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Cross-species variation in gaze following and conspecific preference among great apes, human infants and adults

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1 Although previous studies have shown that many species follow gaze, few study directly
2 compared between closely related species, and thus its cross-species variation remains
3 largely unclear. In this study, we compared between three great ape species (bonobos,
4 *Pan paniscus*, chimpanzees, *Pan troglodytes*, orangutans, *Pongo abelii*) and humans
5 (12-month-olds and adults) in their gaze-following responses to the videos of
6 conspecific and allospecific models. In the video, the model turned his head repeatedly
7 to one of the two identical objects. We used a non-invasive eye-tracking technique to
8 measure participants' eye movements, and used both conspecific and allospecific
9 models as stimuli to examine their potential preference in following conspecific rather
10 than allospecific gaze. Experiment 1 presented to great apes the videos of conspecific
11 and human models. We found that all species follow the conspecific gaze.
12 Chimpanzees did not follow the human gaze, while bonobos did. Bonobos reacted
13 overall more sensitively than chimpanzees to both conspecific and human gaze.
14 Experiment 2 presented to human infants and adults the videos of human, chimpanzee
15 and orangutan models. Both infants and adults followed the human gaze. Unlike adults,
16 infants did not follow the ape gaze. Experiment 3 presented to great apes the videos of
17 allospecific ape models. Consistent with Experiment 1, chimpanzees did not follow the
18 allospecific ape gaze, while bonobos and orangutans did. Importantly, preferential
19 following of conspecific gaze by chimpanzees (Experiment 1) and human infants
20 (Experiment 2) was mainly explained by their prolonged viewing of conspecific face.
21 Thus, it seems to reflect their motivation to selectively attend to the conspecific models.
22 Taken together, we conclude that, gaze following is modulated by both Subject species
23 and Model species in great apes and humans, presumably a reflection of the subjects'
24 intrinsic sensitivity to gaze and also their selective interest in particular models.

25 Keywords; conspecific model, gaze following, great apes, human infants, species
26 difference

27

28 Gaze following, defined as looking in the same direction as others after seeing their
29 gaze direction, is one of the best studied social behaviours in comparative cognition.

30 Gaze following functions in various ways depending on the species and contexts; from
31 simply exploiting the same information that others have acquired to making inferences

32 about others' intentions and knowledge (Hare, Call, & Tomasello, 2000). Gaze

33 following has been documented in numerous species, including primates [great ape:

34 (Bräuer, Call, & Tomasello, 2005); Old World monkeys: (Anderson & Mitchell, 1999;

35 Emery, Lorincz, Perrett, Oram, & Baker, 1997; Scerif, Gomez, & Byrne, 2004); New

36 World monkeys: (Amici, Aureli, Visalberghi, & Call, 2009; Burkart & Heschl, 2006),

37 lemurs (Ruiz, Gómez, Roeder, & Byrne, 2009; Sandel, MacLean, & Hare, 2011;

38 Shepherd & Platt, 2008)], nonprimate mammals [dogs: (Téglás, Gergely, Kupán, Miklósi,

39 & Topál, 2012); goats (Kaminski, Riedel, Call, & Tomasello, 2005)], birds [ravens:

40 (Bugnyar, Stöwe, & Heinrich, 2004); bald ibises: (Loretto, Schloegl, & Bugnyar, 2010)],

41 and reptiles (Wilkinson, Mandl, Bugnyar, & Huber, 2010). Although gaze following

42 appears quite widespread in phylogeny, studies have also documented its variation

43 among closely related species. Thus, stumptailed macaques follow gaze more

44 frequently than other macaque species (Tomasello, Call, & Hare, 1998), bonobos more

45 than chimpanzees (Herrmann, Hare, Call, & Tomasello, 2010) and human children more

46 than great apes (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007),

47 especially when only the model's eyes (not the head direction) served as a gaze cue

48 (Tomasello et al., 2007).

49 Moreover, rather than simply co-orienting with the model, in more complex
50 settings where individuals have to take into account the position and nature of visual
51 barriers in relation to both the model and themselves, the distribution of gaze following
52 among species appears more restricted. Thus, following gaze around barriers has
53 been documented in apes, ravens, capuchin and spider monkeys but not in marmosets
54 and bald ibises (Amici, et al., 2009; Bräuer, et al., 2005; Bugnyar, et al., 2004; Loretto, et
55 al., 2010; Tomasello, Hare, & Agnetta, 1999). Moreover, bonobos and chimpanzees,
56 unlike orangutans, take barrier opacity into consideration when following the gaze of
57 others (Okamoto-Barth, Call, & Tomasello, 2007) and double-looks (i.e., looking back at
58 the model's face after following her gaze and detecting nothing remarkable) have been
59 observed in great apes and Old world monkeys but not in capuchin and spider monkeys
60 (Amici, et al., 2009; Bräuer, et al., 2005; Scerif, et al., 2004).

61 Taken together, these studies show that even though the presence of gaze
62 following is displayed by numerous species, its expression in terms of strength and
63 flexibility vary substantially among species. Data like these are crucial to be able to test
64 evolutionary hypotheses linking gaze following with social and ecological factors that
65 may contribute to explain the differences among species, including the differences
66 between human and nonhuman animals (Rosati & Hare, 2009). However, this sort of
67 evolutionary analysis is currently hindered by two major difficulties. First, gaze
68 following is modulated not only by the individuals' potential abilities but also by
69 motivational or contextual factors. For example, in the previous studies with macaque
70 species, the subjects preferentially followed the gaze of particular individuals depending
71 on the social relationship with, and emotional status of the model (Goossens, Dekleva,
72 Reader, Sterck, & Bolhuis, 2008; Micheletta & Waller, 2012; Shepherd, Deaner, & Platt,

73 2006; Teufel, Gutmann, Pirow, & Fischer, 2010). Most relevant for the species
74 comparison is that many previous studies have used human models rather than
75 conspecific models for pragmatic reasons, and thus it is possible that the species differ
76 in the sensitivities to only human but not conspecific gaze. For example, Hattori, Kano,
77 & Tomonaga (2010) found that chimpanzees followed the gaze of a conspecific but not
78 of a human model when they were presented with the still pictures of those models (but
79 see Itakura, Agnetta, Hare, & Tomasello (1999), while human adults followed the gaze
80 of both types of models. Ideally, when comparing between two or more species, one
81 should use a crossed design with two factors: Subject species and Model species; i.e.
82 presenting the models of both species to the subjects of both species.

83 Second, the dependent measure most often used in previous studies has been
84 head turning frequency due to the difficulty in recording the eye movements directly.
85 However, species may differ in their physical constraints to move their head, body, and
86 eyes. For example, orangutans frequently move eyes but not heads to shift their gaze
87 (i.e. sideways gaze) (Kaplan & Rogers, 2002). Therefore, additional measurements
88 based on eye direction alone may reveal gaze following that goes undetected when
89 using more coarse measures based on head turning.

90 The developmental differences should also be taken into consideration when
91 comparing between species, especially between species that may follow different
92 developmental trajectories. Previous studies have shown that the sensitivity and
93 flexibility of gaze following change with age in human and nonhuman primates. That is,
94 human infants begin to follow the gaze of others from 3-6 month of age (D'Entremont,
95 Hains, & Muir, 1997; Hood, Willen, & Driver, 1998) and establish a robust pattern from 1
96 year of age (Corkum & Moore, 1998; von Hofsten, Dahlstrom, & Fredriksson, 2005).

97 Moreover, around 1 year of age human infants begin to follow gaze geometrically to
98 regions beyond their immediate view (Moll & Tomasello, 2004). Similarly to nonhuman
99 primates, human infants' gaze following is modulated by the motivational and contextual
100 factors. For example, they preferentially follow the gaze of those who have looked
101 toward interesting things versus nothing in the past (Chow, Poulin - Dubois, & Lewis,
102 2008), and take into account whether individuals have their eyes opened or closed
103 (Brooks & Meltzoff, 2002). In non-human primates, studies have shown that
104 macaques and chimpanzees begin to follow gaze by around one and three years of age,
105 respectively, and continue to increase the frequency of gaze following with age (Ferrari,
106 Kohler, Fogassi, & Gallese, 2000; Tomasello, Hare, & Fogleman, 2001) (but see
107 Okamoto et al. 2002 for the earlier onset of gaze following in a chimpanzee). Moreover,
108 macaques and chimpanzees display a relatively late onset for voluntary control of gaze
109 following such as habituation to unreliable observers (Tomasello et al. 2001) and
110 double-looks (Braeuer et al., 2005).

