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Research article

Face and eye scanning in gorillas (*Gorilla gorilla*), orangutans (*Pongo abelii*), and humans (*Homo sapiens*): unique eye-viewing patterns in humans among hominids

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19 Abstract

20 Because the faces and eyes of primates convey a rich array of social information, the way in which  
21 primates view faces and eyes reflects species-specific strategies for facial communication. How are  
22 humans and closely related species such as great apes similar and different in their viewing patterns for  
23 faces and eyes? Following previous studies comparing chimpanzees with humans, this study used the  
24 eye-tracking method to directly compare the patterns of face and eye scanning by humans, gorillas,  
25 and orangutans. Human and ape participants freely viewed pictures of whole bodies and full faces of  
26 conspecifics and allospecifics under the same experimental conditions. All species were strikingly  
27 similar in that they viewed predominantly faces and eyes. No particular difference was identified  
28 between gorillas and orangutans, and they also did not differ from the chimpanzees tested in previous  
29 studies. However, humans were somewhat different from apes, especially with respect to prolonged  
30 eye viewing. We also examined how species-specific facial morphologies, such as the male flange of  
31 orangutans and the black–white contrast of human eyes, affected viewing patterns. Whereas the male  
32 flange of orangutans affected viewing patterns, the color contrast of human eyes did not. Humans  
33 showed prolonged eye viewing independently of the eye color of presented faces, indicating that this  
34 pattern is internally driven rather than stimulus dependent. Overall, the results show general  
35 similarities among the species and also identify unique eye-viewing patterns in humans.

36

37 Introduction

38 Human and non-human primates have highly sophisticated forms of facial communication. Faces and  
39 eyes convey a wide variety of information such as identity, age, sex, emotion, and direction of  
40 attention. Thus, primates perceive faces and eyes differently from the way they perceive other visual  
41 stimuli (Emery, 2000; Tomonaga, 2010). Moreover, primates often engage in prolonged face-to-face  
42 interactions that are accompanied by eye contact (looking into another individual's eyes) or its  
43 avoidance (Gomez, 1996; Kleinke, 1986; Thomsen, 1974). How and when such unique forms of facial  
44 communication evolved in primates have long been of interest, particularly from a comparative  
45 perspective (Chevalier-Skolnikoff, 1973; Darwin, 1872/1999; van Hooff, 1967).

46 Humans and great apes such as chimpanzees, gorillas, and orangutans are known to share  
47 several forms of facial communication with one another. For example, prolonged eye contact indicates  
48 mild threat, and thus gaze avoidance indicates submission (Goodenough, McGuire, & Jakob, 1993;  
49 Redican, 1975). Eye contact is also used in an affiliative context, such as the solicitation of play/sex  
50 and post-conflict appeasement (de Waal, 1990; Goodall, 1986; Kano, 1980; Yamagiwa, 1992). Gaze  
51 following (looking in the same direction) frequently occurs after the establishment of eye contact with  
52 another individual (Bräuer, Call, & Tomasello, 2005; Itakura, 2004; Okamoto-Barth, Call, &  
53 Tomasello, 2007; Tomasello, Hare, Lehmann, & Call, 2007). Additionally, studies have suggested that  
54 these species use eye contact ostensibly (i.e., viewing another individual's eyes with communicative  
55 intent) (Gomez, 1996).

56 On the other hand, notable differences among the species have also been identified. For  
57 example, although close-range long-bout affiliative communication typically accompanies intense eye  
58 contact in humans, this kind of communication seems to occur more frequently in tactile than in visual  
59 forms in great apes (e.g., grooming; Goodall, 1986; Shaller, 1963). Several studies have suggested that  
60 mutual gaze (returning another individual's gaze) is uncommon and that gaze avoidance is frequent in

61 gorillas (Shaller, 1963; but see Yamagiwa, 1992) and orangutans (Kaplan & Rogers, 2002). Kobayashi  
62 and Kohshima (2001) found that, compared with other primates, humans have exceptionally large  
63 white sclera that clearly contrasts with the colors of their iris and skin. These authors hypothesized that  
64 human eyes have evolved to enhance gaze signals such as eye direction. Tomasello et al. (2007) found  
65 that great apes (chimpanzees, bonobos, and gorillas) were less sensitive than human infants were to the  
66 eye direction of a human experimenter when the experimenter's head was immobile. Okamoto-Barth  
67 et al. (2007) found that, compared with chimpanzees, bonobos, and gorillas, orangutans were less  
68 sensitive to gaze (head) directions and more attracted to target objects.

69         These results suggest that, although humans and great apes share a basic set of facial  
70 communicative skills, significant species differences characterize their habitual styles. Direct  
71 comparisons are necessary to reveal such differences among these species. Kano and Tomonaga (2009,  
72 2010) used the eye-tracking method to measure how humans and chimpanzees scanned the faces and  
73 eyes of conspecifics and allospecifics. Both species were presented with pictures of whole bodies and  
74 faces, and they viewed the pictures freely. The species were strikingly similar in their patterns of face  
75 and eye scanning. For example, both species fixated on faces and eyes more frequently than on other  
76 parts of bodies and faces. However, several species differences were also identified. For example,  
77 chimpanzees viewed faces and eyes more briefly than did humans; typically, chimpanzees only  
78 glanced at eyes, whereas humans viewed both eyes (left and right eyes) alternately. Additionally, when  
79 presented with facial expressions including conspicuous mouth actions, humans viewed the eyes  
80 rather than the mouth, and chimpanzees viewed the mouth rather than the eyes. Thus, previous studies  
81 have shown both striking similarities among the species and unique eye-viewing patterns in humans.

82         At present, such face- and eye-scanning data are not available for other ape species. Thus,  
83 this study aimed to obtain a broader comparative picture about this issue. Following previous studies  
84 comparing chimpanzees with humans ([Kano & Tomonaga, 2009, 2010](#)), we compared the patterns of

85 face and eye scanning by humans, gorillas, and orangutans, We had three primary reasons for  
86 examining the patterns of face and eye scanning in gorillas and orangutans. First, gorillas and  
87 especially orangutans are phylogenetically more distant from humans than are chimpanzees. Thus,  
88 this study enabled us to test whether the unique eye-viewing patterns of humans indicate general  
89 differences between humans and great apes or isolated differences among species. Based on previous  
90 studies showing intense eye contact, especially in humans, it would be expected that humans would  
91 view eyes for longer durations than do gorillas and orangutans. Second, several of the previous studies  
92 have reported a high probability of gaze avoidance in gorillas and orangutans (Kaplan & Rogers,  
93 2002; Shaller, 1963). Additionally, orangutans lead semi-solitary lives in their natural habitats, which  
94 is the least socially specialized form among the great apes. The simple experimental design of this  
95 study (presenting facial pictures) enabled us to test gorillas' and orangutans' default motivation for  
96 viewing eyes (i.e., in the absence of social interaction).

97         Finally, each species has species-specific morphological facial features that have  
98 presumably evolved for purposes of communication. This study enabled us to test the role of these  
99 facial features in visual perception. For example, humans have a color contrast between the dark iris  
100 and white sclera in their eyes (Kobayashi & Kohshima, 2001), adult male gorillas have a high crest on  
101 the top of their heads, and adult male orangutans have developed flanges on the sides that are thought  
102 to be sexual signals (Ankel-Simons, 2000; Kuze, Malim, & Kohshima, 2005). Infant and juvenile  
103 orangutans have pale coloring around their eyes and mouth, thought to signal immaturity (Kuze, et al.,  
104 2005). As those facial features are visually conspicuous, they would be expected to automatically  
105 attract viewers' attention. That is, the viewing patterns would be expected to be dependent on the  
106 presence/absence of such conspicuous facial features. However, if viewing patterns were independent  
107 of the types of faces presented, such patterns would be internally driven rather than stimulus  
108 dependent.

109 Following previous studies comparing chimpanzees with humans ([Kano & Tomonaga, 2009](#), [2010](#)),  
110 this study used the eye-tracking method to perform direct comparisons among humans, gorillas, and  
111 orangutans with regard to their patterns of face and eye scanning. We employed a cross-species design,  
112 presenting both conspecific and allospecific pictures. We initially presented whole-body pictures and  
113 examined how humans and apes scanned faces versus bodies. We then presented facial pictures and  
114 examined how they scanned each facial feature (e.g., eyes, nose, and mouth). Picture models included  
115 both conspecific and allospecific individuals, males and females (adults), and familiar and unfamiliar  
116 individuals. To examine the effect of species-specific facial morphologies on viewing patterns,  
117 juvenile faces of gorillas and orangutans were prepared in addition to male adult and female adult  
118 faces, and the viewing patterns for all types of faces were compared with one another.

