Neural representation of face familiarity in an awake chimpanzee

Evaluating the familiarity of faces is critical for social animals as it is the basis of individual recognition. In the present study, we examined how face familiarity is reflected in neural activities in our closest living relative, the chimpanzee. Skin-surface event-related brain potentials (ERPs) were measured while a fully awake chimpanzee observed photographs of familiar and unfamiliar chimpanzee faces (Experiment 1) and human faces (Experiment 2). The ERPs evoked by chimpanzee faces differentiated unfamiliar individuals from familiar ones around midline areas centered on vertex sites at approximately 200 ms after the stimulus onset. In addition, the ERP response to the image of the subject's own face did not significantly diverge from those evoked by familiar chimpanzees, suggesting that the subject's brain at a minimum remembered the image of her own face. The ERPs evoked by human faces were not influenced by the familiarity of target individuals. These results indicate that chimpanzee neural representations are more sensitive to the familiarity of conspecific than allospecific faces.

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Introduction

As social animals, primates rely on face recognition to identify individuals and recognize

their emotional states. Until recently, vast knowledge of the primate visual system has been

primarily obtained from the brains of macaque monkeys and humans. Previous research has

suggested that the ventrolateral visual areas are central for face recognition both for monkeys and

humans (Perrett, Rolls, & Caan, 1982; Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003).

However, the neural mechanisms responsible for face recognition in our closest living species,

the chimpanzee, remain relatively unknown. Examining these mechanism would shed new light

on the physiological and evolutionary origins of human social cognition. Behavioral studies of

chimpanzees have revealed that face stimuli attract their visual attention, just as in humans,

indicating the importance of face perception for chimpanzees (Kano & Tomonaga, 2009). It has

been further reported that chimpanzees process face configurations in a similar manner to humans

(Hirata, Fuwa, Sugama, Kusunoki, & Fujita, 2010; Parr, 2011; Tomonaga, 2007), they understand

conspecific facial expressions (Parr, 2003), and they have sophisticated abilities to identify

individuals in terms of kinship detection (Parr & de Waal, 1999).

Direct examinations of the chimpanzees' neural activities have also been conducted since the

1960s (Adey, Kado, & Rhodes, 1963; Boysen & Berntson, 1985), and are currently a growing

research topic (Fukushima et al., 2010; Hirata et al., 2013; Parr, Hecht, Barks, Preuss, & Votaw,

34   2009; Rilling et al., 2007; Taglialatela, Russell, Schaeffer, & Hopkins, 2008, 2009; Ueno et al.,

35   2008, 2010). In particular, several research groups have reported neural examinations of

36   chimpanzee visual processing (Boysen & Berntson, 1985; Fukushima et al., 2010; Parr et al.,

37   2009). For instance, Parr and colleagues (Parr et al., 2009) conducted a functional neuroimaging

38   study of chimpanzee face processing using positron emission tomography (PET). In their study,

39   the subject chimpanzees were given an isotope marker and performed a matching task with

40   conspecific faces and objects, and they were then sedated before their brains were scanned. Their

41   results explicitly revealed that the chimpanzees recruit similar neurocognitive substrates to

42   humans for face perception. However, measurements of neural metabolism using methods such

43   as PET imaging are poor metrics of the temporal aspects of the neural processing. Furthermore,

44   non-invasive measurements of primates' brains often require sedation (Boysen & Berntson, 1985;

45   Parr et al., 2009; Rilling et al., 2007; Taglialatela et al., 2008, 2009), and this severely limits real-

46   time measurement of their cognitive functions, particularly for elucidating socio-emotional

47   responses.

48   We have developed a protocol of non-invasive measurement of electrophysiological activities

49   in an adult female chimpanzee by means of scalp event-related potentials (ERPs) while she is

50   fully awake (Fukushima et al., 2010; Hirata et al., 2013; Ueno et al., 2008, 2010). Using this

51   protocol, we previously revealed neural evidence that this chimpanzee discriminates human faces

52   from other categories of objects, as there was a divergence of ERPs in response to face stimuli at

53   approximately a 100 ms latency at posterior temporal regions (Fukushima et al., 2010).

54   Furthermore, we demonstrated that chimpanzee neural activities are influenced by observing

55   emotional expressions of conspecifics with an approximately 210 ms latency (Hirata et al., 2013).