111 This study aimed to reveal the variation of gaze following among
112 closely-related species by addressing the above-mentioned issues. We used a
113 crossed design with two factors, Subject species and Model species, and studied four
114 hominid species, bonobos (*Pan paniscus*) chimpanzees (*Pan troglodytes*) orangutans
115 (*Pongo abelii*) and human infants (12-month-olds) and control adults (*Homo sapiens*)
116 (Figure 1). We implemented a relatively simple setting to examine the basic
117 performances of gaze following among species. That is, we measured the frequency
118 of gaze following when each species was observing a human or conspecific model
119 repeatedly turning his head to one of the two identical objects. We adopted the
120 eye-tracking method for two reasons: (1) to present controlled gaze cues of both

121 conspecific and allospecific models on the computer monitor and (2) to rely on the eye
122 movement measurement which is relatively independent of physical constraints. We
123 examined whether species (1) showed any evidence of gaze following for each model
124 species, (2) differentiated between conspecific and allospecific gaze, and (3) differed
125 from one another in their overall gaze sensitivities (frequency and/or response time)
126 when presented with either conspecifics or allospecifics. A previous study confirmed
127 that the great apes did not differ from one another in their basic patterns of eye
128 movement (Kano, Hirata, Call, & Tomonaga, 2011). However, the same previous study
129 also confirmed that humans, especially infants (Hood & Atkinson, 1993) tend to shift
130 their gaze less frequently (the fixations were “stickier”) than apes. Due to this species
131 difference and some procedural differences that existed for pragmatic reasons (e.g. the
132 type of attracting stimuli), we did not compare between great apes and humans in a
133 single experiment. Experiment 1 presented to great apes the videos of conspecific and
134 human model. Experiment 2 presented to human infants and adults the videos of
135 human and allospecific ape model (chimpanzee and orangutan). Experiment 3 returned
136 to great apes and presented the videos of allospecific ape models.

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Figure 1 around here
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143 Experiment 1

144 We examined the gaze following responses in bonobos, chimpanzees, and orangutans
145 when they were presented with a conspecific or a human model repeatedly turning his
146 head to one of the two identical objects. Based on previous studies using eye-tracking
147 (Hattori, et al., 2010), we predicted that chimpanzees would preferentially follow the
148 conspecific gaze rather than the human gaze. In addition, based on previous studies
149 using a different behavioural paradigm (Bräuer, et al., 2005; Herrmann, et al., 2010), we
150 predicted that bonobos would follow gaze, at least the human gaze, more frequently
151 than chimpanzees. Finally, based on previous studies using behavioural paradigms
152 (Bräuer, et al., 2005; Okamoto-Barth, et al., 2007), we predicted that orangutans would
153 follow the gaze of either conspecific or human models; however, it was unclear whether
154 they would follow gaze differentially depending on the observed species.

155

156 *Method*

157 *Participants*

158 Eight bonobos (*Pan paniscus*), 14 chimpanzees (*Pan troglodytes*), and 7 orangutans
159 (*Pongo abelii*) participated (mean age 16.5 years; 16 females, 13 males). All apes lived
160 in groups (> 10 individuals) with their conspecifics (but not with their allospecifics) in the
161 Wolfgang Köhler Primate Research Centre (WKPRC). Most of the apes were raised by
162 their biological mothers. Although some of them were reared by humans early in
163 ontogeny (hand reared), they mostly grew up with conspecifics from an early age (for
164 the details about participants, see Table A1). All great apes were housed in semi-natural
165 indoor enclosures (175-430 m²) with sleeping and testing rooms, and also in outdoor
166 enclosures during the summer time (1400-4000 m²). Both enclosures were equipped

167 with climbing structures, natural vegetation, and enrichment devices to foster extractive
168 foraging activities. They were provided with fresh fruits, vegetables, eggs, meats,
169 cereals, and leaves distributed in three main meals and occasional enrichment
170 programmes. Water was available ad libitum throughout the day. They voluntarily
171 participated in the study and were never food or water deprived. Animal husbandry and
172 research complied with the EAZA Minimum Standards for the Accommodation and Care
173 of Animals in Zoos and Aquaria and the WAZA Ethical Guidelines for the Conduct of
174 Research on Animals by Zoos and Aquariums, respectively. All apes were tested in
175 testing rooms located at WKPRC.

176

177 *Apparatus*

178 The eye movements of ape participants were non-invasively recorded with an infrared
179 eye-tracker (60 Hz; Tobii X120, Tobii Technology AB, Stockholm, Sweden) in an
180 approximately 60-cm viewing distance. We tested them unrestrained but separated
181 from the experimenter and eye-tracker with a transparent acrylic panel. However, in
182 order to keep their heads relatively still, we implemented a nozzle and tube attached to
183 the acrylic panels, which produce grape juice little by little, and let the apes suck the
184 nozzle during the recording (Figure 1a; also see Figure A1). No explicit training was
185 conducted for the apes. Stimuli were presented on a 22-inch LCD monitor (1366x768
186 pixel) with Tobii Studio software (version 3.2.1).

187 Two-point automated calibration was conducted for great apes by presenting a
188 small object or video clip on each reference point. A relatively small number of reference
189 points was adopted for apes because they tended to view those reference points only
190 shortly. However, we manually checked the accuracy at five points after the initial

191 calibration and repeated the calibration if necessary. As a result, our preliminary session
192 confirmed the comparable accuracy between apes and humans (see Kano, Call, &
193 Tomonaga 2012 for the accuracy estimate). Before every test session for apes, we
194 checked the accuracy manually and started the session when we confirmed that the
195 error value was less than 1-2 degree.

196

197 *Stimuli and Procedure*

198 The stimuli were 10-second videos in which a model repeatedly looked at one of the two
199 identical objects (hereafter “target” as opposed to “distractor”). The model was either a
200 male bonobo, chimpanzee, orangutan (one of the members from WKPRC), or a male
201 human (F.K.) (Figure 1b). These models were familiar to the ape participants (the apes
202 had at least some regular visual access even to allospecific models). Each model’s
203 head turn was videotaped at the testing room of WKPRC, and then later edited in Adobe
204 Premiere Pro so that the model appeared to look at the target repeatedly in the final video.
205 The brightness and contrast were matched across stimuli as much as possible. The
206 objects were plain coloured square shapes (the colour was selected not to stand out too
207 much from the background; green for the bonobo video and red for the other videos,
208 depending on the greenish/reddish background tones). In each video, the model faced
209 forward for 1 second, and for the remaining of time (9 s), repeatedly looked at the target
210 by turning both eyes and head back and forth. The head turning frequency varied
211 among stimuli in order to conserve the natural speed of each model’s head turn (4, 5, 5,
212 3 times respectively for bonobo, chimpanzee, human, and orangutan video; each head
213 turn was thus about 1.8-3 s; see Video S1).

214 Each ape viewed the videos of both conspecific and human model. Each video
215 was repeated for 3 times (total 6 trials). Each ape viewed a single video in a day (total 6
216 days). The order of presenting model type (conspecific or human) and direction of the
217 model's gaze (left or right) was counterbalanced across individuals. The experimenter
218 initiated the presentation of each video when apes were attending to the monitor.

219

220 *Data analysis*

221 Participants' fixations were detected by the Tobii fixation filter using Tobii Studio (version
222 3.2.1) with a default setting. To determine which areas each fixation landed on, we
223 defined the area of interest (AOI) as a circle shape respectively for target, distractor
224 (diameter 350 pixels), and model's face (diameter 400-700 pixels depending on the size
225 of model's face; Figure 1c).

