2	1, 3	Play	1 F, 1 M	0 I, 1 J, 1 S, 0 A	100	100	100
Scalp backward	The ears are flattened against the head, and the scalp and cheek are retracted backward.	Visual	206	41	1, 2, 3	Affiliative, other, parental care, play, sexual	30 F, 11 M	3 I, 7 J, 6 S, 25 A	100	100	85 ²
Slap	The monkey hits the recipient with an opened hand.	Tactile	44	15	1, 2, 3	Affiliative, agonistic, grooming, parental care, play	9 F, 6 M	0 I, 6 J, 3 S, 6 A	98	100	55
Somersault	The monkey makes a flip.	Visual	12	5	1, 2, 3	Play	1 F, 4 M	0 I, 5 J, 0 S, 0 A	100	100	92
Spread leg	The monkey stretches one hind leg backward, without touching the recipient.	Visual	42	16	1, 2, 3	Affiliative, agonistic, play	15 F, 1 M	2 I, 2 J, 4 S, 8 A	93	98	74
Spread leg touch	The monkey stretches one hind leg backward, gently touching the recipient with its foot.	Tactile	19	6	1	Affiliative	6 F, 0 M	0 I, 1 J, 3 S, 2 A	100	100	42
Stare	The body of the monkey is tense, the head is placed forward, the eyes are wide open and directed to the recipient.	Visual	102	33	1, 2, 3	Affiliative, agonistic, other, play, submissive	22 F, 11 M	1 I, 8 J, 4 S, 20 A	100	100	92
Stretch arm	The monkey stretches its arm(s) toward the recipient, the palm being downward or to the side.	Visual	222	38	1, 2, 3	Affiliative, agonistic, parental care, play, submissive	25 F, 13 M	4 I, 8 J, 4 S, 22 A	99	99	91
Tail raising	The monkey holds its tail vertically straight, like a flag.	Visual	83	27	1, 2, 3	Affiliative, agonistic, grooming, other, play, sexual, submissive	20 F, 7 M	1 I, 6 J, 5 S, 15 A	59	94	89
Teeth grind	The monkey rubs its canines against each other, making exaggerated chewing movements with its jaws.	Audible	33	10	1, 2, 3	Agonistic, play, submissive	6 F, 4 M	0 I, 5 J, 1 S, 4 A	100	100	100
Ventral presentation	The monkey stands on two legs and presents its belly/genitals to the recipient.	Visual	17	12	1, 2, 3	Affiliative	11 F, 1 M	0 I, 2 J, 2 S, 8 A	100	100	76

386 *Flexibility*

387 Several gestures in one context

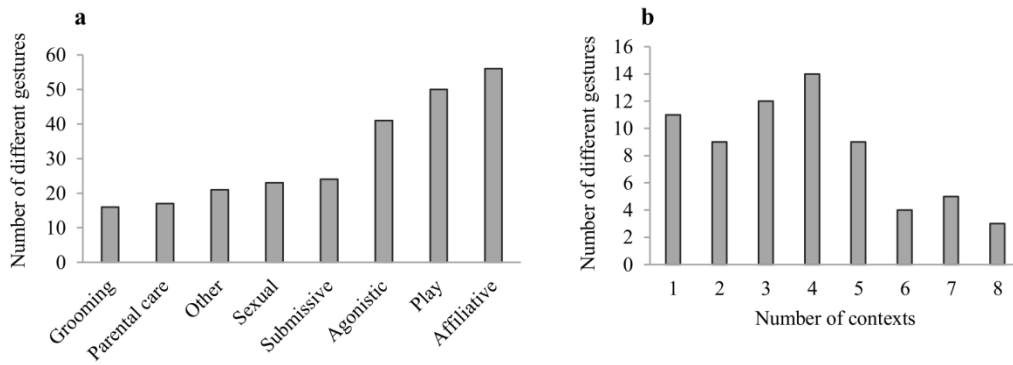
388 Several gesture types were systematically recorded for each of the 8 contexts (from 16 to
389 56 gestures, Figure 2a) emphasizing the diversity of the gestural lexicon used by baboons to
390 fulfil social functions. On average 31 different gesture types were used in each context (mean
391 \pm SE = 31.1 ± 5.5). Most of the gesture types were used in the affiliative (83.6% of the
392 repertoire), play (74.6%) and agonistic (61.2%) contexts. On average a third of the gesture types
393 were used in the submissive (35.8%), sexual (34.3%), and other (31.3%) contexts. A smaller
394 number of different gesture types were used in the context of parental care (25.4%) and
395 grooming (23.9%).