56   Along this line of research, one issue to be further clarified is the influence of experience on

57   face processing. Particularly, *familiarity* is considered to be the basis of individual recognition

58   and an important factor in the modulation of social behaviors, by means of in-group and out-

59   group differentiation, for example. Human ERP studies show that a negative deflection around

60   140–200 latency ('N170') reflects a primal stage of face processing (Bentin, Allison, Puce, Perez,

61   & McCarthy, 1996; George, Evans, Fiori, Davidoff, & Renault, 1996). Importantly, it has been

62   shown that the effects of facial familiarity appear in latencies later than 200 ms after stimulus

63   onset.That is, they appear later than the initial processing of basic facial configuration (Bentin &

64   Deouell, 2000; Eimer, 2000; Henson et al., 2003; Schweinberger, Pfütze, & Sommer, 1995).

65   Neuroimaging studies have further elucidated that facial familiarity modulates not only ventral

66   visual areas, but also distributed networks, including affective and memory-related regions,

67   including the amygdala and medial parietal areas (Gobbini & Haxby, 2007; Natu & O'Toole,

68   2011). Concerning chimpanzees, behavioral studies have revealed that familiarity with the target

69   enhances identification of individuals (Parr, Siebert, & Taubert, 2011), but neural responses to

70 familiarity during face perception remain unknown.

71   Based on these studies, the primary aim of the present study was to examine the effects of

72 familiarity on neural activities during face processing. The first experiment in this study

73 compared ERPs during the perception of familiar and unfamiliar conspecific faces. As a topic

74 somewhat related to familiarity perception, *self-face* recognition in chimpanzees is a research

75 topic that has received a great deal of attention (Bard, Todd, Bernier, Love, & Leavens, 2006;

76 Gallup, 1970; Povinelli, 1987). The subject chimpanzee in the present study showed evidence of

77 mirror self-recognition, as indicated by self-exploratory behaviors of her own body while

78 watching a mirror (Hirata, unpublished data). Although the present study primarily examined the

79 effects of familiarity on face processing, the experiment also included an image of the subject's

80 own face as a stimulus category, as a first preliminary investigation of neural correlates of self-

81 perception in the chimpanzee.

82   It is also known that the *species* shown in a target stimulus can influence visual processing of

83 the displayed faces. However, whether or not primates have a specialized mechanism for

84 perceiving the faces of conspecifics is controversial (Martin-Malivel & Okada, 2007; Parr,

85 Heintz, & Pradhan, 2008). Among previous behavioral studies in chimpanzees, some findings

86 have suggested differential perception between conspecific and allospecific faces (Dahl,

87 Wallraven, Bulthoff, & Logothetis, 2009; Fagot & Tomonaga, 1999; Fujita, 1990; Hattori, Kano,

88 & Tomonaga, 2010; Parr, Dove, & Hopkins, 1998; Parr, Heintz, & Akamagwuna, 2006; Parr et

89 al., 2011; Tomonaga, Itakura, & Matsuzawa, 1993), but some research has also suggested that

90 chimpanzees process human faces in a similar manner to conspecific faces (Kano & Tomonaga,

91 2009; Martin-Malivel & Okada, 2007; Tomonaga, 2007). These inconsistent findings from

92 behavioral studies motivate further elucidation of the species dependency of face processing by

93 identifying the neural responses to conspecific and non-conspecific faces and examining possible

94 differences in their patterns. Therefore, in the second experiment in this study, we presented the

95 subject with faces of allospecific humans, and compared the ERP responses with familiar and

96 unfamiliar human faces, to examine whether chimpanzee brain activity is differentially

97 responsive to the familiarity of conspecific and allospecific faces.

98 **Materials and Methods**

99 *Subject*

100 The subject was a female chimpanzee (*Pan troglodytes*) named Mizuki, who was housed at

101 the Great Ape Research Institute of Hayashibara Biochemical Laboratories, Inc., Okayama,

102 Japan. She was raised by human caregivers from a few days after birth. Since the subject arrived

103 at the Great Ape Research Institute when she was 2 years and 1 month old, she has spent the

104   majority of her time with other chimpanzees in outdoor and indoor compounds. At the time of

105   experimentation, the subject was 10–11 years old and living in the institute with other group

106   members (two were male, two were female, and one was an infant). At that time, the subject had

107   undergone other behavioral cognitive experiments (Hirata & Fuwa, 2007; Idani & Hirata, 2006)

108   and earlier ERP experiments (Fukushima et al., 2010; Hirata et al., 2013; Ueno et al., 2008,

109   2010). She had also participated in informal tests of mirror self-recognition, recognition of self-

110   images on TV monitors, and match-to-sample tasks of the faces of conspecifics (Hirata,

111   unpublished data). A playground for the chimpanzees in the institute had a small wall covered

112   with stainless-iron, and it was observed that chimpanzees including the present subject looked at

113   the reflective wall and made some gestures, such as opening the mouth and looking into it.