226 The main measurement was the proportion of trials in which the participants
227 first looked at the target or distractor after the initiation of model's head turn (hereafter,
228 the proportion of first look) with respect to total number of trials (including the trials in
229 which participants looked at neither). We also measured the total number of fixations
230 onto the target or the distractor (after the initiation of model's head turn). As this
231 measure yielded very similar results with the first look measure throughout this study,
232 we report these results in detail in the Supplementary Material.

233 In addition, to examine how rapidly each species responded to the gaze, we
234 measured the response time when the participants first looked at the target (the
235 initiation of looks at the target from the initiation of the model's head turn). Moreover, to
236 examine whether the occurrence of gaze following was mediated by the strength of
237 attention to the model's face, we measured the amount of time spent viewing for the

238 model's face before the model's first head turn (hereafter, face viewing time) and
239 correlated that value with the proportion of first look at the target. We standardized the
240 face viewing time as the proportion of viewing time for face with respect to the total
241 viewing time for the entire scene.

242 For the statistical analyses, we distinguished between within-species and
243 between-species analyses. Within-species analysis tested whether each species show
244 any evidence of gaze following and differential sensitivity to the conspecific versus
245 human gaze (a repeated-measures ANOVA with Object and Model species as factors).
246 Between-species analysis tested whether those species quantitatively differed from one
247 another in their frequency of gaze following and their sensitivity to conspecific versus
248 human gaze (a repeated-measures ANOVA with Subject species, Object, and Model
249 species as factors). All analyses were conducted in SPSS (version 20).

250

251 *Results*

252 *Between-species analysis*

253 Figure 2 presents the means and standard errors of first look. A repeated-measures
254 three-way ANOVA revealed a significant main effect of Object ($F_{1,26} = 24.93$, $P < 0.001$,
255 $\eta^2 = 0.49$). Thus, overall, great apes first looked at the target rather than the distractor
256 more frequently than *vice versa*, indicating that they followed the model's gaze. There
257 was a significant main effect of Subject species ($F_{2,26} = 15.59$, $P = 0.040$, $\eta^2 = 0.22$).
258 However, we also found a significant two-way interaction between Subject species and
259 Object ($F_{2,26} = 4.16$, $P = 0.027$, $\eta^2 = 0.24$). Thus, species also differed from one another
260 in their frequency of first look at the target versus the distractor. More specifically,
261 bonobos followed the gaze more frequently than chimpanzees ($F_{1,20} = 16.74$, $P = 0.001$,

262 $\eta^2 = 0.45$). Bonobos differed from chimpanzees particularly in their responses to the
263 human gaze ($F_{1,19} = 7.22, P = 0.015, \eta^2=0.27$) rather than to the conspecific gaze ($F_{1,19}$
264 $= 1.62, P = 0.21, \eta^2 = 0.07$). Although bonobos and chimpanzees responded to
265 conspecific versus human gaze somewhat differently, we did not find a significant
266 three-way interaction between Model species, Subject species, and Object ($F_{2,26} = 0.87,$
267 $P = 0.43, \eta^2 = 0.06$). Orangutans did not significantly differ from either bonobos or
268 chimpanzees in their frequency of first look at the target versus the distractor ($P_s > 0.1$).

269 We also examined the individual differences in terms of sex (male, female), age
270 (young ≤ 9 year of age, adult > 9 year of age), and rearing history (mother, hand
271 reared) by including those factors into the same analysis. However, we did not find any
272 significant effect of these factors ($P_s > 0.1$), and importantly, the species difference in
273 first look at the target versus the distractor was still detected in this follow-up analysis
274 (Species \times Object ; $F_{2,16} = 3.96, P = 0.040, \eta^2 = 0.33$).

275 We then examined whether the species difference in first look at the target was
276 related to the species difference in face viewing time (how long they spent viewing the
277 face before the model's first head turn). Species did not significantly differ from one
278 another in their face viewing time ($F_{2,28} = 2.62, P = 0.092$). In addition, there was no
279 significant correlation between first look at the target and face viewing time (Pearson's r
280 $= -0.12, N = 29, P=0.51$). Thus, it is unlikely that the species difference in overall
281 frequency of gaze following was due to the variations of face viewing time.

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Figure 2, Table 1 and 2 around here

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286

287 *Within-species analysis*

288 We then examined the pattern of first look respectively in each species using two-way
289 ANOVAs. In bonobos, we found a significant main effect of Object ($F_{1,7} = 19.38$, $P =$
290 0.003 , $\eta^2 = 0.73$) but not a significant interaction between Object and Model species ($F_{1,7}$
291 $= 0.038$, $P = 0.85$, $\eta^2 = 0.005$), indicating that they followed the gaze of both conspecific
292 and human models. Similarly, in orangutans, we found a trend in the main effect of
293 Object ($F_{1,6} = 5.25$, $P = 0.062$, $\eta^2 = 0.46$) (we found a significant main effect of Object in
294 the total number of fixations, see Supplementary Material) but not a significant
295 interaction between Object and Model ($F_{1,6} = 0.60$, $P = 0.46$, $\eta^2 = 0.09$). In chimpanzees,
296 we did not find a significant main effect of Object ($F_{1,13} = 1.63$, $P = 0.22$, $\eta^2 = 0.11$); yet
297 we found a significant interaction between Object and Model ($F_{1,13} = 5.06$, $P = 0.042$, η^2
298 $= 0.28$). Follow-up paired t-tests indicated that chimpanzees followed the gaze of
299 conspecific model ($t_{13} = 2.82$, $P = 0.014$) but not that of human model ($t_{13} = 0.51$, $P =$
300 0.61).

301 We then examined whether chimpanzees' differential responses to the
302 conspecific versus human gaze may be because of their differential viewing of the
303 conspecific versus human face. As shown in Table 1, we indeed found that
304 chimpanzees viewed the conspecific face longer than human face (0.90 vs. 0.68; $t_{13} =$
305 3.87 , $P = 0.002$). Moreover, as shown in Table 2, they viewed the face AOI longer on
306 those trials in which they looked at the target (followed the gaze) than on those trials in
307 which they looked at the distractor (0.88 vs. 0.70; $t_8 = 3.03$, $P = 0.016$). Thus,
308 chimpanzees' preferential following of conspecific gaze may be simply explained by
309 their preferential viewing of conspecific face. No such relation was confirmed for

310 bonobos and orangutans ($P_s > 0.07$).

311

312 *Response time*

313 We examined the response time for first look (the time at which they first looked at the
314 target). We restricted this analysis to the presentation of conspecific models because
315 chimpanzees did not follow the human gaze. The response times were 1989 ± 451 ,
316 3364 ± 359 , and 2621 ± 501 ms (mean \pm S.E.), respectively for bonobos, chimpanzees,
317 and orangutans. Overall, there was some indication that species might differ in
318 response time ($F_{2, 27} = 2.85$, $P = 0.076$, $\eta^2 = 0.41$). Bonobos followed the conspecific
319 gaze significantly faster than chimpanzees ($t_{19} = 2.37$, $P = 0.028$). Orangutans did not
320 differ from either bonobos or chimpanzees in their response time ($P_s > 0.05$).

321

322 *Discussion*

323 All species followed at least conspecific gaze in this eye-tracking paradigm. That is, they
324 more frequently looked into the same than opposite direction with the conspecific model.
325 As for the species difference, we found that bonobos followed human gaze more
326 frequently than chimpanzees, which extends the similar finding in a previous study
327 using a different behavioural paradigm (Herrmann, et al., 2010). Although the two
328 species did not differ from one another in their frequency of following the conspecific
329 gaze, bonobos followed the conspecific gaze faster than chimpanzees. Thus, bonobos
330 seem to be more sensitive than chimpanzee to the gaze in general. Orangutans were
331 not statistically different from the other two species in their frequency or timing of gaze
332 following.