396

397 Same gesture in several contexts

398 If gestures were bound to specific contexts, we would observe specific gestures used in
399 single social contexts. However, most of the gesture types were used in more than one context
400 (from 1 to 8 contexts, Figure 2b), with on average each gesture type being used in 4 different
401 contexts (mean \pm SE = 3.7 ± 0.2). While 83.6% of the gesture types of the repertoire were used
402 in several contexts, only a small proportion of gestures was actually used in only one social
403 context (16.4%, Table 1), which statistically differed from a uniform distribution (Binomial test
404 compared to the proportion 0.5, $p < 0.001$, $N = 67$). Among the 11 gesture types that were
405 recorded in only one context, 7 were observed less than 15 times (see Table 1). The gestures
406 'lip smack', 'mock bite' and 'peer' were used in all 8 contexts.

407



408

409 **Figure 2:** Flexibility of the repertoire (a) Number of gesture types recorded in each context. (b)
 410 Number of gesture types as a function of the number of contexts in which they were recorded.

411

412 *Variability*

413 When looking at individual repertoire size, there was high variability across individuals
 414 (from 15 to 45 gestures), with on average 31 gesture types per subject (mean \pm SE = 31.1 \pm 1;
 415 Figure 3a). None of the 47 subjects showed the entirety of the 67 gesture types observed.

416 Across age classes

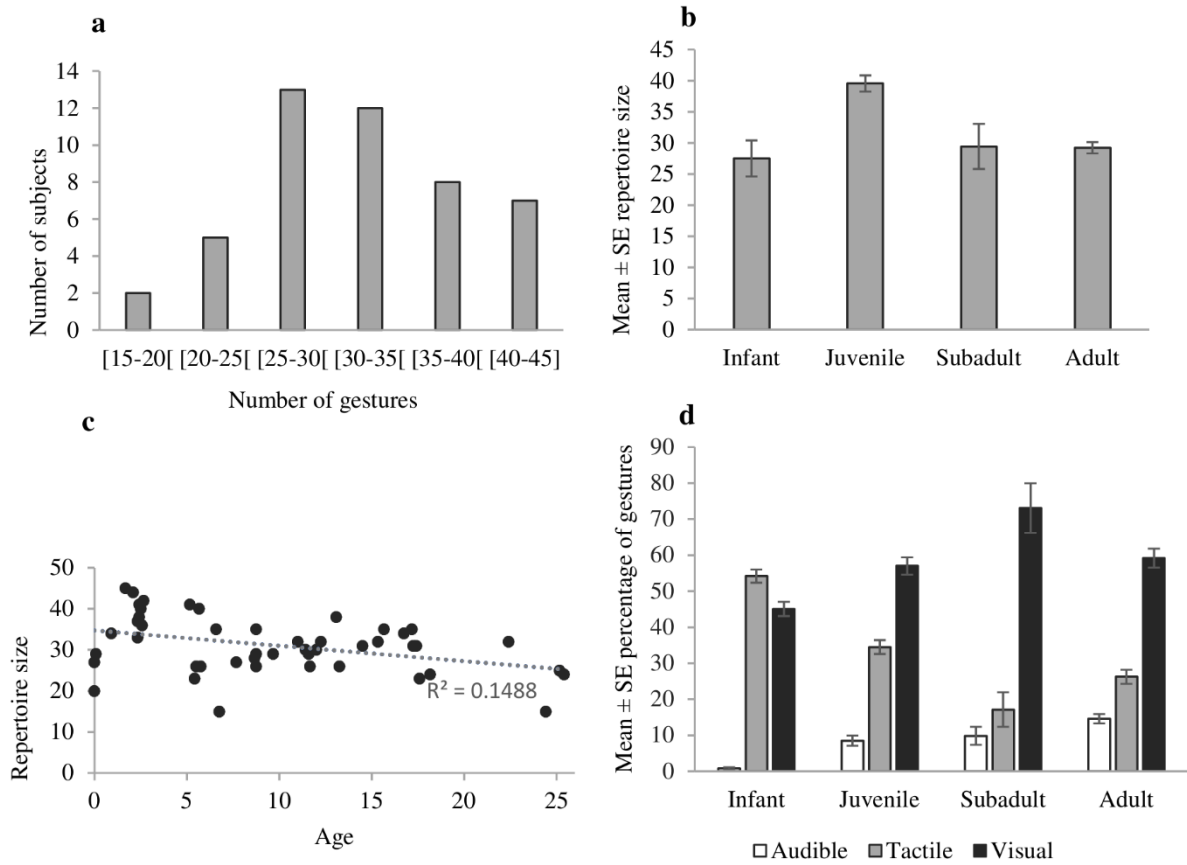
417 The size of individual repertoires differed significantly across age classes (One-way
 418 ANOVA, $F_{3,43} = 8.5$, $p < 0.001$; Figure 3b). Bonferroni post hoc analyses indicated that
 419 juveniles had significantly bigger repertoire than infants ($p = 0.006$), subadults ($p = 0.005$), and
 420 adults ($p < 0.001$). There was no statistically significant difference between the other age classes
 421 ($p > 0.05$ in all other cases). Furthermore, the size of the repertoire significantly decreased when
 422 age (in years) increased (Spearman correlation, $r_{45} = -0.35$, $p = 0.016$, Figure 3c). The gesture
 423 ‘invite young’ was produced only by adults, while the gesture ‘somersault’ was produced only
 424 by juveniles and the gesture ‘headstand’ was produced only by two infants.