114   This research was conducted in accordance with the "Guide for the Care and Use of

115   Laboratory Animals" of Hayashibara Biochemical Laboratories, Inc., and the Weatherall report,

116   "The use of non-human primates in research". The research protocol was approved by the Animal

117   Welfare and Animal Care Committee of The University of Tokyo and Hayashibara Biochemical

118   Laboratories, Inc. (GARI-051101).

119   *Apparatus and stimuli*

120   The overall methodology basically followed our previous study (Fukushima et al., 2010). The

121   experimental room consisted of concrete walls, with moderate lighting. The subject sat on a

122   concrete platform and was fully awake during recordings. A 17-inch CRT display (IIyama

123   LA702U) was set up in front of her approximately 40 cm away, at the horizontal level of her

124   head. An infrared video camera was fixed on top of the CRT display to monitor the subject from a

125   frontal view. We used this camera to check if the subject's gaze was directed to the stimulus

126   display.

127   Experimental stimuli in Experiment 1 were color photographs of the faces of chimpanzees

128   (Figure 1). The stimuli consisted of seven chimpanzee faces: three of unfamiliar (out-group)

129   chimpanzees that were novel to the subject, three of familiar (in-group) chimps, and the one of

130   the subject's own face. The images were digitally processed in 24-bit color by graphics software.

131   The stimuli in Experiment 2 consisted of six human faces: three of familiar persons who were the

132   caregivers of the subject, and three of unfamiliar humans who were novel to the subject. All of

133   the human models were Japanese subjects in their 30s, and two male subjects and one female

134   subject were included in both categories. In both experiments, all stimuli were displayed on a

135   black background with a visual field approximately 15° high and 13° wide. The average

136   luminance (mean, 119.29 cd/m^2; SD, 0.73 cd/m^2) and number of pixels (mean, 94213; SD, 265)

137   among stimulus categories were matched, varying less than 0.8%.

138   *Procedure*

139   Experiment 1 was conducted in three recording sessions in separate days, each consisting of

140   five blocks with 105 trials (1575 trials in total). Experiment 2 was also conducted in three

141   recording sessions with different days from Experiment 1, each consisting of five blocks with 60

142   trials (900 trials in total). On each trial of both experiments, one of the stimuli (seven images in

143   Experiment 1 and six images in Experiment 2) was presented for 500 ms in a pseudo-randomized

144   order with no consecutive repetition of the same stimulus. Each stimulus was followed by a 700

145   ms inter-stimulus interval (an empty black screen). To maintain the subject's attention to the

146   display, occasional images of several objects that were not related to faces or animals (e.g.,

147   geometric figures or patterns) were also presented randomly at a rate of once every several trials.

148   Between blocks, the subject was given a rest period of approximately 1 min, which allowed her

149   to make considerable body movements and to receive fruit rewards. During the recordings, an

150   experimenter (one of the subject's caregivers) stood beside her to keep her still and facing the

151   display. The subject's gaze appeared to occasionally avert from the monitor. When this occurred,

152   another experimenter, who was monitoring the subject's gaze direction, manually added a marker

153   in the electroencephalography (EEG) data via a keyboard connected to the measurement

154   computer.

155   *ERP recording and analysis*

156   EEG was recorded from Ag/AgCl electrodes attached to five scalp positions (Fz, Cz, Pz, T5,

157   and T6), according to the international 10-20 system for humans. The signals were referenced to

158   the forehead midline (FPz) and a ground electrode was positioned at the left earlobe (Fukushima

159   et al., 2010). The electrodes were filled with Quick GEL and impedances were kept below 6 kΩ.

160   Signals were amplified by NuAmp-40 and processed by Acquire 4.3 software (NeuroScan Inc.)

161   with a 1,000 Hz sampling rate. A 0.1–20 Hz band-pass filter (24 dB/oct) was applied in the

162   offline analysis. All data were segmented into 700-ms epochs, including a 100-ms pre-stimulus

163   baseline period, based on time markers of the stimulus onset. These epochs were baseline

164   corrected with respect to the mean amplitude over the 100-ms pre-stimulus period. Epochs that

165   exceeded ±60 μV were excluded from the analysis. Epochs that contained 'non-looking' markers

166   described above were also excluded in the analysis. The numbers of epochs accepted for the

167   analysis were as follows: in Experiment 1, 115, 126, and 52, for unfamiliar, familiar, and self

168   faces, respectively; in Experiment 2, 121 and 105 for unfamiliar and familiar faces, respectively.

169   In Experiment 1, a successive ANOVA with a single factor of stimulus type

170   (unfamiliar/familiar/self) was applied along each data point of each channel to test differentiation

171   among the ERP amplitudes for stimulus categories. In Experiment 2, a successive two-tailed t-

172   test was applied to explore the difference between ERPs to unfamiliar and familiar human faces.

173   To avoid the detection of spurious differentiation among categories, we considered a time range

174   of 30 consecutive time points (30 ms) of p-values < 0.05 to indicate a significant main effect.