119 Method

120 Participants

121 Five gorillas (*Gorilla gorilla*), 10 orangutans (*Pongo pygmaeus*), and 12 humans (five males  
122 and seven females; all European adults; 21–52 years, mean: 30.5 years) participated in this study. All  
123 apes were housed in semi-natural indoor and outdoor enclosures (total 2,564 m<sup>2</sup> for gorillas, 1,910 m<sup>2</sup>  
124 for orangutans) at the Wolfgang Köhler Primate Research Center (WKPRC), Leipzig Zoo, Germany.  
125 All apes received regular food, enrichment, and water *ad libitum*. They were not deprived of food or  
126 water. All apes and humans voluntarily participated in the study. Animal husbandry and research  
127 complied with the EAZA Minimum Standards for the Accommodation and Care of Animals in Zoos  
128 and Aquaria and the WAZA Ethical Guidelines for the Conduct of Research on Animals by Zoos and  
129 Aquariums, respectively. Informed consent was obtained from all human participants. Table 1 lists the  
130 sex, age, and rearing history of each ape. Most of the ape participants were reared by their biological  
131 mothers. All apes and humans had extensive and regular experience interacting with both apes and  
132 humans at the zoo and were thus highly familiar with both kinds of faces.

133 -----  
134 Table 1 about here

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136 -----  
137 Figure 1 about here

138 -----  
139 Apparatus

140 All apes were tested in a chamber that separated the ape from the eye-tracking apparatus and  
141 the experimenter with transparent acrylic panels. The gaze movements of the apes were  
142 non-invasively recorded while their heads were unrestrained. We were able to implement this

143 unrestrained eye-tracking method by using two devices. First, we employed a table-mounted infrared  
144 eye tracker with wide-angle lenses ( $\pm 40$  degrees in the semicircle above the camera; 60 Hz; Tobii  
145 X120, Tobii Technology AB, Stockholm, Sweden). This eye tracker recorded both eyes of participants  
146 (the average value was used to estimate the single gaze point) and allowed relatively large head  
147 movements by participants. Second, the eye tracker and the 17-inch LCD monitor ( $1280 \times 1024$   
148 pixels) were mounted on a movable platform, and the distance between the platform and the  
149 participants was adjusted by the experimenter to the point at which the gaze could be most accurately  
150 recorded (approx. 60 cm). This adjustment was performed before each trial if necessary (but not  
151 during the trial).

152           To encourage the apes to sit still in front of the acrylic panel and face the eye tracker, the  
153 experimenter offered small pieces of fruit *ad libitum*. These were given to the apes before each trial if  
154 necessary (but not during the trial). However, eight of the 15 apes tested (Gorgo, Louna, Zola, Batak,  
155 Kila, Maia, Suaq, and Tanah; mostly juveniles) had difficulty in approaching the acrylic panel upon  
156 the request of the experimenter. We thus used a nozzle and tube attached to the acrylic panel, which  
157 produced regular drops of grape juice during the experiment; this motivated the apes to keep their  
158 heads in front of acrylic panel (Fig. 1a and b). The eye tracker was unable to track both eyes of one  
159 male adult gorilla (Gorgo) due to the wide distance between his eyes, and of one juvenile female  
160 gorilla (Louna) due to her strabismus. Therefore, we concealed the left eye of these apes from the eye  
161 tracker by attaching opaque tape to the panel and tracked only the right eye. Although these apes  
162 viewed stimuli only with their right eyes, they still had a full view of all stimuli with the typical 60-cm  
163 viewing distance. The preliminary analysis revealed no specific pattern of face and eye scanning in  
164 these two apes, so we did not exclude their data from the analysis. Although experiments were  
165 conducted for apes in the presence of the experimenter, the apes rarely attended to the experimenter  
166 during the presentation of stimuli. Also, the apes who received grape juice during the presentation of



167 pictures did not look at the nozzle but freely viewed the pictures.

168           Humans were tested using the same apparatus but in another room with no panel between  
169 the eye tracker and participants. Our preliminary tests for accuracy revealed that the acrylic panels  
170 (1.5–2 cm thick, with no scratches or dirt) had no influence on the eye-tracking data. Each  
171 participant's gaze was recorded as a relative coordinate with respect to the monitor size (i.e., not as the  
172 gaze angle). One degree of gaze angle corresponded to approximately 1 cm on the screen at a typical  
173 60-cm viewing distance.

174

#### 175 Calibration

176           An automated calibration process was employed. Several reference points were presented  
177 sequentially at different locations on the screen to guide the participants to look at those points. The  
178 system then automatically matched the raw-gaze data of participants with those reference points.  
179 Humans were instructed to view the small dots that appeared on the screen, whereas a short video clip  
180 or a piece of fruit was presented to attract the apes' gaze. Five reference points were used for humans,  
181 whereas two were used for apes to reduce the time required for each calibration process.

182           After completing the calibration process, the calibration accuracy at five points on the  
183 screen was inspected by attracting the participants' gaze to those points in the same way. The  
184 calibration process was repeated if necessary (the calibration was usually repeated more frequently for  
185 apes than for humans because of the limited calibration conditions mentioned above.). The accuracy  
186 check was conducted before every session and occasionally during the session (between the trials). In  
187 a preliminary session, we estimated the error value (the average distance between recorded and  
188 intended gaze positions) with two gorillas, six orangutans, six chimpanzees, and six humans. We  
189 found that the error was small and comparable among the species (average  $\pm$  s.e.m.  $0.61 \pm 0.06$ ,  $0.72 \pm$   
190  $0.04$ , and  $0.52 \pm 0.05$  degrees at the typical 60-cm viewing distance, respectively).

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Figure 2 about here

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## Stimuli

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## Procedure

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Figures 2a and 2b present examples of the stimuli. Color still pictures were prepared for this study, including 16 whole-body and 56 facial pictures. Gorillas and orangutans viewed eight human and eight conspecific whole-body pictures (total of 16 whole-body pictures) and eight human and 24 conspecific facial pictures (32 facial pictures); each ape viewed a total of 48 pictures. Humans viewed pictures of both apes and humans (16 whole-body and 56 facial pictures). Half of the pictures were of familiar apes/humans that interacted with the participants on a daily basis, and the other half included unfamiliar apes/humans that had been never exposed to the participants. Pictures were taken when the models were in calm, relaxed states. Their eyes were open, and their mouths were closed. The facial pictures of gorillas and orangutans consisted of three types of faces (eight stimuli for each type): adult male face, adult female face, and juvenile face. Whole-body pictures were converted to  $1280 \times 1024$  pixels ( $37 \times 30$  degrees at a typical 60-cm viewing distance). Facial pictures were converted to  $768 \times 1024$  pixels ( $22 \times 30$  degrees at a typical 60-cm viewing distance) with a gray frame around the background (total  $1280 \times 1024$  pixels). The internal parts of faces (eyes, nose, and mouth) were thus approximately 10–15 degrees in size at a typical 60-cm viewing distance.

In each trial, a picture was presented after participants fixated on a red mark that appeared at the center of the screen. Participants then scanned the picture freely (without any training or instruction). They never kept gazing at the point where the initial red mark appeared, and sequential scanning of the picture was almost always observed. Each stimulus was presented for 3 sec. No

215 specific instructions were given to humans except to view the pictures freely.

216           The presentation order of the pictures was randomized for each participant. The entire  
217 session was conducted over 2 days for humans (36 pictures each day), but the session was divided  
218 across 12 days for apes (four pictures each day). The purpose of dividing the entire session for apes  
219 was to reduce the time required for daily sessions and to maintain the apes' interest in the pictures.  
220 Daily sessions lasted 10–15 min for apes and 15–20 min for humans. Trials in which participants  
221 viewed a picture for less than 1 sec were repeated after the whole session, and the original trials were  
222 replaced by the new trials; otherwise, those trials were eliminated from the analysis. As a result, we  
223 excluded 6.2% and 8.7% of the trials of the whole-body pictures and 10.0% and 7.1% of the trials of  
224 the facial pictures for gorillas and orangutans, respectively (no trials were eliminated for humans). The  
225 exclusion of trials (especially those of facial pictures) was largely attributable to two male  
226 human-raised individuals, Gorgo (gorilla) and Bimbo (orangutan). These individuals sometimes  
227 averted their heads from facial pictures. The reason for this behavior is uncertain; it could have been  
228 active gaze avoidance in response to the social stimuli or simply a lack of interest in the pictures.