425 The rate of gestures produced by each individual differed across age classes (Kruskal-
 426 Wallis test, $H_3 = 13.2$, $p = 0.004$, $N = 47$). Dunn-Bonferroni pairwise comparisons indicated

427 that juveniles (mean \pm SE = 55.4 \pm 4.8 gestures/h) produced more gestures than adults (mean \pm
428 SE = 33.5 \pm 2.2 gestures/h; $p = 0.004$) and subadults (mean \pm SE = 34.5 \pm 7.3 gestures/h; $p =$
429 0.018). There was no significant difference between the other age classes (mean \pm SE = 36 \pm
430 8.3 gestures/h for infants; $p > 0.05$ for all the other comparisons). The rate of production of
431 gestures significantly decreased when age (in years) increased (Spearman correlation, $r_{45} = -$
432 0.38, $p = 0.008$).

433 The best fitting model revealed an interaction effect between the modalities of the
434 gestures produced and the age class of the individuals (Wald test: $\chi^2 = 374.28$, $p < 0.0001$, $N =$
435 47; Best fitting model: AICc = 1697.68; Figure 3d; Online Resource 2, Table S1). Indeed, the
436 proportion of tactile gestures produced decreased significantly with the increase of age (in
437 years; Spearman correlation, $r_{45} = -0.35$, $p = 0.016$), whereas the proportion of audible gestures
438 increased significantly (Spearman correlation, $r_{45} = 0.55$, $p < 0.001$). There was no significant
439 correlation between the age and the proportion of visual gestures (Spearman correlation, $r_{45} =$
440 0.08, $p = 0.58$). However, when adults were removed from the sample, the proportion of visual
441 gestures produced increased significantly with age (Spearman correlation, $r_{18} = 0.66$, $p =$
442 0.001).

443



444

445 **Figure 3:** (a) Distribution of individual repertoire size. (b) Mean \pm SE individual repertoire size
 446 across age classes. (c) Individual repertoire size as a function of age (in years). (d) Mean \pm SE
 447 percentage of gestures produced for each modality and for each age class.

448

449 Between sexes

450 No significant difference was found between the repertoire size of males (mean \pm SE =
451 33.7 ± 2.2 gestures) and females (mean \pm SE = 30.1 ± 1.1 gestures; T-test, $t_{45} = 1.6$, $p = 0.11$).
452 The gestures ‘pursed lips’, ‘spread leg touch’, ‘pelvic thrusts’ and ‘invite young’ were produced
453 only by females, while ‘mating intention’ was, following our definition of this specific
454 behaviour, only produced by males. There was no significant difference between the rate of
455 gestures produced by males (mean \pm SE = 43.5 ± 5.8 gestures/h) and females (mean \pm SE = 36
456 ± 2.3 gestures/h; Mann-Whitney U test, $U = 179$, $z = -1$, $p = 0.33$, $N = 47$).