Results

Experiment 1

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176

177   The images of seven chimpanzee faces (three unfamiliar [out-group] chimpanzees, three

178   familiar [in-group] chimps, and the subject herself; Figure 1) were pseudo-randomly presented

179   during EEG measurements. ERPs time-locked to the presentation of the face stimuli were

180   calculated for each category (i.e., unfamiliar/familiar/self).

181   The basic morphologies of the ERP waveforms remarkably resembled those reported in our

182   previous studies with the same subject (Fukushima et al., 2010; Hirata et al., 2013). The ERPs

183   from midline sites (Fz, Cz, and Pz) showed three dominant deflections (Figure 2): early negative

184   components within a 100 ms latency, positive deflections peaking around a 140–150 ms latency,

185   and a negative slow wave, which was visible after approximately a 200 ms latency. At the lateral

186   occipitotemporal sites (T5 and T6), additional negative components appeared over the time range

187   of 100–150 ms.

188   A successive analysis of variance (ANOVA) with a factor of stimulus type

189   (unfamiliar/familiar/self) was applied along each ERP data point of each channel to test

190   differentiation among the stimulus categories. A significant main effect of stimulus type was

191   detected over the midline electrode sites (Fz, Cz, and Pz), as indicated in Figure 2 (all F-values >

192   3.027 [*df1*=2, *df2* = 290], *p*-values < 0.05). This differentiation was found in the time range from

193   approximately a 200 to 450 ms latency, most prominently at the Cz site. The details of the

194   latencies that differentiated each category at each electrode position are depicted in Table 1. Post-

195   hoc two-tailed *t*-test revealed that the waveforms for unfamiliar faces significantly diverged from

196   those of familiar and self faces and no differences in the ERPs related to familiar and self faces

197   were detected (Table 1).

198   **Experiment 2**

199   Following Experiment 1, in which we examined the effects of familiarity in ERP responses to

200   conspecific faces, Experiment 2 was conducted to investigate the same effect s of familiarity in

201   ERP responses to allospecific human stimuli. The images of six human faces (three persons

202   familiar and three persons unfamiliar to the subject) were pseudo-randomly presented using the

203   same basic design as in Experiment 1.

204   Figure 3 illustrates ERP waveforms elicited by the images of familiar and unfamiliar human

205   faces. A successive *t*-test (*df* = 224) along each data point of the ERP waveforms on each channel

206   failed to detect any significant differences in the ERPs related to familiar and unfamiliar human

207   faces.

Discussion

208

209   This study examined whether and how the familiarity of faces is reflected in chimpanzee

210   ERPs. Based on the results of Experiment 1, we propose that familiarity modulates the ERPs

211   evoked by conspecific faces, differentiating faces of familiar subjects from the subject's own

212   face. The familiarity effect was observed in a time range later than approximately 200 ms post-

213   stimulus onset. Our previous study reported that face-specific modulation of the chimpanzee's

214   visual ERP was initiated as early as around a 100 ms latency in comparison with images of

215   scrambled faces or non-face objects (Fukushima et al., 2010). Thus, the results of our previous

216   study and the current study together indicate an early response to face processing and relatively

217   late modulation by face familiarity. This pattern is consistent with humans studies, in which ERPs

218   differentiate familiar and unfamiliar faces in a time period *after* the primary processing of face

219   configuration (i.e., after the occurrence of the N170 component) (Bentin & Deouell, 2000; Eimer,

220   2000; Henson et al., 2003; Kaufmann, Schweinberger, & Burton, 2009; Miyakoshi, Kanayama,

221   Nomura, Iidaka, & Ohira, 2008; Paller, Hutson, Miller, & Boehm, 2003), although a few research

222   groups have reported earlier latencies of this familiarity effect (Caharel et al., 2002; Caharel,

223   Courtay, Bernard, Lalonde, & Rebai, 2005; Jemel, Schuller, & Goffaux, 2010; Leleu et al., 2010).

224   It is considered that the familiarity effect basically occurs in later stages of face recognition

225 because it interacts with multiple face-related processing steps (Gobbini & Haxby, 2007).

226 Interestingly, the latency of the familiarity effect in the present study resembled that of our

227 previous study of affective processing, in which the ERP differentiation of affective vs. non-

228 affective pictures initiated about a 210 ms latency (Hirata et al., 2013). Thus, the familiarity effect

229 in the current study may be partially modulated by affective processing.