229

230 Data analysis

231 *Fixation definition*

232           Fixation was defined as a stationary gaze within a radius of 50 pixels for at least 75 ms (more  
233 than five measurement samples). Otherwise, the recorded sample was defined as part of a saccade.  
234 Records during the first 200 ms were eliminated from the analysis, thereby eliminating fixations that  
235 might have begun before the onset of stimuli.

236 *Area of interest (AOI)*

237           Each stimulus was divided into areas of interest (AOI) for quantitative comparison. Each  
238 whole-body picture was divided into background, face, and body. Each AOI was defined to be 20

239 pixels larger than the precise outline of the features to compensate for error in gaze estimation. The  
240 AOIs were generated in the following order: background, body, and face. If two or more AOIs were  
241 duplicated, gaze samples were added to the last AOI. Each facial picture was divided into background,  
242 eyes, nose, mouth, and periphery (ears, cheeks, chin, forehead, hair; see Fig. 2c).

#### 243 *Proportion of viewing time*

244 The proportion of viewing time for each AOI was calculated with respect to the viewing  
245 time for the entire scene. Out-of-scene fixations were excluded from the analyses (less than 5% of all  
246 fixations in all species when participants were presented with whole-body pictures; 6.1%, 6.0%, and  
247 1.9% of all fixations in gorillas, orangutans, and humans, respectively, when participants were  
248 presented with facial pictures). To compensate for the differences in area size between AOIs, viewing  
249 time was normalized for area size by subtracting the proportion of viewing time from the proportion of  
250 area size. The chance level was thus set at zero.

#### 251 *Probability of fixation across fixation order*

252 To examine the time course of face viewing in whole-body pictures and of eye viewing in  
253 facial pictures, we calculated the probability of fixation on faces/eyes across fixation order (first  
254 through fifth fixations). The results were calculated as the proportion of fixations with respect to the  
255 total number of sampled fixations for each fixation order.

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257 Results

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Figure 3 about here

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Figure 3 shows examples of scanning paths in each species. First, it is important to note that none of

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the ape participants exhibited a fear response to facial pictures, even though some apes (especially

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juveniles) had never been exposed to facial pictures before this study.

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Figure 4 about here

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267 *Whole-body pictures*

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*Proportion of viewing time.* Figure 4a shows the proportion of viewing time for each AOI

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when participants were presented with whole-body pictures. We conducted a repeated-measures

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ANOVA with species, AOI, stimulus species, and familiarity as factors. We found a significant main

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effect of AOI ( $F(2, 48) = 446.59, P < 0.001, \eta^2 = 0.94$ ). All species viewed each AOI in a different

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way [humans ( $F(2, 22) = 382.82, P < 0.001, \eta^2 = 0.97$ ), gorillas ( $F(2, 8) = 50.41, P < 0.001, \eta^2 =$

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0.92), orangutans ( $F(2, 18) = 178.01, P < 0.001, \eta^2 = 0.95$ )]. *Post hoc* tests (Bonferroni correction)

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revealed that they viewed faces most intensely, followed by bodies and then backgrounds ( $P < 0.001$ ).

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We found a significant interaction between species and AOI ( $F(4, 48) = 18.64, P < 0.001, \eta^2 = 0.60$ ).

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We found significant species differences in viewing patterns for faces ( $F(2, 24) = 28.69, P < 0.001,$

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$\eta^2 = 0.70$ ), bodies ( $F(2, 24) = 5.15, P = 0.014, \eta^2 = 0.30$ ), and backgrounds ( $F(2, 24) = 24.50, P <$

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0.001,  $\eta^2 = 0.67$ ). This is explained by the fact that humans viewed faces more intensely than did apes

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( $P < 0.001$ ). Although we were not able to analyze the effects of age and sex because of the small

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numbers of juveniles and males, excluding juveniles or males from the analysis did not change the

281 overall pattern of results [juveniles (main AOI:  $F(2, 40) = 396.84, P < 0.001, \eta^2 = 0.95$ ; species  $\times$   
282 AOI:  $F(4, 40) = 20.20, P < 0.001, \eta^2 = 0.66$ ), males (main AOI:  $F(2, 44) = 391.20, P < 0.001, \eta^2 =$   
283  $0.94$ ; species  $\times$  AOI:  $F(4, 44) = 17.34, P < 0.001, \eta^2 = 0.61$ )]. To examine whether participants  
284 showed differential patterns over the course of an entire session, we separated the whole session into  
285 two blocks and included that factor in the ANOVA. However, we did not find any effect of session  
286 block (block  $\times$  AOI:  $F(2, 23) = 0.76, P = 0.47, \eta^2 = 0.06$ ; block  $\times$  AOI  $\times$  species:  $F(4, 48) = 1.19, P =$   
287  $0.32, \eta^2 = 0.09$ ).

288 We found a significant interaction between stimulus species and AOI ( $F(2, 48) = 4.72, P =$   
289  $0.013, \eta^2 = 0.16$ ). The effect of stimulus species was significant in viewing patterns for faces ( $F(1, 24)$   
290  $= 10.56, P = 0.003, \eta^2 = 0.30$ ) and bodies ( $F(1, 24) = 6.09, P = 0.021, \eta^2 = 0.20$ ). This is explained by  
291 the fact that all species viewed conspecific faces longer than allospecific faces. Additionally, we found  
292 a significant interaction between familiarity, species, and AOI ( $F(4, 48) = 2.93, P = 0.030, \eta^2 = 0.19$ ).  
293 The interaction between familiarity and AOI was significant only in humans ( $F(2, 22) = 4.34, P =$   
294  $0.026, \eta^2 = 0.28$ ). Humans viewed faces of familiar individuals somewhat longer than those of  
295 unfamiliar individuals (0.65 vs. 0.60).

296 *Probability of fixation on faces across fixation order.* Figure 4b shows the time course of  
297 face-viewing patterns for whole-body pictures. A repeated-measures ANOVA with species and  
298 fixation order as factors revealed a main effect of fixation order ( $F(4, 96) = 18.23, P < 0.001, \eta^2 =$   
299  $0.43$ ). This is explained by the fact that they fixated on faces at an earlier rather than a later time. We  
300 also found a significant interaction between species and fixation order ( $F(8, 96) = 4.22, P < 0.001,$   
301  $\eta^2 = 0.26$ ). This is explained by the fact that humans fixated on faces at an earlier time than did apes.

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303 Figure 5 about here

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305 *Facial pictures*

306 *Proportion of viewing time.* Figure 5a shows the proportion of viewing time for each AOI  
307 when participants were presented with facial pictures. We conducted a repeated-measures ANOVA  
308 with species, AOI, stimulus species, and familiarity as factors. Only adult faces of the three species  
309 were used in this analysis. We found a significant main effect of AOI ( $F(3, 69) = 238.75, P < 0.001,$   
310  $\eta^2 = 0.91$ ). All species viewed each AOI in a different way; humans ( $F(3, 33) = 146.57, P < 0.001,$   
311  $\eta^2 = 0.93$ ), gorillas ( $F(3, 12) = 100.94, P < 0.001, \eta^2 = 0.96$ ), and orangutans ( $F(3, 24) = 65.90, P <$   
312  $0.001, \eta^2 = 0.89$ ). *Post hoc* tests (Bonferroni correction) revealed that they viewed eyes most  
313 intensely, followed by nose/mouth and periphery ( $P < 0.001$ ). We found a significant interaction  
314 between species and AOI ( $F(3, 69) = 3.14, P = 0.009, \eta^2 = 0.21$ ). We found significant species  
315 differences in viewing patterns for the eyes ( $F(2, 23) = 4.00, P = 0.032, \eta^2 = 0.25$ ) and the periphery  
316 ( $F(2, 23) = 6.27, P = 0.007, \eta^2 = 0.35$ ). This is explained by the fact that humans viewed the eyes  
317 more intensely and viewed the periphery less intensely than did orangutans. Although we were not  
318 able to analyze the effects of age and sex because of the small numbers of juveniles and males,  
319 excluding juveniles or males from the analysis did not change the overall pattern of results [juveniles  
320 (main AOI:  $F(3, 57) = 174.85, P < 0.001, \eta^2 = 0.90$ ; species  $\times$  AOI:  $F(6, 57) = 3.20, P = 0.009, \eta^2 =$   
321  $0.25$ ), males (main AOI:  $F(3, 66) = 218.51, P < 0.001, \eta^2 = 0.90$ ; species  $\times$  AOI:  $F(6, 66) = 3.13, P =$   
322  $0.009, \eta^2 = 0.22$ )]. To examine whether the participants showed differential patterns over the course  
323 of entire session, we separated the whole session into two blocks and included that factor in the  
324 ANOVA. However, we did not find any effect of session block (block  $\times$  AOI:  $F(3, 22) = 1.87, P = 0.16,$   
325  $\eta^2 = 0.20$ ; block  $\times$  AOI  $\times$  species:  $F(3, 22) = 1.49, P = 0.20, \eta^2 = 0.16$ ).