457

458 *Intentionality*

459 Orientation

460 Subjects produced significantly more gestures when looking at the recipient than when
461 not looking (Table 2a, Figure 4a; Online Resource 2, Table S2). On average, the subjects
462 produced 90.5% of the gestures (± 0.9) when looking at the recipient (Figure 4a). The
463 percentage of gestures produced when the subjects were looking at the recipient differed
464 significantly across age classes (Kruskal-Wallis test, $H_3 = 12$, $p = 0.008$, $N = 47$). Dunn-
465 Bonferroni pairwise comparisons indicated that infants (mean \pm SE = $75.8\% \pm 1$) produced
466 fewer gestures when looking at the recipient than adults (mean \pm SE = $91.6\% \pm 0.7$; $p = 0.014$)
467 and juveniles (mean \pm SE = $93.2\% \pm 1.1$; $p = 0.004$). There was no significant difference
468 between the other age classes (mean \pm SE = $90.9\% \pm 2.1$ for subadults; $p = 0.06$ for infants vs.
469 subadults and $p > 0.05$ for all the other comparisons).

470

471

472

473 Response waiting

474 Subjects produced significantly more gestures followed by response waiting than gestures
475 that were not (Table 2b, Figure 4a; Online Resource 2, Table S2). On average, the subjects
476 produced 87% of the gestures (± 1) when waiting for a response (Figure 4a). The percentage of
477 gestures followed by response waiting differed significantly across age classes (Kruskal-Wallis
478 test, $H_3 = 13.4$, $p = 0.004$, $N = 47$). Dunn-Bonferroni pairwise comparisons indicated that
479 infants (mean \pm SE = $72.6\% \pm 1.4$) produced significantly fewer gestures followed by response
480 waiting than adults (mean \pm SE = $87.4\% \pm 1.3$; $p = 0.028$) and juveniles (mean \pm SE = 91.4%
481 ± 1.2 ; $p = 0.002$). There was no significant difference between the other age classes (mean \pm
482 SE = $87.8\% \pm 1.4$ for subadults; $p > 0.05$ for all the other comparisons).

483

484 Attention

485 Subjects produced significantly more gestures when the recipient was attending than not
486 attending (Table 2c, Figure 4a; Online Resource 2, Table S2). On average, the subjects
487 produced 81.2% of the gestures (± 1.2) when the recipient was attending (Figure 4a). There was
488 no significant difference across age classes in the percentage of gestures produced when the
489 recipient was attending (Kruskal-Wallis test, $H_3 = 5.3$, $p = 0.15$, $N = 47$).

490 The choice of different modalities varied significantly according to the attentional state
491 of the recipient (Friedman test, $\chi^2_5 = 137.5$, $p < 0.001$, $N = 47$, Figure 4b). Specifically, the use
492 of audible and visual gestures decreased when the recipient was not attending (Wilcoxon signed
493 ranks test, audible: $z = -4.3$, $p < 0.001$, visual: $z = -5.6$, $p < 0.001$), whereas the use of tactile
494 gestures increased (Wilcoxon signed ranks test, $z = -5.8$, $p < 0.001$).