333 Also consistent with the previous study using a similar eye-tracking paradigm

334 (Hattori, et al., 2010), chimpanzees followed the conspecific gaze but not human gaze.
335 This preferential following of conspecific gaze seems to be related to their preferential
336 viewing of conspecific face. In addition, as shown in Figure 2, unlike chimpanzees,
337 bonobos frequently followed the gaze of both conspecific and human model. Thus, the
338 two species may differ from one another in their responses to conspecific versus
339 allospecific gaze. However, in Experiment 1, the statistical support for this idea was
340 insufficient (i.e. the three-way interaction; Model species \times Subject species \times Object).
341 Also, it remains unclear whether each species prefer not to follow only human gaze or
342 allospecific gaze in general. Also, for orangutans, although we did not find a statistical
343 difference between their responses to conspecific and allospecific, we also did not find a
344 clear statistical support for gaze following in response to the human gaze (see Figure 2).
345 Thus, we further explored great apes' responses to the allospecific gaze by presenting
346 the nonhuman allospecific gaze to the same participants in Experiment 3.

347

348

349

350 Experiment 2

351 This experiment examined how infants and adults differently follow the gaze of human
352 and ape model (chimpanzee and orangutan model) with the same method used in
353 Experiment 1. Based on a previous study using an eye-tracking paradigm (Hattori, et al.,
354 2010), we expected that human adults follow the gaze of both human and ape models.
355 Although numerous studies have used nonhuman agents as stimuli to examine infants'
356 social cognition in general, to the best of our knowledge, there is no previous study used
357 nonhuman primates as stimuli to examine infants' gaze following. Thus, two different
358 predictions are possible. One could hypothesize that human infants may follow both
359 human and nonhuman gaze because previous studies have shown that human infants
360 find goal-directedness in nonhuman agents if the agents show certain type of
361 behavioural cues (e.g. self-propelling; Gergely & Csibra 2003). However, some studies
362 also suggest that human infants do not follow the gaze of nonhuman agents if the
363 behavioural cues are limited. For example, infants followed the gaze of a toy animal only
364 when the animal showed contingent movements to the infants prior to gaze cueing
365 (Johnson, Slaughter, & Carey, 1998). Also, the previous studies suggest that human
366 infants, unlike great apes (Tomasello, Hare, Lehmann, & Call, 2007), rely more on the
367 eye than head direction when following the human gaze (Brooks & Meltzoff, 2002). In
368 this study, however, our ape models in the videos did not produce these cues explicitly.
369 Critically, our ape models did not provide a clear signal of eye direction, unlike our
370 human model, due to the nature of their eye morphology (i.e. dark sclera; Kobayashi &
371 Kohshima 1997).

372 Importantly, in this experiment, we made some minor changes in our video
373 stimuli. In our pilot test using the stimuli without any changes from Experiment 1, we

374 found that human infants did not view the target/distractor object and instead kept
375 looking at the face of human and ape model (while human adults followed the gaze).
376 This is probably because infants generally move their gaze less frequently (i.e. sticky
377 fixations) than great apes or human adults. Thus, based on the previous knowledge
378 (Moore, 2008), in this experiment we made two minor changes to the stimuli used in
379 Experiment 1 so that infants could release attention from the model's face and follow at
380 least the gaze of human model (for details, see Method and Supplementary Results) as
381 in many previous studies with the eye-tracking method (Senju & Csibra, 2008; von
382 Hofsten, et al., 2005).

383

384 *Method*

385 *Participants*

386 Twenty-two 12-month-old infants (within two weeks on either side; 11 males, 11
387 females) participated. The participants were recruited by telephone from a database of
388 parents who had volunteered to participate in developmental studies. All parents agreed
389 the informed consent upon coming to the institute. They were tested in a testing room
390 located at the Max-Planck Institute for Evolutionary Anthropology (MPI-EVA), Leipzig,
391 Germany. Two additional infants were tested but excluded from the analysis because of
392 fussiness (n=1) and a software malfunction (n=1). We also asked one of the parents of
393 infants to participate in this study, and so 22 adults (7 males, 15 females, 20-40 years
394 old) completed the same trials as the infants.

395 *Apparatus*

396 The human participants were tested using the same eye-tracker, monitor, and software.
397 Infants were seated on a parent's lap during the recording. Calibration was conducted

398 using five reference points for infants and adults by presenting a small video at each
399 reference point.

400 *Stimuli and Procedure*

401 Compared to the stimuli used in Experiment 1, we (1) increased the object saliency by
402 replacing them with colourful balls and (2) decreased the face saliency by reducing the
403 number of head turns of the model (only 2 times; see Video S2). Each infant and adult
404 viewed the videos of (1) human model and (2) ape species model. Half of the human
405 participants (11 infants and 11 adults) viewed the human and chimpanzee model and
406 the other half viewed the human and orangutan model. Each video was repeated 3
407 times (total 6 trials). Each infant and adult viewed all videos in a single session. The
408 whole session lasted approximately 10 minutes. The presentation order for model type
409 (conspecific or human) and direction of the model's gaze (left or right) was
410 counterbalanced across individuals. At the beginning of each video, we presented small
411 animations and boing sounds to make sure that infants looked at the monitor. Human
412 adults were told to watch the videos as they normally would. They were told neither the
413 contents of videos nor the purpose of experiments (i.e. gaze following) before
414 participating this experiment except that they would see apes and humans in the videos.

415 *Data analysis*

416 All analyses were conducted in the same way as in Experiment 1. Our initial analysis did
417 not reveal any significant difference between the two groups who saw the chimpanzee
418 or orangutan model, and thus we combined the two groups in the following analyses.

419

420 *Results*

421 *Proportion of first look*

422 Figure 3 presents the means and standard errors of first look. A repeated-measures
423 three-way ANOVA revealed a significant main effect of Object ($F_{1,42} = 53.92, P < 0.001,$
424 $\eta^2 = 0.56$), indicating that they followed the gaze of models. There was a significant main
425 effect of Age ($F_{1,42} = 7.0, P = 0.011, \eta^2 = 0.14$), but also a significant interaction between
426 Age and Object ($F_{1,42} = 13.48, P = 0.001, \eta^2 = 0.24$). Thus, adults followed the gaze
427 more frequently than infants. We also found a marginal three-way interaction between
428 Model, Object, and Age ($F_{1,42} = 3.45, P = 0.070, \eta^2 = 0.076$), suggesting that adults and
429 infants followed the gaze of human and ape models differently.

430 We then examined the pattern of first look respectively in each age group using
431 two-way ANOVAs. In adults, we found a significant main effect of Object ($F_{1,21} = 53.76,$
432 $P < 0.001, \eta^2 = 0.71$), but not the significant interaction between Model and Object ($F_{1,21}$
433 $= 0.068, P = 0.79, \eta^2 = 0.003$). Thus, adults followed the gaze of both human and ape
434 models. In infants, we found a significant main effect of Object ($F_{1,21} = 7.73, P = 0.011,$
435 $\eta^2 = 0.26$) but also a significant interaction between Model and Object ($F_{1,21} = 11.29, P =$
436 $0.003, \eta^2 = 0.35$). Follow-up paired t-tests for infants showed that they followed the
437 human gaze ($t_{21} = 3.83, P = 0.001$) but not the ape gaze ($t_{21} = 0.86, P = 0.39$).

438 We also examined whether the age difference in first look was related to the
439 face viewing time (how long they spent viewing the face before the model's first head
440 turn). Adults viewed the model's face significantly longer than infants ($t_{42} = 5.38, P <$
441 0.001). In addition, there was a significant correlation between first look at the target and
442 face viewing time (Pearson's $r = 0.39, N = 44, P = 0.007$). However, when we analysed
443 each age group separately, we did not find any significant correlation in each group (P s
444 > 0.5). Therefore, although adults followed the gaze more frequently and viewed the
445 face longer than infants; the individual difference in face viewing time does not

446 necessarily explain the individual difference in the first look.

447 Finally, we examined whether infants' differential responses to the human
448 versus ape gaze may be because of their differential viewing of the human versus ape
449 face. As shown in Table 1, we indeed found that infants viewed the human face longer
450 than the ape face (0.87 vs. 0.64; $t_{21} = 3.41$, $P = 0.003$). Moreover, as shown in Table 2,
451 they viewed the face AOI longer on those trials in which they looked at the target
452 (followed the gaze) than on those trials in which they looked at the distractor (0.84 vs.
453 0.75; $t_{18} = 3.45$, $P = 0.003$). Thus, infants' preferential following of human gaze may be
454 mediated by their preferential viewing of human face. We did not conduct the same
455 analysis for adults because they viewed both conspecific and allospecific faces over
456 90% of total time and rarely fixated on the distractor

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Figure 3 around here

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462 *Response time*

463 As in Experiment 1, we restricted the analysis for response time to the presentation of
464 human models because infants did not follow the gaze of ape models. The response
465 times were 2518 ± 276 and 1516 ± 231 ms (mean \pm S.E.), respectively for infants and
466 adults. Adults follow the gaze significantly faster than infants ($t_{42} = 2.78$, $P = 0.008$).