230   With respect to its topography, the familiarity effect was observed around the midline

231 electrode sites (i.e., Fz, Cz, and Pz) centered on the vertex. This result was different from our

232 previous study(Fukushima et al., 2010), which demonstrated face-specific patterns around

233 temporal and posterior regions (i.e., T5/T6 as well as Pz electrode sites), suggesting that the

234 familiarity effect in the current study was modulated by neural substrates not limited to those

235 specific to face processing. This consideration is again consistent with neuroimaging studies in

236 human subjects, which indicate that the familiarity effect is subserved by non-visual networks,

237 such as memory or affective networks (Gobbini & Haxby, 2007; Natu & O'Toole, 2011). Another

238 related study from our group examined the ERPs of the same subject while they received auditory

239 presentations of the names of familiar (including her own name) and unfamiliar chimpanzees,

240 showing that the evoked potentials from fronto-central sites differentiated unfamiliar names from

241 familiar ones (Ueno et al., 2010). Although the previous auditory study used different reference-

242 channels (i.e., A1/A2) from the current visual study, it is possible that similar mechanisms

243   subserved familiarity processing across the two studies. Furthermore, a few human ERP studies

244   of face perception have reported a familiarity effect not only at temporo-occipital sites but also in

245   regions around fronto-central sites (Caharel et al., 2002; Miyakoshi et al., 2008). It is difficult to

246   strictly compare ERP topographies from chimpanzees and humans because of structural

247   differences in terms of the shapes of the bone and muscles of the skull between the species

248   (Burrows, Waller, Parr, & Bonar, 2006), and these differences may substantially influence scalp-

249   surface potentials. However, the results of the present experiments are somewhat consistent with

250   those of previous human studies.

251   It is noteworthy that the ERPs elicited by the subject's own face diverged from those evoked by

252   unfamiliar but not familiar faces of conspecifics in Experiment 1. Human studies have shown that

253   self-face perception is reflected in the modulation of face-evoked ERPs, although the latency and

254   topography of this effect are somewhat inconsistent among reports (Caharel et al., 2002; Keyes,

255   Brady, Reilly, & Foxe, 2010; Ninomiya, Onitsuka, Chen, Sato, & Tashiro, 1998; Sui, Zhu, &

256   Han, 2006). In our previous study mentioned above, the ERPs from the same subject chimpanzee

257   showed specific patterns in their response to the auditory presentation of the subject's own name

258   with a 500 ms latency, suggesting that the chimpanzee brain at least differentiated this self-

259   relevant stimulus (Ueno et al., 2010). The reason why the current study failed to detect self-

260   specific patterns in terms of visual face recognition may be quantitative differences in the amount

261 of exposure to this stimulus. Auditory symbols had been much more frequently used in the

262 subject's communication with human caregivers. As for the visual recognition of self-image, the

263 subject chimpanzee was exposed to the image of its own face in a few experimental sessions

264 (Hirata, unpublished), and she also had occasional access to visual images of her own face (see

265 Methods). However, the visual input of her own face may not be sufficient to differentiate ERPs

266 related to self and familiar non-self faces. This study at least suggests that experience with self-

267 face perception can influence neural representations of the self-face by shifting it toward that of

268 "familiar" individuals. In other words, we cannot claim based on our results that the subject

269 chimpanzee recognized an image of her own face as representing herself, but we can claim that

270 the subject's brain did respond differently to her own face. Determining whether there is a

271 chimpanzee neural signature of self-face recognition requires further investigation using

272 matching experience with the stimuli, and examination of the correspondence between neural

273 activities and measures of self-oriented behaviors.

274   In contrast to the responses to the chimpanzee faces, ERPs to human faces did not

275 differentiate familiar and unfamiliar individuals (Figure 2). This result suggests that modulation

276 of face familiarity in the chimpanzee visual system depends on the species displayed in the target

277 stimulus; that is, the chimpanzee was more sensitive to familiarity of conspecific faces than

278 allospecific faces. Behavioral studies in non-human primates have shown that monkeys have a

279   relatively robust preference for conspecific faces despite substantial exposure to other species,

280   even when they lack visual experiences of conspecific faces (Fujita, 1993; Martin-Malivel &

281   Okada, 2007; Sackett, 1966). Chimpanzees have also been shown to have self-species superiority

282   in social cognition, in terms of, for example, fast face recognition (Parr et al., 1998; Tomonaga et

283   al., 1993) and attracting initial looking at a conspecific face (Hattori et al., 2010). Therefore, the

284   differences between chimpanzee vs. human faces in the current study are in line with those

285   reports, and can be further assumed to suggest that visual face processing is an inherent property

286   of chimpanzees. However, in parallel to this view, a few studies have suggested the presence of

287   flexible modulation of cross-species face perception in chimpanzees. For example, captive

288   chimpanzees show similar configural processing to human faces as to conspecific faces (Parr et

289   al., 1998), and chimpanzees reared by humans show better discrimination of human faces than

290   chimpanzee faces (Martin-Malivel & Okada, 2007). Furthermore, recent studies have explicitly

291   examined the effects of experience on cross-species face processing, showing that young

292   chimpanzees predominantly process conspecific faces, whereas old chimpanzees predominantly