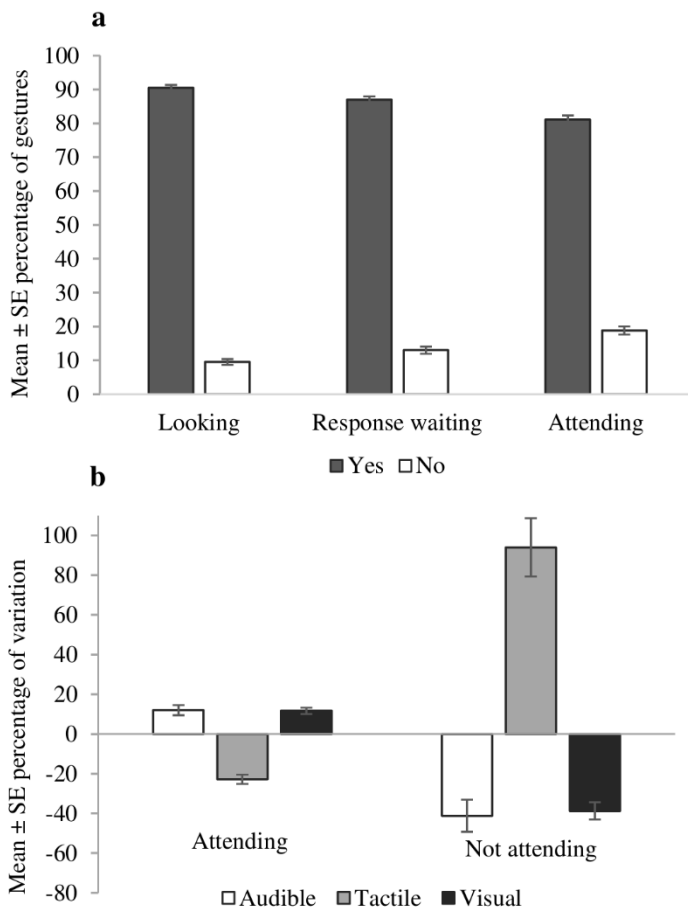
495

496 **Table 2.** Coefficients and significance of the variables entered in the GLMMs with a Poisson
 497 distribution to analyse whether subjects (N = 47) produced (a) more gestures when looking at
 498 the recipient than when not, (b) more gestures when waiting for a response from the recipient
 499 than when not, and (c) more gestures when the recipient was attending than not attending.
 500

Variables	Coefficient ± SE	Z	p	95% CIs
<i>(a) Orientation</i>				
Best fitting model: AICc = 1060				
Chi-square tests for the log-likelihood ratios, best fitting model-null model, p < 0.0001				
Orientation	-2.30 ± 0.04	-62.06	<0.001	-2.37 – -2.23
Age class	-0.12 ± 0.05	-2.30	0.022	-0.22 – -0.02
<i>(b) Response waiting</i>				
Best fitting model: AICc = 1135.1				
Chi-square tests for the log-likelihood ratios, best fitting model-null model, p < 0.0001				
Response waiting	-1.98 ± 0.03	-60.60	<0.001	-2.04 – -1.91
Age class	-0.12 ± 0.05	-2.30	0.021	-0.22 – -0.02
<i>(c) Attention</i>				
Best fitting model: AICc = 1096.6				
Chi-square tests for the log-likelihood ratios, best fitting model-null model, p < 0.0001				
Attention	-1.50 ± 0.03	-53.40	<0.001	-1.55 – -1.44
Age class	-0.13 ± 0.05	-2.64	0.008	-0.23 – -0.03

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505 **Figure 4:** (a) Mean \pm SE percentage of gestures produced when the subject was looking or not
 506 looking at the recipient, when the subject was waiting or not waiting for a response from the
 507 recipient, and when the recipient was attending or not attending. (b) Mean \pm SE percentage of
 508 variation in the use of each modality according to whether the recipient was attending or not
 509 attending. The deviation above and below the zero-line indicates the direction of the signaller's
 510 adjustment to the recipient's attention.

511

512 **Discussion**

513 This study is the first comprehensive and quantitative description of the types and
 514 properties of an old-world monkey species' gestural communication. Over one year of
 515 observation, 67 gestures were consistently recorded and compose the gestural repertoire of olive
 516 baboons. This repertoire may serve as a tool for researchers, as it can notably be used to select
 517 which type of gesture can be of interest for further studies, based on criteria of variability (i.e.