467

468 *Discussion*

469 Both human infants and adults followed at least the human model in this eye-tracking
470 paradigm, consistent with many previous studies. Human adults followed the gaze more
471 sensitively (more frequently and faster) than infants. Unlike adults, infants followed the
472 conspecific (human) but not ape gaze. This preferential following of conspecific face by
473 infants seems to be related to their preferential viewing of human face.

474 . It is not surprising to find that human adults follow both human and allospecific
475 ape gaze more sensitively than infants, given their sensitivity to both human and
476 allospecific ape eyes (Kano & Tomonaga, 2010) and a strong contagious tendency
477 toward the other's behaviours (Driver et al., 1999; Gallup et al., 2012). Also, human
478 adults are usually given numerous opportunities to view humans and nonhumans in
479 media and to interact with them in a real life. On the other hand, it is somewhat
480 surprising to find that human infants showed marked differences in their responses to
481 conspecific versus allospecific faces given that human infants attribute
482 goal-directedness of nonhuman agents in many contexts (Gergely & Csibra, 2003).
483 Infants' preferential gaze following was analogous to chimpanzees'. We will discuss the
484 possible mechanism underlying this apparent similarity between human infants and
485 chimpanzees in the General Discussion.

486

487

488 Experiment 3

489 This experiment further investigated whether great apes followed the allospecific gaze;
490 yet this time, we used other ape species as models. The purpose of this experiment was
491 to complement the crossed design with two factors, Subject species and Model species.
492 In particular, in Experiment 1, we found (1) chimpanzees' conspecific preference and (2)
493 bonobos' gaze sensitivity over chimpanzees'. However, since humans are very familiar
494 allospecifics to ape participants (e.g. caregivers), it is not entirely clear whether
495 Experiment 1's findings derive from their special response to the human model or from
496 general response to the allospecific model. If the latter were the case, the same pattern
497 of results of Experiment 1 would emerge also in this experiment.

498 *Method*

499 We tested the same ape participants using the same stimuli as in Experiment 1, but
500 presenting the chimpanzee and bonobo models to the bonobo and chimpanzee
501 participants, respectively. We also presented the bonobo model to the orangutan
502 participants (because the orangutan participants at the WKPRC had a better visual
503 access to the bonobo model than the chimpanzee model used in this study). The
504 presentation order of direction of the model's gaze (left or right) was counterbalanced
505 across individuals. The apparatus and other procedures are the same as in Experiment
506 1

507 *Results and Discussion*

508 Figure 4 presents the means and standard errors of first look . A repeated-measures
509 two-way ANOVA revealed a significant main effect of Object ($F_{1, 26} = 24.31, P = 0.012, \eta^2$
510 $= 0.28$) but also a significant interaction between Object and Subject species ($F_{2, 26} =$
511 $5.29, P < 0.001, \eta^2 = 0.48$). Specifically, bonobos followed the gaze of chimpanzee

512 model ($t_7 = 3.45$, $P = 0.011$), and orangutans followed the gaze of bonobo model ($t_6 =$
513 6.0 , $P = 0.001$). In contrast, chimpanzees did not follow the gaze of bonobo models (t_{13}
514 $= 0.51$, $P = 0.61$). We omitted the correlation analysis with the first look and face viewing
515 time in this experiment due to the insufficient number of trials. The response times for
516 the first look at the target were 2165 ± 463 and 3469 ± 715 (mean \pm S.E.), respectively
517 for bonobos and orangutans (not significantly different, $P > 0.1$).

518 Thus, taken together with the results from Experiment 1, chimpanzees seem to
519 differ from the other two species in their responses to the allospecific gaze. That is,
520 while bonobos and orangutans followed the gaze of allospecific models, chimpanzees
521 did not follow the gaze of allospecific models, either human or allospecific ape (bonobo)
522 model.

523 Finally, it should be noted that, although this study (and the previous study)
524 showed that chimpanzees followed the conspecific gaze, further studies are necessary
525 to pin down what type of conspecific models they prefer to follow. That is, this study (and
526 the previous study) used a familiar chimpanzee as a model, and thus it is possible that
527 their preferential gaze following may reflect their preference for familiar individuals (or
528 in-group individuals) rather than their preference for conspecific individuals in general.
529 This issue will be further discussed in General Discussion.

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Figure 4 around here

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536 General Discussion

537 In this study, we found that all species similarly followed the gaze of conspecific model.
538 However, while bonobos, orangutans, and human adults followed the gaze of both
539 conspecific and allospecific models, chimpanzees and human infants followed the gaze
540 of only conspecific models. Importantly, all stimulus models elicited the gaze following
541 responses in at least two species, and overall patterns for the presence/absence of
542 gaze following were unrelated to the low-level stimulus differences (e.g. colour,
543 brightness, and contrast of objects/models; but note some changes in the stimuli in
544 Experiment 2). Rather, the absence of following the allospecific gaze by chimpanzees
545 and human infants was related to their inattentiveness to the allospecific face.. This
546 seems to indicate that motivational differences of participants, not the competence
547 differences of participants nor the low-level differences of stimuli, are responsible for the
548 observed patterns of gaze following in these species.

549 Preferential following of conspecific gaze by chimpanzees and infants suggests
550 that they may preferentially learn from or acquire information from the conspecifics, the
551 most relevant others. That is, rather than reflexively following any individual's gaze, they
552 may first selectively view the relevant others and then follow the gaze. This behavioural
553 strategy, "select-then-follow", may be particularly important for those species like
554 chimpanzees and young humans who need to learn efficiently from particular
555 individuals.. Thus, at least in this sense, this study is consistent with the previous
556 studies reporting selective social referencing or selective behavioural copying of
557 particular others, such as majorities and dominants, by chimpanzees, capuchin
558 monkeys, vervet monkeys, and human children (Dindo, Whiten, & de Waal, 2009; Haun,
559 Rekers, & Tomasello, 2012; van de Waal, Renevey, Favre, & Bshary, 2010).

560 However, our findings about conspecific preference by chimpanzees and
561 human infants are limited in scope because it is unclear whether they followed the gaze
562 of conspecifics in general or only that of particular individuals (e.g. familiar/unfamiliar
563 individuals). Since previous studies have shown that the familiarity of the model
564 modulates the gaze following in monkeys and human infants and adults (Deaner,
565 Shepherd, & Platt, 2007; Gredebäck, Fikke, & Melinder, 2010; Micheletta & Waller,
566 2012), it is possible that our human and ape participants have some specific preference
567 for particular individuals. This is an issue that deserves further investigation especially
568 given that several studies have shown that communicative signals of strangers may
569 function differently for human infants and nonhuman animals (Topál, Gergely, Erdőhegyi,
570 Csibra, & Miklósi, 2009).

571 In this study, we observed particularly intriguing species differences between
572 bonobos and chimpanzees. First, unlike chimpanzees, bonobos did not show
573 preference in following the conspecific versus allospecific gaze. Thus, bonobos followed
574 the allospecific gaze more frequently than chimpanzees. Second, although the two
575 species did not significantly differ from one another in their frequency of following the
576 conspecific gaze, bonobos followed the conspecific gaze significantly faster than
577 chimpanzees. These species differences in gaze following seem to be unrelated to their
578 attentiveness to the model's face. Taken together, bonobos seem to differ from
579 chimpanzees in their intrinsic sensitivity to the gaze. One proximate explanation for this
580 species difference is that bonobos may follow the gaze more reflexively and thus less
581 selectively than chimpanzees. In support of this view, a previous study based on a
582 behavioural paradigm showed that bonobos and chimpanzees followed the
583 experimenter's gaze but chimpanzees inferred the location of hidden objects more

584 flexibly (thus perhaps less reflexively) in various experimental contexts than bonobos
585 (MacLean & Hare, 2012). As for the underlying mechanism, several previous studies
586 with macaques and humans have suggested that the relative strength of reflexive and
587 voluntary components in gaze following may be modulated by androgen-related
588 mechanisms (Shepherd, et al., 2006). Previous studies have also shown that bonobos
589 and chimpanzees are different in their levels or reactivity of androgens (Wobber et al.,
590 2010). Thus, the physiological differences between species may contribute to how much
591 reflectively or selectively each species follows gaze. To test this possibility, again future
592 studies should examine to what extent bonobos and chimpanzees are selective in
593 following the gaze of particular conspecific individuals.