293   process human faces (Dahl, Rasch, Tomonaga, & Adachi, 2013a, 2013b). Their mathematical

294   simulations predicted that this shift in face processing occurs around the age of 15 years in

295   chimpanzees (Dahl et al., 2013a). The subject of our study was 10–11 years old at the time of the

296   experiments, thus it is reasonable to speculate that she still had a dominant sensitivity to

297   conspecific faces, and this was reflected in the ERP responses. Such flexibility is also observed in

298 humans, as it has been shown that human infants have a bias to conspecific faces (de Haan,

299 Pascalis, & Johnson, 2002), but it may be also flexible as human adults perceive chimpanzee

300 faces with a quite similar process to that used for ose of human faces (Carmel & Bentin, 2002).

301 Further investigations of face processing mechanism of primates should take into account

302 interactions between innate tendencies and acquired properties (de Haan, Humphreys, & Johnson,

303 2002).

304 .Finally, we should be cautious of a couple of issues when interpreting the present findings.

305 First, it may be the case that neural differentiation of human familiarity did occur in Experiment 2

306 but it was so small that it was below the limit of detection of EEG or occurred in a manner that is

307 not amenable to measurement by cross-trial averaging of scalp-surface potentials (Luck, 2005;

308 Tallon-Baudry & Bertrand, 1999). Therefore, it is still premature to conclude that the chimpanzee

309 is differentially sensitive to the conspecific and allospecific faces. Second, as pointed out in our

310 earlier discussion of the response to the self-face image, it is also possible that our results simply

311 reflect quantitative differences in the amount of exposure to the target categories. The present

312 subject was reared by humans, and interacted every day with the human staff whose faces were

313 presented as the stimuli of the "familiar" category in Experiment 2. Thus, we suggest that the

314 subject was very familiar with these human faces, and it is valid to define the set of pictures

315 depicting her caregivers as the "familiar" category for this subject. However, the amount of

316 exposure to the familiar chimpanzees and humans, particularly the total amount of time

317 previously spent looking at their faces, could not be exactly and quantitatively matched in this

318 study. In common with the topic of self-face recognition, the current study was a preliminary

319 attempt to clarify the effects of familiarity on face processing and cross-species differences in

320 these effects. Further examinations of how experience modulates face perception should apply

321 strict control over exposure to the target stimuli and behavioral indices.

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478 **Acknowledgments**

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Figure 1

Figure 1

Stimulus images used in the present study. In Experiment 1, the subject was presented seven images of chimpanzee faces in the three categories of unfamiliar, familiar, and self-images. In Experiment 2, the subject was presented six images of human faces with unfamiliar and familiar categories. Note that only one example of each category is shown for Experiment 2 for privacy protection.
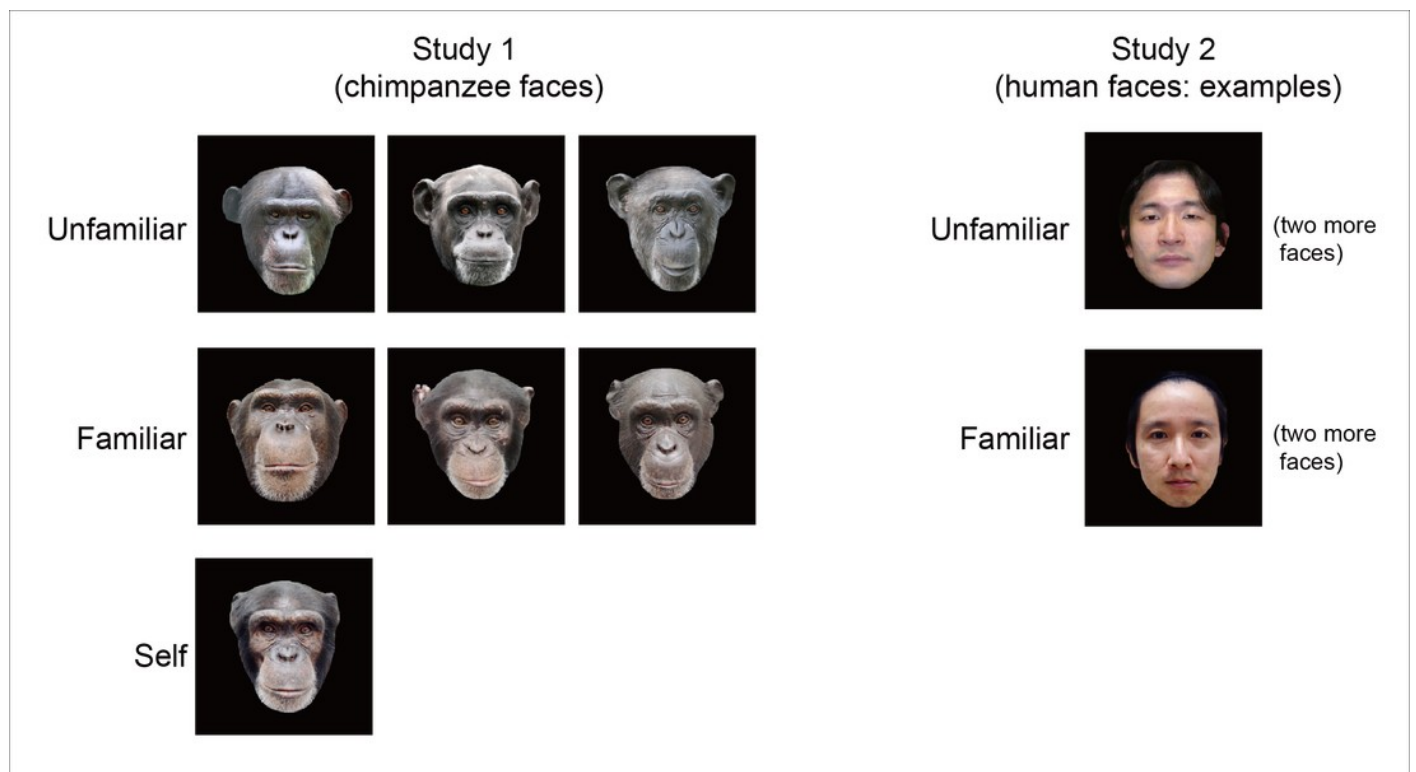
Figure 2