518 across individuals, sexes, and ages), flexibility across contexts, and intentionality (i.e.
519 signaller's orientation, response waiting and recipient's attention). Olive baboons used a variety
520 of audible, tactile and visual gestures, that were produced by movements of the whole body,
521 parts of the body, and parts of the face. This repertoire included a majority of visual gestures
522 (58% of the repertoire), which is consistent with the hypothesis that the type of gestures used
523 by a species may be related to its degree of terrestriality (Marler 1965; Liebal and Pika 2005).
524 Indeed, the nature of the communication of a species depends notably of its ecology, social
525 structure, and cognitive skills (e.g. Maestriperi 2005; Pika et al. 2005a; Parr et al. 2015).
526 Specifically, it has been suggested that more terrestrial species such as olive baboons (e.g. Patel
527 and Wunderlich 2010), that do not live under dense vegetation compare to more arboreal
528 species (e.g. siamangs; Liebal et al. 2004b), could rely on the use of visual modality of
529 communication because their environment does not constrain the perception of this type of
530 communication (Marler 1965; Liebal and Pika 2005; Pika et al. 2005a; Parr et al. 2015). In this
531 regard, baboons have evolved in an environment comparable to the paleo-environment of early
532 humans (Cerling et al. 2011), and they also form multi-tiered societies that closely resemble
533 human societies (Smuts et al. 2008). Hence, they offer a precious model to study the
534 evolutionary pathways from intentional communication to language.

535 In this regard, our results provide some of the first evidence of intentional gesture use
536 towards conspecifics by monkeys. When producing a gesture, olive baboons looked at the
537 recipient, waited for a response, and took into account the attentional state of the recipient.
538 Moreover, we also found evidence for means-ends dissociation as baboons flexibly selected
539 among different gestures to achieve one function, while a same gesture could be used to
540 different ends. Our results also indicate variations in the use of gestures by baboons which is
541 comparable to the variability reported in apes. Indeed, individuals did not produce the same set

542 of gestures. In addition, the gesture's types, rate and modality changed with individual's age,
543 but not with sex.

544

545 Repertoire size varied a lot across individuals, and baboons used around 46% of all
546 gesture types within their own repertoire, and actually none of the 47 subjects used the entirety
547 of the repertoire, which is consistent with what has been found in apes (Tomasello et al. 1994,
548 1997; Liebal and Pika 2005; Hobaiter and Byrne 2011a; Roberts et al. 2014). Moreover,
549 juveniles showed the largest repertoire and the highest rate of gestures produced, and these
550 values decreased with age. In apes, the active repertoire of juveniles is also larger than the ones
551 of adults and infants (Tomasello et al. 1989; Liebal et al. 2004b, 2006; Genty et al. 2009;
552 Hobaiter and Byrne 2011b). It has been suggested that young individuals first explore the
553 variety of gestures available, using a large number of gestures in a variety of interactions, before
554 retaining the ones that have proved to be the most effective in their social interactions and group
555 (Hobaiter and Byrne 2011b; Byrne et al. 2017). In chimpanzees, the likelihood of choosing an
556 effective gesture increases with age (Hobaiter and Byrne 2011b). In baboons, the use of tactile
557 gestures decreased with age, in contrast to audible and visual gestures. This corroborates the
558 observation made in ape species where gestures that are potentially effective over distance (i.e.
559 audible and visual gestures) increase with age, while gestures that involve contact with the
560 recipient (i.e. tactile gestures) decrease (Schneider et al. 2012; Fröhlich et al. 2016; Liebal et al.
561 2018). One explanation may be that young individuals use more tactile gestures because of their
562 close proximity with their mother, and reliance on this modality may decrease with the increase
563 of independence (Liebal et al. 2018). No difference of repertoire size and production of gestures
564 was found between males and females. In non-human primates, differences between sex are
565 scarcer and often limited to sexual context (e.g. Liebal et al. 2004b; Hesler and Fisher 2007;
566 Scott 2013).