326 We found a significant interaction among stimulus species, AOI, and species ( $F(6, 69) =$   
327  $6.62, P < 0.001, \eta^2 = 0.36$ ). This is explained by the fact that, whereas gorillas and orangutans viewed  
328 the conspecific eyes more intensely than the allospecific eyes, humans exhibited an opposite tendency,

329 viewing the allospecific eyes more intensely than the conspecific eyes. The effect of familiarity was  
330 not significant ( $P > 0.05$ ).

331 *Probability of fixation on eyes across fixation order.* Figure 5b shows the time course of eye  
332 viewing for facial pictures. A repeated-measures ANOVA using species and fixation order as factors  
333 revealed a main effect of fixation order ( $F(4, 96) = 35.03, P < 0.001, \eta^2 = 0.59$ ), which is explained by  
334 the fact that they fixated on eyes at an earlier rather than a later time. The interaction between species  
335 and fixation order was not significant ( $F(8, 96) = 1.69, P = 0.11, \eta^2 = 0.12$ ).

336 *Viewing patterns for the eyeball region.* Differences between apes and humans in eye  
337 viewing were not as clear as those previously found between chimpanzees and humans (Kano &  
338 Tomonaga, 2009, 2010). However, this possible inconsistency may be attributable to the definition of  
339 the eye AOI. That is, the visual inspection of each scanning path (Fig. 3) suggested that humans more  
340 directly fixated on eyes than did apes (i.e., fixation on eyeballs rather than on the region around the  
341 eyes). Therefore, we also delineated an eyeball AOI, which was inside the eye AOI and included only  
342 the eyeball, and compared the viewing times for eyeballs between the species. We found significant  
343 species differences in viewing patterns for eyeballs (Fig. 5a;  $F(2, 23) = 8.09, P = 0.002, \eta^2 = 0.41$ ).  
344 This is explained by the fact that humans viewed eyeballs more intensely than did apes ( $P < 0.05$ ). We  
345 also analyzed the probability of fixation on eyeballs across fixation order. We found a significant  
346 interaction between species and fixation order (Fig. 5b;  $F(8, 96) = 2.28, P = 0.028, \eta^2 = 0.16$ ). This is  
347 explained by the fact that, whereas humans showed an increasing tendency for viewing eyeball regions,  
348 apes showed a decreasing tendency in this regard.

349 -----  
350 Figure 6 about here  
351 -----

352 *Probability of saccade destination.* Visual inspection of the scanning data (Fig. 3) suggested



353 that humans viewed left and right eyes alternately, whereas apes did not. To clarify this issue, we  
354 quantified the typical scanning path of each species when participants were presented with facial  
355 pictures. We divided the eye AOI into right and left eye AOIs (i.e., right eye, left eye, nose, mouth, and  
356 periphery) and calculated the probability of saccade destination. Each saccade (the path that joins two  
357 consecutive fixations) was classified based on the two AOIs in which the saccade started and ended;  
358 thus, each saccade was classified into one of 10 possible combinations of beginning and ending AOIs.  
359 Saccades for out-of-face start or end points were excluded from analyses. The results were calculated  
360 as the proportion of the total number of sampled saccades. Data for conspecific and allospecific faces  
361 were combined. As suggested, humans shifted their gaze between the left and right eyes more  
362 frequently than did gorillas ( $t(15) = 2.26, P = 0.039$ ) and orangutans ( $t(20) = 4.82, P < 0.001$ ) (Fig. 6).

363 -----  
364 Figure 7 about here  
365 -----

366 *The effect of face type.* Figure 7 shows the proportion of viewing time for each AOI as a  
367 function of face type in gorillas and orangutans. A repeated-measures ANOVA with face type and AOI  
368 did not reveal an effect of face type in gorillas ( $F(6, 24) = 1.97, P = 0.10, \eta^2 = 0.33$ ), whereas it did in  
369 orangutans ( $F(6, 54) = 6.09, P < 0.001, \eta^2 = 0.40$ ). *Post hoc* tests revealed that orangutans viewed the  
370 juvenile eyes more intensely than the male or female eyes ( $P < 0.05$ ). We also found that they viewed  
371 the periphery of male faces (i.e., cheek flange) more intensely than that of female or infant faces ( $P <$   
372  $0.05$ ). Human participants did not demonstrate this pattern (gorilla faces:  $F(6, 66) = 0.08, P = 0.99,$   
373  $\eta^2 = 0.008$ ; orangutan faces:  $F(6, 66) = 1.53, P = 0.18, \eta^2 = 0.12$ ).

374

375 Discussion

376 First, it is important to note that humans and great apes showed striking similarities in their  
377 patterns of face and eye scanning. All species viewed faces for longer durations and at earlier times  
378 than they viewed bodies and backgrounds when presented with whole-body pictures. Additionally, all  
379 species viewed inner features of faces, especially eyes, for longer durations and at earlier times than  
380 they viewed the periphery when presented with facial pictures. The same patterns were observed for  
381 chimpanzees in previous studies (Kano & Tomonaga, 2009, 2010) (Table S1 and S2). Selective  
382 attention to faces as opposed to complex naturalistic backgrounds clearly eliminated the possibility  
383 that viewing patterns were simply dependent on visual saliency (e.g., color, shape, contrast). In  
384 support of this notion, a previous study demonstrated that the chimpanzees' viewing patterns for faces  
385 were not explained by the saliency model of Itti and Koch (2001) (Kano & Tomonaga, 2011).

386 None of the ape species avoided viewing eyes in this study. Rather, they viewed eyes  
387 predominantly, regardless of the type of face (conspecific/allospecific, male/female) presented. A  
388 possible inconsistency between these data and previous findings that gorillas and orangutans  
389 frequently avoided viewing faces/eyes during natural interactions may exist (Kaplan & Rogers, 2002;  
390 Shaller, 1963). However, this apparent inconsistency may be explained by the fact that this study  
391 presented apes with faces in the absence of interactive contexts. Previous studies have also shown that  
392 eye contact (or its avoidance) is highly dependent on the interactive contexts in which such eye contact  
393 occurs. Thus, this study's finding that all great ape species are similar in their eye-viewing tendencies  
394 may indicate that the ape species do not differ in their default motivation for viewing eyes. However, it  
395 should be noted that two adult males in this study frequently averted their heads when presented with  
396 facial pictures (see Methods). It is possible that notable sex, age, rank, or individual differences  
397 characterize their eye-viewing tendencies (cf. Yamagiwa, 1992)

398 Although no significant differences were found between gorillas and orangutans, humans

399 differed from apes in their patterns of face and eye scanning. Humans viewed faces for longer  
400 durations than did apes when presented with whole-body pictures. Additionally, humans viewed eyes,  
401 especially eyeballs, for longer durations than did apes when presented with facial pictures.  
402 Furthermore, humans often alternated their gaze between the left and right eyes, whereas apes rarely  
403 showed this gaze movement (Fig. 3, 6). By alternating their gaze between the left and right eyes and  
404 shifting their gaze occasionally to the mouth, humans exhibited triangular scanning paths in response  
405 to faces. As the upper component of this triangular shape was absent in apes, their scanning paths  
406 appear to be more linear than those of humans. A similar species difference was observed between  
407 chimpanzees and humans in previous studies (Kano & Tomonaga, 2009, 2010). Therefore, active,  
408 prolonged eye viewing is a unique characteristic of humans as compared with great apes.

409         One possible interpretation for this species difference is that eyes may have evolved  
410 additional communicative functions not found in ape species. Compared with those of other primates,  
411 human eyes have a notable dark–white contrast between the iris and sclera (Kobayashi & Kohshima,  
412 2001), which enhances directional cues. Moreover, fine motor control of the muscles around the eyes  
413 (Ekman & Friesen, 1978) enables humans to communicate a variety of emotional cues. As these cues  
414 are subtle, the active and prolonged eye-viewing patterns of humans may benefit them by facilitating  
415 the efficient retrieval of such communicative information. That is, humans may employ eyes for  
416 bidirectional communication between senders and receivers. Tomasello et al. (2007) hypothesized that  
417 the importance of close-range joint attentional and communicative interactions may have shaped the  
418 unique eye morphology of humans. It is also possible that the behavioral tendency to actively collect  
419 eye information has evolved along with eye morphology.