Figure 2

Averaged ERP waveforms elicited by images of unfamiliar and familiar conspecific faces as well as the subject's own face in Experiment 1. The blue-shaded squares overlaid on the waveforms show the periods of statistically significant main effects of stimulus category. The solid lines below the waveforms show the periods of significant difference between unfamiliar and familiar (green) and unfamiliar and self (orange) images.
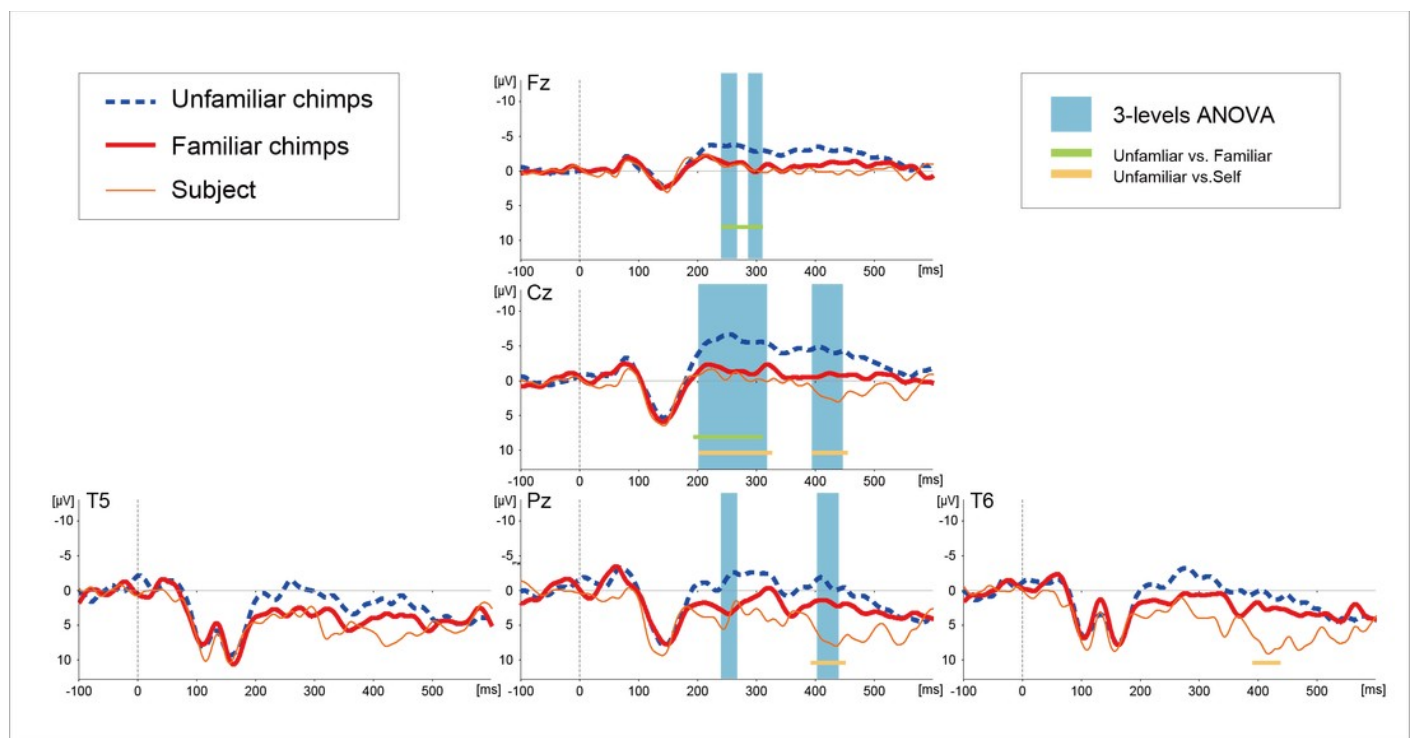
Figure 3