594 The observed patterns of gaze following by orangutans fit somewhat in
595 between bonobos and chimpanzees in terms of the frequency and selectiveness.
596 Importantly, in this study, orangutans reliably followed the model's gaze, and in no case
597 they were significantly inferior to the other two species. One of the main differences
598 between this study and previous ones is that this study measured their eye- rather than
599 head/body-movements. Thus, orangutans in this study should have been free of
600 physical constraints derived from their relatively slow head/body movements. Also, this
601 study used a straightforward experimental setting which only required orangutans to
602 glance at the object existing in their visual fields. Thus, at least at the basic level, it is
603 reasonable to conclude that orangutans do not differ from the other great ape species in
604 their ability of gaze following.

605 Human infants preferentially followed human but not ape gaze in this study. As
606 discussed above, this pattern resembles that of chimpanzees, and the function may be
607 also similar between the two species. The underlying mechanisms may be also similar

608 between chimpanzees and infants. That is, human infants may have tried to selectively
609 acquire information from the human models as relevant others, thereby viewed the
610 human face longer than ape face, and followed the human gaze more frequently than
611 the ape gaze. However, based on the previous studies with human infants, alternative
612 explanations are also possible. That is, first, acknowledging the model's communicative
613 intent, which is provided as such signal as eye contact and contingent movements, is
614 important to elicit gaze following in infants (Farroni, Csibra, Simion, & Johnson, 2002;
615 Senju & Csibra, 2008). Thus, our infants may have failed to see the communicative
616 intent in the ape models because they had little experience in seeing and interacting
617 with great apes or similar kinds. Second, human infants, but not great apes, are
618 sensitive to the eye rather than head direction of human models (Brooks & Meltzoff,
619 2002; Tomasello, Hare, Lehmann, & Call, 2007). Thus, our infants may have failed to
620 perceive the eye direction of ape models because the apes do not have a clear contrast
621 between iris and sclera unlike humans (Kobayashi & Kohshima, 1997). Neither of those
622 accounts could be applied to our chimpanzees' preferential gaze following of
623 conspecific chimpanzee models. Thus, it is possible that distinct mechanisms underlie
624 the apparently similar pattern of gaze following between chimpanzees and human
625 infants. Likewise, although bonobos' and human adults' sensitivity to the allospecific
626 gaze may reflect a similar mechanism to some extent, e.g. reflexive following of any
627 gaze, it is also possible that distinct mechanisms underlie the apparent similarities,
628 especially given human adults' extensive experience with allospecific faces.

629 Finally, as a methodological lesson, the species variation of sensitivity to the
630 allospecific gaze suggests the importance of using conspecific models in the
631 comparative studies of gaze following and perhaps any social behaviours relying on

632 gaze following (also see Hare, et al., 2000; Tomasello, et al., 1998). However, it should
633 be noted that, although chimpanzees in this study did not follow the human gaze,
634 numerous previous studies have documented their robust responses to the human
635 experimenter's gaze. Parsimoniously, this disparity can be explained by the
636 methodological differences; in this study chimpanzees spontaneously pay less attention
637 to the human face than the conspecific face, but in the previous studies, the human
638 experimenter typically establishes the eye contact with chimpanzees before giving a
639 gaze cue (by presenting a food in front of the face or calling the chimpanzee's name).
640 Also, the relevance of stimuli (i.e. video versus live) may also contribute to the
641 chimpanzees' motivation of attending to the human face.

642

643 *Conclusion*

644 Using a crossed design with two factors, Subject species and Model species, we
645 showed that (1) all species followed the conspecific gaze, (2) unlike bonobos,
646 orangutans and human adults, chimpanzees and human infants preferentially followed
647 the conspecific but not allospecific gaze, and (3) bonobos followed both conspecific and
648 allospecific gaze more sensitively than chimpanzees. Thus, we conclude that gaze
649 following is modulated by both Subject species and Model species in great apes and
650 humans, presumably a reflection of the subjects' intrinsic sensitivity to gaze and also
651 their selective interest in particular models.

652

653

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796 Appendix

797 **Total number of fixations**

798 Overall, we obtained similar results with this measure as compared to the proportion of
799 first look.

800 *Experiment 1*

801 Figure A2 presents the means and standard errors of total number of fixations. A
802 repeated-measures three-way ANOVA (Object, Subject species, Model species)
803 revealed a significant main effect of Object ($F_{1, 26} = 6.77, P < 0.001, \eta^2 = 0.41$) and
804 Subject species ($F_{2, 26} = 9.82, P = 0.001, \eta^2 = 0.43$) and a significant interaction between
805 Subject species and Object ($F_{2, 26} = 6.97, P = 0.004, \eta^2 = 0.34$). Bonobos and
806 chimpanzees differ from one another in their total number of fixations on the target
807 versus the distractor ($F_{1, 20} = 11.77, P = 0.003, \eta^2 = 0.37$). Orangutans did not differ from
808 the other two species ($P > 0.1$). Within-species analysis revealed a significant main
809 effect of Object for bonobos ($F_{1, 7} = 8.58, P = 0.022, \eta^2 = 0.55$) and for orangutans ($F_{1, 6}$
810 $= 8.09, P = 0.029, \eta^2 = 0.57$), but not for chimpanzees ($F_{1, 13} = 0.21, P = 0.65, \eta^2 = 0.01$).
811 There was a significant interaction between Object and Model for chimpanzees ($F_{1, 13} =$
812 $5.41, P = 0.037, \eta^2 = 0.29$) but not for the other two species ($Ps > 0.5$).

813 *Experiment 2*

814 Figure A3 presents the means and standard errors of total number of fixations. A
815 repeated-measures three-way ANOVA (Object, Age, Model species) revealed a
816 significant main effect of Object ($F_{1, 42} = 147.88, P < 0.001, \eta^2 = 0.59$) and Age ($F_{1, 42} =$
817 $4.33, P = 0.044, \eta^2 = 0.09$) and a significant interaction between Object and Age ($F_{1, 42} =$
818 $19.62, P < 0.001, \eta^2 = 0.31$). When we analysed each group separately, in adults, we
819 found a significant main effect of Object ($F_{1, 21} = 40.88, P < 0.001, \eta^2 = 0.66$) but not a

820 significant interaction between Model and Object ($F_{1,21} = 1.91, P = 0.18, \eta^2 = 0.08$). In
821 infants, we found a significant main effect of Object ($F_{1,21} = 40.88, P < 0.001, \eta^2 = 0.66$)
822 but also a significant interaction between Model and Object ($F_{1,21} = 10.69, P = 0.004, \eta^2$
823 $= 0.33$).

824 *Experiment 3*

825 Figure A4 presents the means and standard errors of total number of fixations. A
826 repeated-measures two-way ANOVA revealed a significant main effect of Object ($F_{1,26} =$
827 $15.84, P < 0.001, \eta^2 = 0.37$). We did not find a significant interaction between Object and
828 Subject species ($F_{2,26} = 2.28, P = 0.12, \eta^2 = 0.14$). When we analysed each species
829 separately, we found a significant effect of Object for orangutans ($t_6 = 4.76, P = 0.003$), a
830 trend for bonobos ($t_7 = 2.29, P = 0.056$), and no significant effect for chimpanzees ($t_{13} =$
831 $0.88, P = 0.39$).