567 It is difficult to directly compare the repertoire size between species because of the
568 variation in sampling methods across studies. Indeed, there are noticeable discrepancies (i) in
569 the definition of gesture (e.g. some studies only considered as ‘gestures’ the movements of the
570 hand(s); Hobaiter and Byrne 2017; Liebal et al. 2018), (ii) in the level of details used to define
571 and categorise each gesture type (i.e. granularity of description; Cartmill and Byrne 2011;
572 Byrne et al. 2017; Hobaiter and Byrne 2017), as well as (ii) in how gestures are described (e.g.
573 action-based or meaning-based; Hobaiter and Byrne, 2017). However, the repertoire size of
574 olive baboons is large and quite similar to the ones reported in apes such as bonobos (e.g. 68
575 gestures, Graham et al. 2017), chimpanzees (e.g. 66 gestures, Hobaiter and Byrne 2011a) and
576 orangutans (e.g. 64 gestures, Cartmill and Byrne 2010). Two idiosyncratic gestures were found
577 in this study, which may indicate that olive baboons may be able to invent new gestures.
578 However, this result might be taken with caution, because recent studies have shown that
579 increasing sampling effort or confronting gesture categorization choices could dismiss the
580 hypothesis of idiosyncrasy (Genty et al. 2009; Hobaiter and Byrne 2011a; Byrne et al. 2017;
581 Graham et al. 2017). Qualitative differences with some great ape gestural repertoires include
582 the absence of gesturing with detachable object in baboons. This latter difference requires
583 further investigation so as to specify whether this lack of behaviour in baboons is species-
584 specific or related to their captive environment which offered very limited opportunities with
585 detachable object. While chimpanzees, orangutans and gorillas often incorporate objects when
586 producing gestures (e.g. throwing an object or hitting the recipient with an object), this is less
587 the case in bonobos, siamangs and Barbary macaques (Liebal et al. 2004b, 2006; Hesler and
588 Fisher 2007; Genty et al. 2009; Liebal and Call 2012; Byrne et al. 2017). In apes, repertoires
589 have been found to overlap across species, despite differences in body shape and locomotion
590 (Hobaiter and Byrne 2011b; Byrne and Cochet 2017; Byrne et al. 2017; Graham et al. 2017). It
591 has been suggested that because gestures overlapped between apes, and because these gestures

592 were only a part of all possible gestures that an ape body could perform (Hobaiter and Byrne
593 2017), these gestures may have a common descent and the gestural repertoire may be inherited
594 (Byrne et al. 2017). It is worth noting that some gestures described in olive baboons (e.g.
595 embrace, grab, presentation, hand body touch, stretch arm, bared-teeth, lip-smack) seem not
596 only to overlap with gestures described in other monkeys such as macaques (Maestriperi 1996,
597 1997, 2005; Hesler and Fisher 2007) and other baboon's species (Rowel 1967; Kummer 1968),
598 but also with gestures described in ape's species (Liebal et al. 2004b, 2006; Parr et al. 2015;
599 Byrne et al. 2017). If some gestures are actually shared by apes, macaques and baboons, it may
600 imply that their phylogenetic origin may be relatively old, going back to the ancestor of
601 catarrhine primates. Overall, an effort to increase consistency between studies is still necessary
602 to provide a solid comparison basis of the gestural repertoires across species (Byrne et al. 2017;
603 Hobaiter and Byrne 2017; Graham et al. 2018; Liebal et al. 2018; Pika and Fröhlich 2018).

604

605 Flexibility assessment showed that approximately 31 gestures were used within the same
606 context, and each gesture was on average used in 4 different contexts. Such level of flexibility
607 is similar to the one found in the gestural communication of apes (e.g. Tomasello et al. 1994;
608 Pika et al. 2005b; Liebal et al. 2006; Genty et al. 2009), but also in macaques (Maestriperi
609 1996, 1997; Hesler and Fischer 2007). This emphasizes the diversity of the gestural lexicon
610 used by baboons to fulfil social functions. Note, however, that the diversity of gestures used
611 across contexts may depend on how the contexts had previously been defined and classified in
612 the study (e.g. the more the definition of the context is broad, the more behaviours can
613 potentially be included in this context). Byrne and colleagues investigated the flexibility of the
614 gestural lexicon of apes using a different approach. Instead of looking at functional contexts,
615 they used the meaning of gestures to assess flexible use (Cartmill and Byrne 2010; Hobaiter
616 and Byrne 2014; Byrne et al. 2017; Hobaiter and Byrne 2017). Using this approach, it has been

617 found that in chimpanzees and bonobos, flexibility resides mostly in the use of several gestures
618 for a specific meaning, and one gesture can have several meanings which are disambiguated by
619 the social context like in human pragmatics (Roberts et al. 2012; Hobaiter and Byrne 2014;
620 Byrne et al. 2017). Further investigation is required to explore the flexibility of meaning in
621 baboon gestures, by relying on the behavioural response of the recipient and whether the
622 signaller is apparently satisfied by this response or not (e.g. Apparently Satisfactory Outcome,
623 ASO, Hobaiter and Byrne 2017).