420         Humans and apes viewed conspecific faces for longer durations than they viewed allospecific  
421 faces when presented with whole-body pictures. This may indicate their greater interest in conspecific  
422 than in allospecific individuals. However, their patterns of face and eye scanning were, in general,

423 highly consistent across stimuli despite the fact that various types of faces were presented. This was  
424 also the case for chimpanzees and humans in the previous study. Thus, their viewing patterns may  
425 reflect general responses to face-like configurations rather than specific responses to particular facial  
426 information. This result may be explained by the fact that study participants were not required to  
427 collect particular information from the faces (free viewing). Thus, we would expect that their viewing  
428 patterns would be more variable if they viewed faces under an experimental situation in which they  
429 were required to sort faces based on certain facial information or in an interactive situation in which  
430 they reacted emotionally to faces. Further studies are necessary to test these possibilities.

431         Although orangutans' viewing patterns were generally consistent across stimuli, they were  
432 clearly affected by species-specific facial features. They viewed the periphery of adult male faces  
433 (flange on the sides) for longer durations than those of adult female or juvenile faces. Furthermore,  
434 they viewed the eyes of juvenile faces (surrounded by pale coloring) for longer durations than those of  
435 adult faces. These results suggest that these conspicuous facial features are indeed visually appealing.  
436 Human participants who viewed the same orangutan faces did not follow the same patterns, perhaps  
437 because their viewing patterns are more standardized than are those of orangutans.

438         The color contrast in human eyes did not attract viewers' attention to the eyes. That is, apes  
439 did not view human eyes for longer durations than they viewed conspecific eyes, and humans showed  
440 prolonged eye viewing for both conspecific and allospecific faces. Thus, unlike the male flange and  
441 the skin color of juvenile orangutans, the color contrast in human eyes is not particularly conspicuous.  
442 Humans showed prolonged eye viewing independently of the effect of eye color. Thus, this pattern is  
443 internally driven rather than stimulus dependent. We speculate that the color contrast of human eyes  
444 conveys information most efficiently when the eyes receive such active attention.

445         Further comparative studies on face and eye scanning may reveal similarities and differences  
446 between apes and other primate species. For example, this study demonstrated a remarkably strong

447 tendency for apes and humans to view the internal features of faces, and successive fixations on  
448 internal features were frequent (i.e., successive on-feature fixations rather than repetition of on- and  
449 off-feature fixations; see Fig. 3). It remains unclear how apes and monkeys differ in this regard when  
450 tested using the same experimental settings. Further studies using the eye-tracking method are also  
451 necessary to perform direct comparisons between humans and great apes in terms of gaze-following  
452 tendencies. Previous studies have shown that humans, chimpanzees, gorillas, and orangutans show  
453 differential gaze-following tendencies in response to a human experimenter's gaze (Okamoto-Barth,  
454 et al., 2007; Tomasello, et al., 2007). It remains unclear how these species differ from one another  
455 when tested using a cross-species design (presenting both conspecific and allospecific faces).

456         The aim of this study was to reveal how humans and great apes are similar and different in  
457 their pattern of face and eye scanning. Following a previous study comparing chimpanzees with  
458 humans, we directly compared the viewing patterns of gorillas, orangutans, and humans in response to  
459 whole-body and facial (full-face) pictures of conspecifics and allospecifics. The general conclusion is  
460 that all species are strikingly similar in patterns of face and eye scanning. However, we also identified  
461 unique eye-viewing patterns among humans. Unlike the species-specific facial features of orangutans  
462 (e.g., male flange), the black–white contrast in human eyes, a unique trait of humans, did not attract  
463 viewers' attention. Humans showed prolonged eye viewing independently of the eye color of  
464 presented faces. Thus, active eye viewing may be a unique characteristic of humans as compared with  
465 great apes, and given that humans have unique eye morphology, facial communication among humans  
466 may be specialized for the eyes.

467

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477

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- 539
- 540

Table 1. Age, sex, and rearing history of each ape.

	<b>Sex</b>	<b>Age (years)</b>	<b>Rearing History</b>
<b>Gorilla</b>			
Gorgo	M	29	Nursery
Kibara	F	6	Mother
Louna	F	4	Mother
Viringika	F	15	Mother
Zola	F	2	Mother
<b>Orangutan</b>			
Batak	M	1 (+ 1 month)	Mother
Bimbo	M	30	Nursery
Dukana	F	21	Mother
Kila	F	10	Mother
Maia	F	3	Mother
Padana	F	13	Mother
Pini	F	22	Mother
Raja	F	7	Mother
Suaq	M	1 (+ 6 months)	Mother
Tanah	F	1 (+ 5 months)	Mother

541

542

543 Figure captions

544

545 Figure 1. Apes and apparatus. (a) Eye-tracking apparatus. An eye tracker and a monitor are mounted  
546 on the movable platform (front). The experimenter controlled the apparatus using the computer  
547 mounted on the other platform (behind). See also:

548 <http://www.youtube.com/watch?v=zHx2KwQEHq0>.

549 (b) A juvenile gorilla drinking grape juice *via* a tube attached to the transparent acrylic panel. (c) An  
550 adult female orangutan on the apparatus.

551

552 Figure 2. Examples of stimuli: (a) whole-body pictures; (b) facial pictures; (c) areas of interest (AOI)  
553 for facial pictures.

554

555 Figure 3. Examples of scanning paths for facial pictures. The scanning paths of five participants from  
556 each species were superimposed on the facial pictures. The pictures were dimmed for clarity.

557

558 Figure 4. Scanning pattern for whole-body pictures in each species. (a) Proportion of viewing time for  
559 each AOI with respect to the total scene-viewing time. (b) Probability of fixation for each AOI across  
560 fixation order. All data are normalized for area sizes. Error bars represent the upper and lower bounds  
561 of the 95% confidence intervals.

562

563 Figure 5. Scanning pattern for facial pictures in each species. (a) Proportion of viewing time for each  
564 AOI with respect to total face-viewing time. (b) Probability of fixation for each AOI across fixation  
565 order. All data are normalized for area sizes. Error bars represent the upper and lower bounds of the  
566 95% confidence intervals.

567 Figure 6. Typical scanning paths for facial pictures. Probabilities of saccade destination are presented  
568 in percentages and scaled to size. If a human participant is currently looking at the right eye of a human  
569 face (top center), he/she would re-fixate the right eye with a probability of 2.6, the left eye with a  
570 probability of 15.6, the nose with a probability of 7.7, etc. (see text for details).

571

572 Figure 7. The proportion of total face-viewing time spent viewing each AOI as a function  
573 of face type in gorillas and orangutans. All data were normalized for area sizes. Error  
574 bars represent the upper and lower bounds of the 95% confidence intervals. Asterisk  
575 indicates  $P < 0.05$  in *post hoc* tests.

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579 The English in this document has been checked by at least two professional editors, both native  
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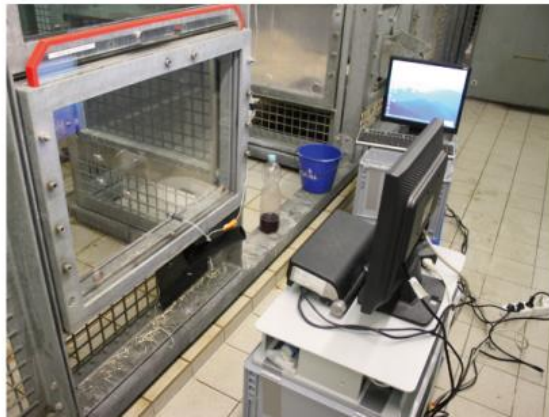
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(a)



(b)



(c)