832

833 **The pilot test for Experiment 2 (infants and adults)**

834 A pilot test was conducted for Experiment 2 with a separate group of infants and adults
835 using the same stimuli as in Experiment 1.

836 *Method*

837 Eleven infants (6 males, 7 females) and 11 adults (3 males, 8 females) participated in
838 this pilot test. They were presented with the videos of chimpanzee and human model,
839 which were the same as those used in Experiment 1. All the other procedures were
840 same as those in the main test (Experiment 2).

841 *Results*

842 As shown in Figure A5 and A6, although control adults followed the gaze of both models
843 ($P_s < 0.01$), infants did not follow the gaze of either ($P_s > 0.2$). In most of the trials,

844 infants did not view the objects but instead kept viewing the faces of models.

845 *Discussion*

846 Such “sticky” fixations of infants to the faces may derive from their immaturity of
847 attention (Hood, Willen, & Driver, 1998). In particular, the objects in our stimuli may be
848 too simple in the forms (plain colored squares), and also the faces of models may be too
849 attractive in the motions (frequent head turns) to release their attention from faces. We
850 therefore changed those parameters In Experiment 2 and improved their performance
851 (see the main text).

852 One might expect that, by applying the same changes, great apes would also
853 show improved gaze-following performances. However, we doubt this possibility
854 because apes fixated the face far more briefly than do any humans (in this experiment
855 and also in general; Kano, Call, & Tomonaga 2012).

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860 Tables

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Table 1. Proportion of face viewing time (mean, S.E.) for each model species

Subject species	Model species	
	Ape	Human
Bonobos (Exp. 1)	0.66 (0.069)	0.57 (0.051)
Chimpanzees (Exp. 1)	0.90 (0.032)	0.68 (0.039)
Orangutans (Exp. 1)	0.83 (0.051)	0.70 (0.019)
Human infants (Exp.2)	0.71 (0.052)	0.88 (0.023)

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Table 2. Proportion of face viewing time (mean, S.E.) as a function of the looking patterns for the objects.

Subject species	Looking pattern		
	Looked at neither	Looked at target	Looked at distractor
Bonobos (Exp. 1)	0.60 (0.14)	0.62 (0.057)	0.62 (0.059)
Chimpanzees (Exp. 1)	0.80 (0.054)	0.88 (0.030)	0.70 (0.045)
Orangutans (Exp. 1)	0.79 (0.031)	0.75 (0.049)	0.78 (0.071)
Human infants (Exp. 2)	0.78 (0.060)	0.84 (0.029)	0.76 (0.044)

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Table A1. Species, sex, age, and rearing history of the ape subjects

Name	Species	Sex	Age	Rearing history
Fimi	Bonobo	F	5	Mother
Luiza	Bonobo	F	8	Mother
Yasa	Bonobo	F	15	Mother
Ulindi	Bonobo	F	19	Mother
Loto	Bonobo	M	3	Mother
Kuno	Bonobo	M	16	Hand Reared
Jasongo	Bonobo	M	23	Mother
Joey	Bonobo	M	30	Hand Reared
Kara	Chimpanzee	F	8	Mother
Fifi	Chimpanzee	F	20	Mother
Jahaga	Chimpanzee	F	20	Mother
Sandra	Chimpanzee	F	20	Mother
Getrudia	Chimpanzee	F	20	Mother
Riet	Chimpanzee	F	35	Hand Reared
Ulla	Chimpanzee	F	36	Hand Reared
Fraukje	Chimpanzee	F	37	Hand Reared
Bangolo	Chimpanzee	M	4	Mother
Kofi	Chimpanzee	M	8	Mother
Lobo	Chimpanzee	M	9	Mother
Alex	Chimpanzee	M	12	Hand Reared
Lome	Chimpanzee	M	12	Mother
Robert	Chimpanzee	M	37	Hand Reared
Raja	Orangutan	F	9	Mother
Padana	Orangutan	F	15	Mother
Dokana	Orangutan	F	24	Mother
Pini	Orangutan	F	25	Mother
Batak	Orangutan	M	3	Mother
Suaq	Orangutan	M	4	Mother
Tanah	Orangutan	M	4	Mother

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865

866 Figure legends

867 Figure 1: Overview of experiments. (a) The participants and (b) the models in this study.
868 (c) An example of area of interest (AOI) defined for the fixation analysis. In this study,
869 bonobos were presented with the bonobo, chimpanzee, and human models.
870 Chimpanzees were presented with the chimpanzee, bonobo, and human models.
871 Orangutans were presented with the orangutan, human, and bonobo models. Human
872 infants and adults were presented with the human, chimpanzee, and orangutan models.
873 Thus, each species was presented with three types of models, and each model was
874 presented to at least three species.

875 Figure 2: Proportion of first look in great apes when they were viewing conspecific and
876 human models. Error bars denote the standard error of mean. + $P < 0.07$, * $P < 0.05$,
877 *** $P < 0.001$.

878 Figure 3: Proportion of first look in human infants and adults when they were viewing
879 human and ape models. Error bars denote the standard error of mean. *** $P < 0.001$.

880 Figure 4: Proportion of first look in great apes when they were viewing allospecific ape
881 models. Error bars denote the standard error of mean. * $P < 0.05$, *** $P < 0.001$.

882 Figure A1: An ape on the apparatus (a) and the apparatuses in Experiment 1 (great
883 apes).

884 Figure A2: Total number of fixations in great apes when they were viewing conspecific
885 and human models. Error bars denote the standard error of mean. * $P < 0.05$, *** $P <$
886 0.001.

887 Figure A3: Total number of fixations in human infants and adults when they were

888 viewing human and ape models. Error bars denote the standard error of mean. *** $P <$
889 0.001.

890 Figure A4: Total number of fixations in great apes when they were viewing allospecific
891 ape models. Error bars denote the standard error of mean. + $P < 0.07$, ** $P < 0.01$

892 Figure A5: Proportion of first look in human infants and adults when they were viewing
893 human and ape models (Pilot test for Experiment 2). Error bars denote the standard
894 error of mean. ** $P < 0.01$, *.* $P < 0.001$

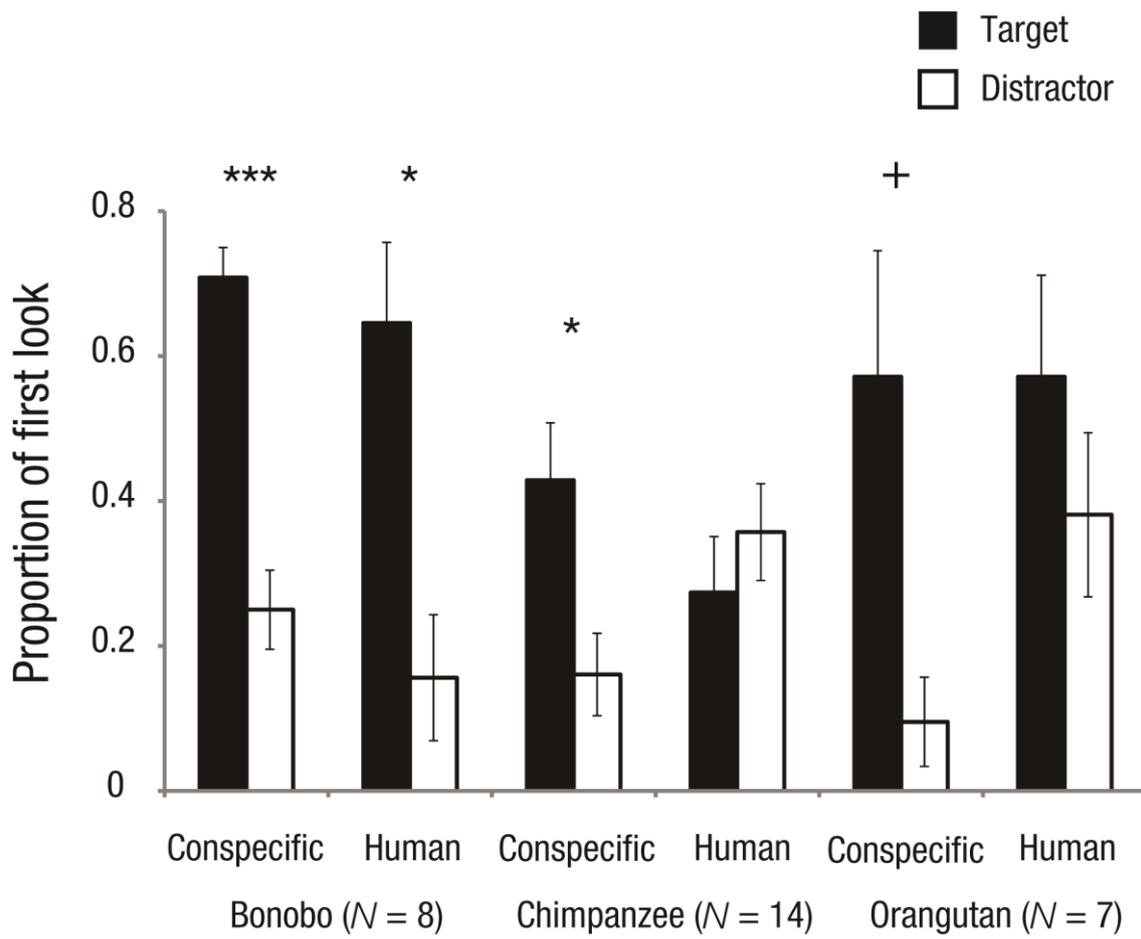
895 Figure A6: Total number of fixations in human infants and adults when they were
896 viewing human and ape models (Pilot test for Experiment 2). Error bars denote the
897 standard error of mean. ** $P < 0.01$, *.* $P < 0.001$