Figure 3

Averaged ERP waveforms elicited by images of unfamiliar and familiar human faces in Experiment 2.
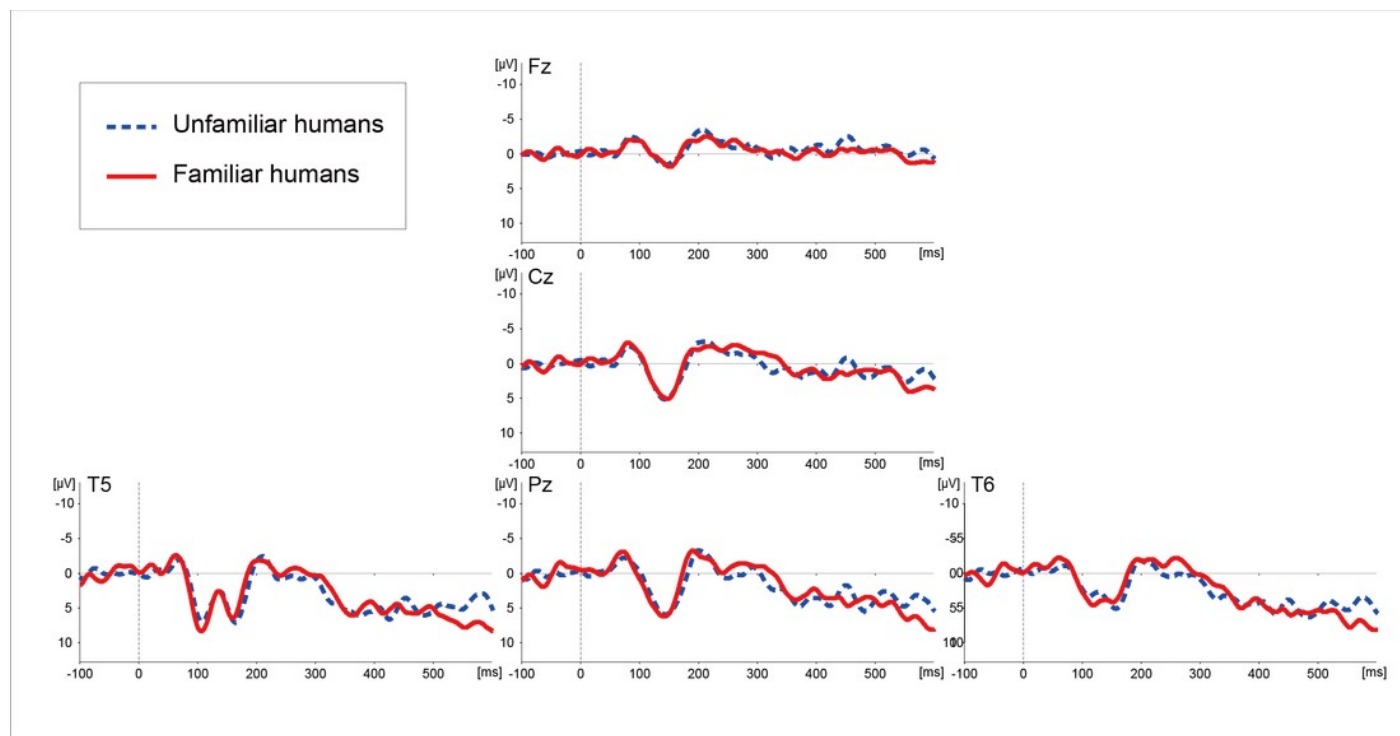
Table 1 (on next page)

Table 1

Time ranges where ERPs for each category differed significantly in Experiment 1 (post stimulus latencies in ms).

Test	Electrodes	Time ranges of statistical significance
3-levels ANOVA	Fz	232 - 269, 286 - 309
	Cz	201 - 317, 393 - 445
	Pz	232 - 269, 402 - 438
Unfamiliar vs. Familiar	Fz	232 - 310
	Cz	192 - 309
Unfamiliar vs. Self	Cz	201 - 325, 392 - 453
	Pz	396 - 453
	T6	393 - 434