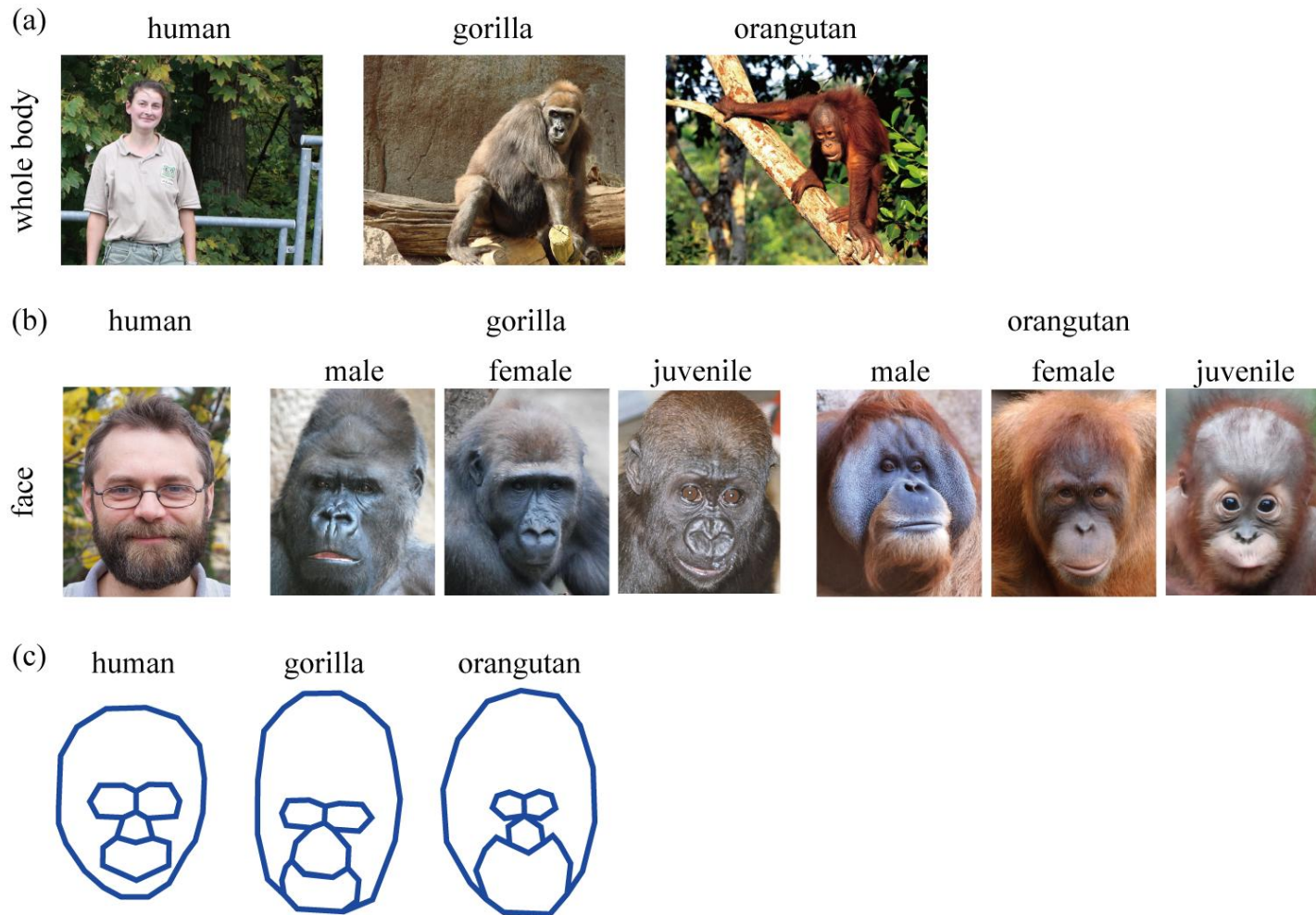


585

586 Figure 1

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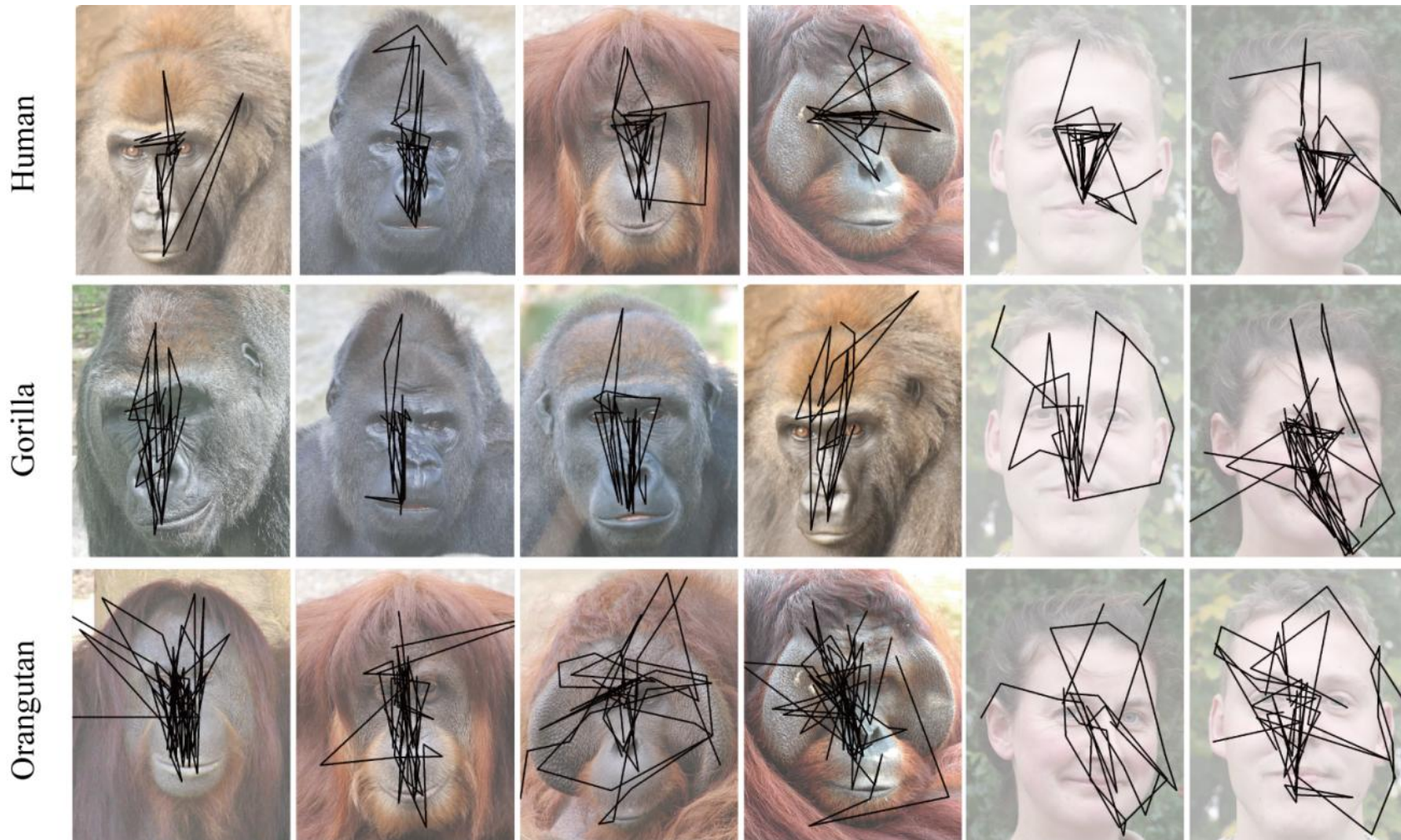
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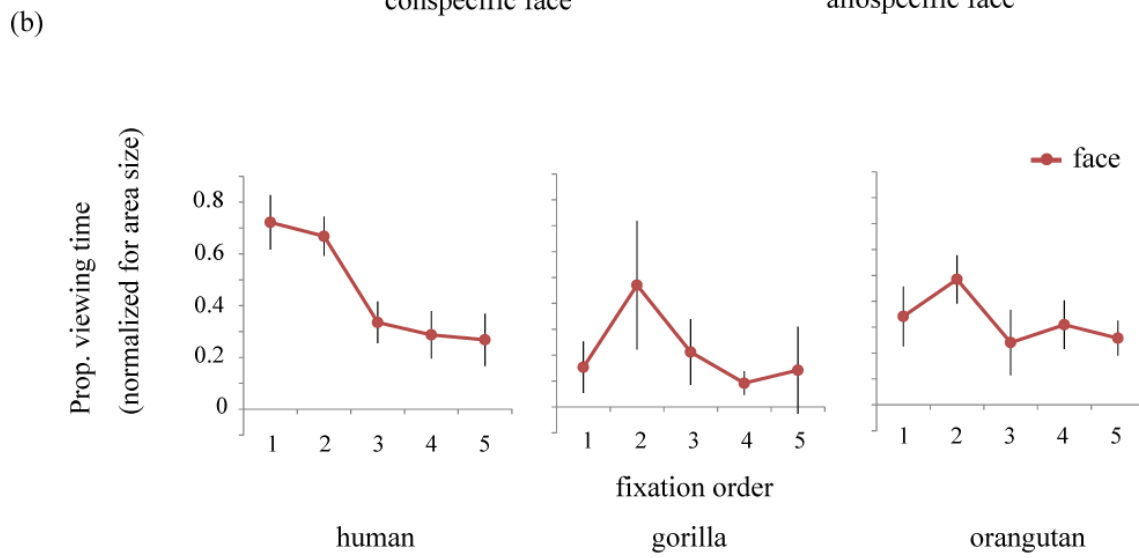
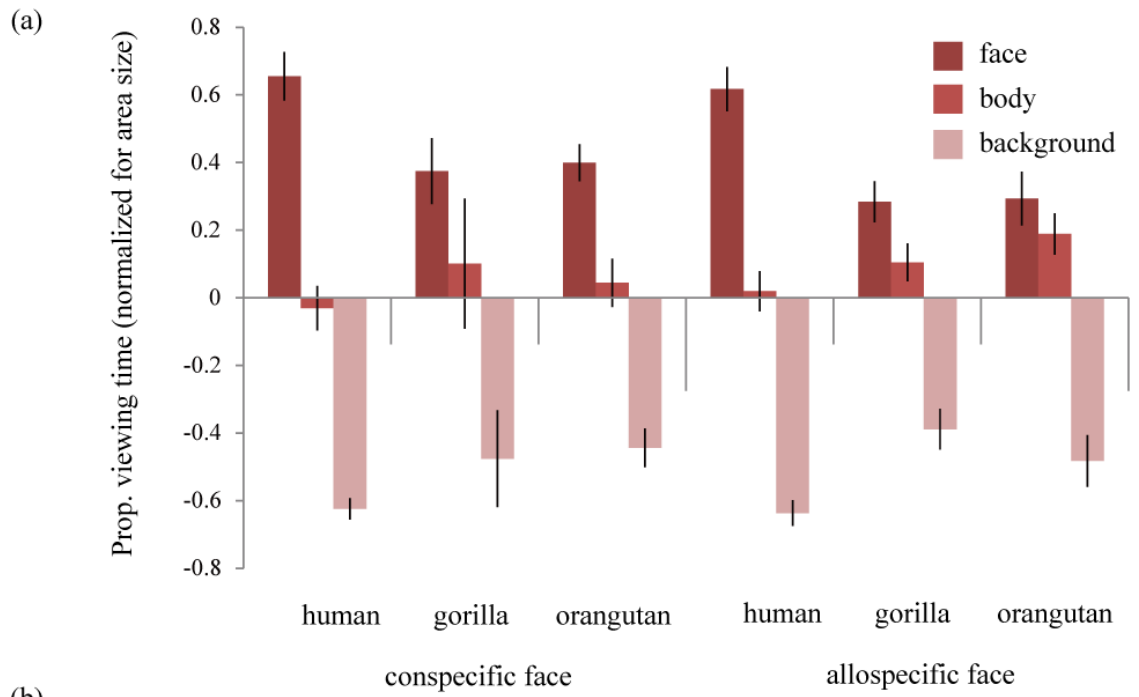
590 Figure 2