624

625 Importantly, our study provides a comprehensive evidence of the ability of a monkey
626 species to communicate intentionally with congeners, and outside experimental design
627 involving human-monkey communication. Specifically, our study showed that olive baboons
628 looked at their communication partner in 90.5% of cases, waited for a response and actively
629 adjusted the modality of their gestures to the attentional state of the recipient. Indeed, they
630 increased the production of tactile gestures while decreasing the production of audible and
631 visual gestures when the recipient was not visually attending. Tactile gestures involve physical
632 contact with the recipient and can thus be effective without the recipient being attending. Some
633 tactile gestures may also serve as attention getters, to trigger the attention of an inattentive
634 recipient (e.g. Tomasello et al. 1989, 1994; Liebal and Call 2012). For example, young
635 chimpanzees poke their recipient to initiate play when this one is not attending (Tomasello et
636 al. 1989). Note that here, baboons favoured tactile gestures over audible gestures when the
637 recipient was not visually attending. It can be noted that their repertoire includes only 4 audible
638 gestures and that these gestures have also a strong visual component. Thus, it is possible that
639 olive baboons use this type of modality more as a visual signal, with the audible component
640 remaining secondary. Overall these findings are consistent with the evidence of signallers'
641 sensitivity to the recipient's attention in apes (Genty et al. 2009; Hobaiter and Byrne 2011a;

642 Roberts et al. 2014; Waller et al. 2015), as well as in monkeys gesturing to humans in
643 experimental settings (Hattori et al. 2010; Maille et al. 2012; Meunier et al. 2013; Bourjade et
644 al. 2014; Canteloup et al. 2014, 2015). Therefore, the gestural communication of olive baboons
645 fulfils the main criteria of intentional communication, which means that olive baboons gesture
646 in a goal-directed way to influence specific target audiences. To go further in analysing the
647 intentionality of gesture production in olive baboons, future studies may also look at whether
648 they persist in using the same gesture, or whether they elaborate by using another gesture, when
649 the response they received is unsatisfactory (Liebal et al. 2004a; Leavens et al. 2005; Hobaiter
650 and Byrne 2011b; Roberts et al. 2013).

651 In addition, in spite of the very small sample size for infants, our results in infant baboons
652 must be stressed for at least one reason: they suggested that intentional communication might
653 not be there from birth. Infants actually were less likely to look at the recipient when producing
654 a gesture and they were also less likely to wait for a response. Thus, the intentional use of
655 gesture may develop over lifetime. Similar patterns are observed in infant chimpanzees where
656 markers of intentional communication increase with age (Bard et al. 2014; Fröhlich et al. 2018),
657 as well as in human infants. Indeed, children within their first year go through a pre-intentional
658 stage where their communication is not directed to communicative partners but seem to reflect
659 their internal states (Bates et al. 1979; Harding 1984). Through repeated interactions with their
660 caregiver who answers appropriately to these behaviours, children develop intentional
661 communication in which they direct their signals appropriately to their caregiver to receive a
662 particular response at around 9 months of age (Bates et al. 1979; Harding 1984; Carpenter et al.
663 1998). Thereby, through repeated interactions with their mother and other group mates, infants
664 may learn to direct their gestures to appropriate audience in a goal-directed way. Longitudinal
665 studies looking at the development of gestures and intentionality from birth may help to shed

666 light on how intentional gestural communication develops in non-human primates (e.g. see
667 Liebal et al. 2018 for a review).

668

669 Our investigation of the gestural communication system of olive baboons provides some
670 evidence of an evolutionary continuity with some key properties of human language in the
671 catarrhine lineage. Further studies are needed to investigate the gestural repertoire and
672 properties of other catarrhine primates, but also of other clades such as Platyrrhini, to track
673 down the precursors to human language. To conclude, this study offers a comprehensive
674 description of the gestural communicative system of olive baboons with empirical evidence of
675 flexibility, variability and intentionality. These core properties of human language that are
676 found in all natural languages, may have been present in the common ancestor of baboons and
677 humans, around 30-40 million years ago.

678

679 **Compliance with Ethical Standards**

680 All applicable international, national, and/or institutional guidelines for the care and use of
681 animals were followed.

682

683 **Conflict of Interest:** The authors declare that they have no conflict of interest.

684

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