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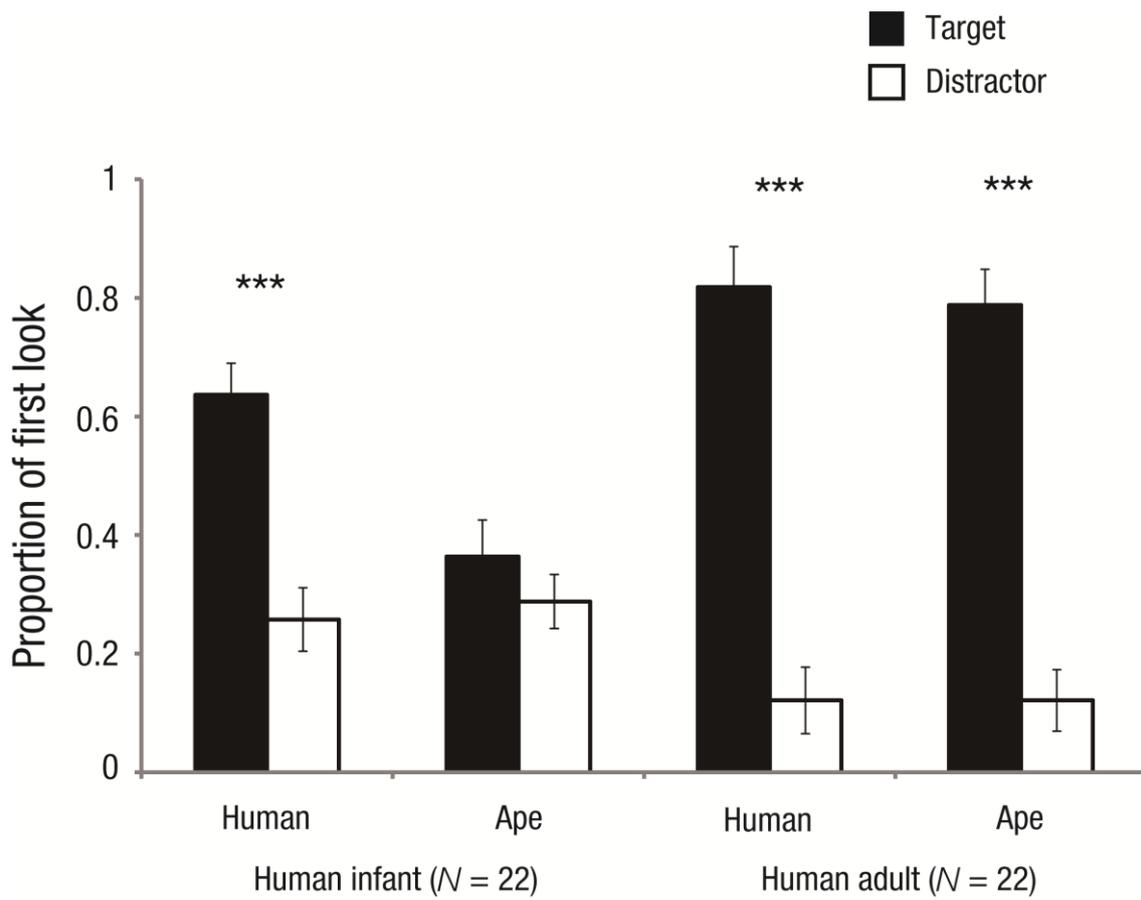
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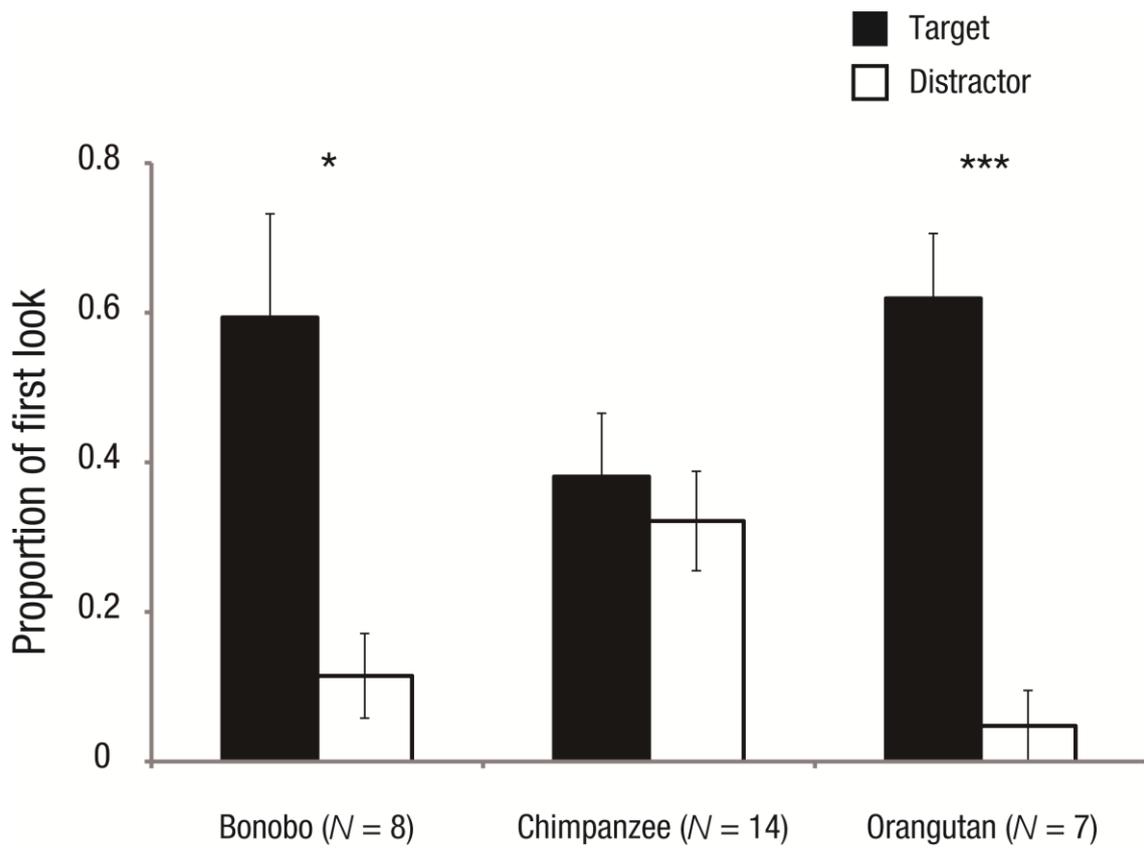


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