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593 Figure 3

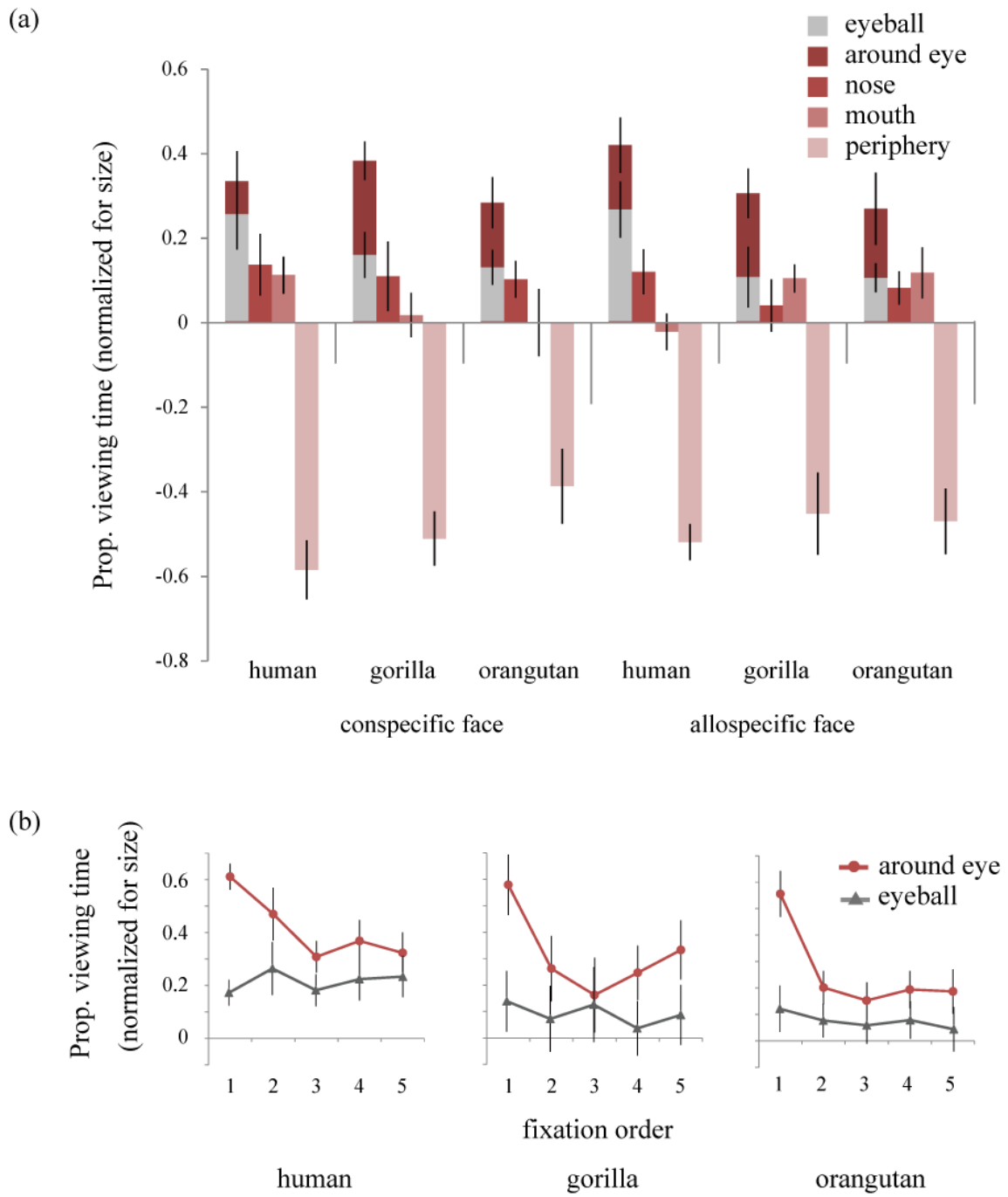


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596 Figure 4



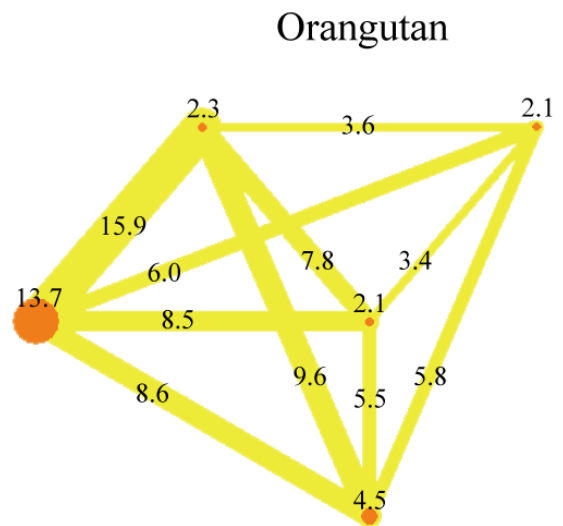
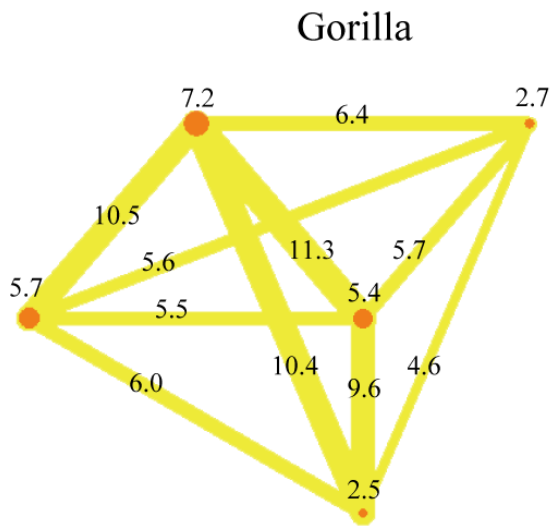
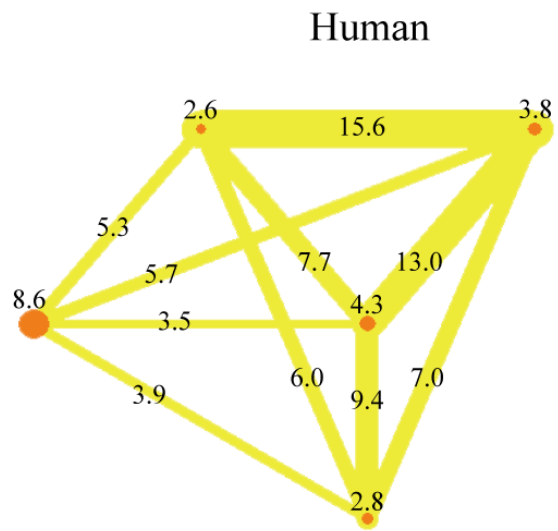
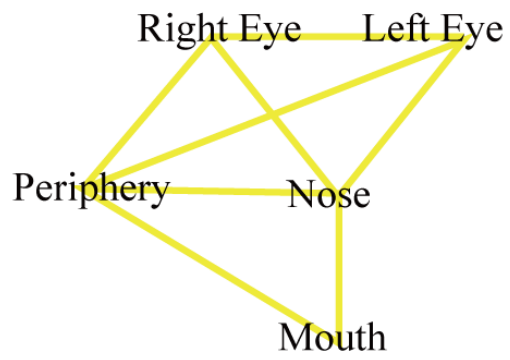


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599 Figure 5

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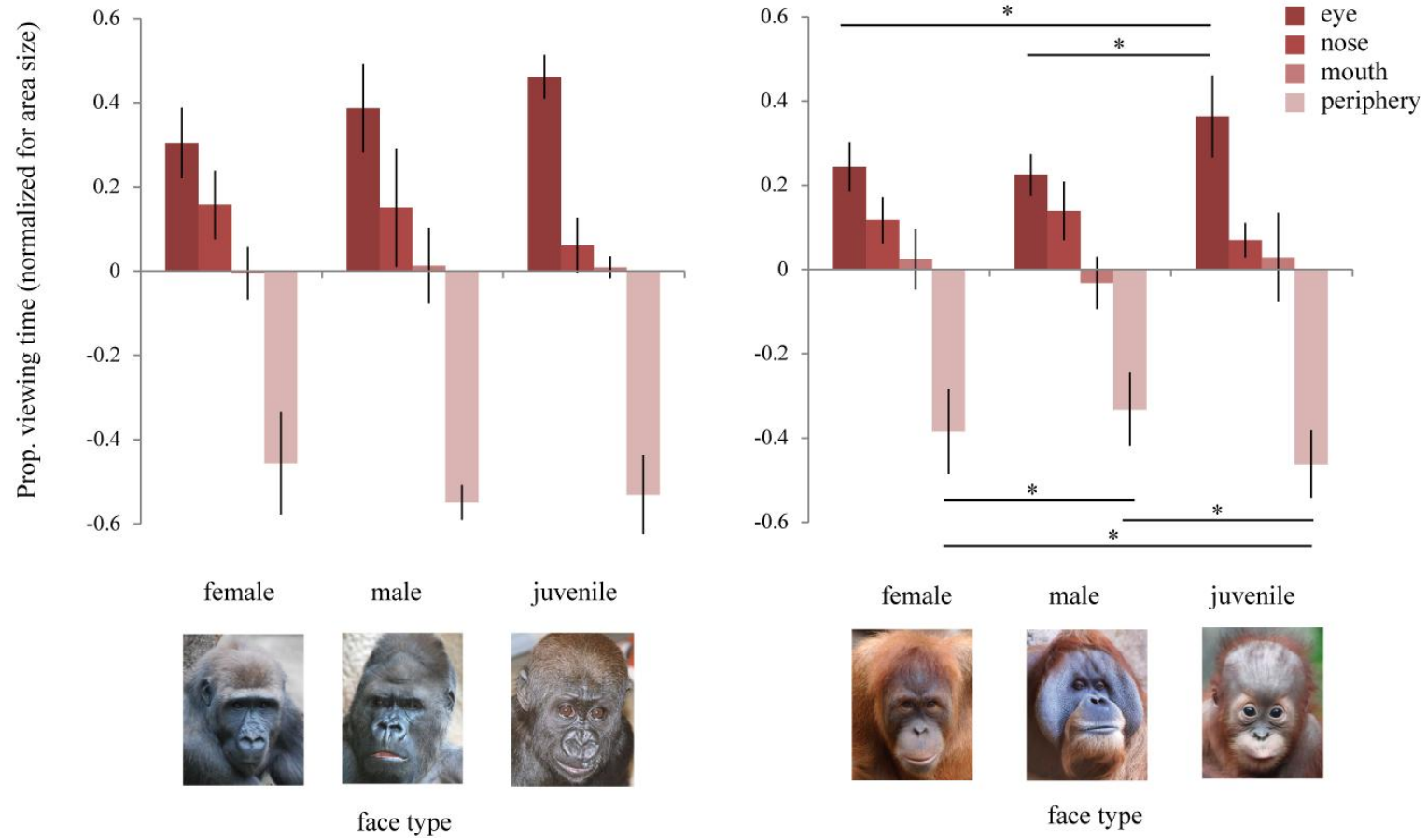


601

602 Figure 6

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604



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606 Figure 7

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608 Supporting material

609

Table S1. Proportion of viewing time for each part of a scene (not normalized for size) in each species across studies.

<b>Participant</b>	<b>Conspecific scene</b>			<b>Allospecific scene</b>		
	Face	Body	Background	Face	Body	Background
Human (1)	0.7	0.21	0.08	0.66	0.28	0.05
Gorilla (1)	0.42	0.38	0.25	0.33	0.34	0.32
Orangutan (1)	0.45	0.29	0.19	0.34	0.43	0.22
Human (2)	0.57	0.21	0.21	0.72	0.18	0.09
Chimpanzee (2)	0.37	0.43	0.18	0.31	0.34	0.34

(1) This study

(2) Kano and Tomonaga (2009)

610

Table S2. Proportion of viewing time for each part of a face (not normalized for size) in each species across studies.

<b>Participant</b>	<b>Conspecific face</b>				<b>Allospecific face</b>			
	Eye (Eyeball)	Nose	Mouth	Periphery	Eye (Eyeball)	Nose	Mouth	Periphery
Human (1)	0.64 (0.23)	0.23	0.04	0.07	0.68 (0.26)	0.15	0.08	0.07
Gorilla (1)	0.48 (0.18)	0.2	0.13	0.17	0.41 (0.13)	0.07	0.18	0.31
Orangutan (1)	0.36 (0.15)	0.13	0.19	0.29	0.38 (0.12)	0.12	0.2	0.29
Human (2)	0.44 (0.27)	0.17	0.19	0.18	0.51 (0.28)	0.18	0.13	0.16
Chimpanzee (2)	0.37 (0.11)	0.16	0.25	0.2	0.28 (0.07)	0.24	0.15	0.31

(1) This study

(2) Kano and Tomonaga (2010)

Table S3. Average fixation duration (ms) for each AOI of whole-body/facial pictures.

	Human (1)	Gorilla (1)	Orangutan (1)	Human (2)	Chimpanzee (2)
<b>Whole Body</b>					
Face	821	375	356	1002	354
Body	299	212	286	313	207
Background	237	217	280	289	224
Whole Scene	607	255	318	739	259
<b>Face</b>					
Eye	410	293	357	484	257
Nose	303	250	337	415	275
Mouth	348	285	366	305	225
Periphery	287	232	318	272	221
Whole Face	374	282	366	464	255
(1) This study					
(2) Kano and Tomonaga (2009/2010)					

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613