Familiar face + novel face = familiar face? Representational bias in the perception of morphed faces in chimpanzee

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Highly social animals possess a well-developed ability to distinguish the faces of familiar from novel conspecifics to induce distinct behaviors for maintaining society. However, the behaviors of animals when they encounter ambiguous faces of familiar yet novel conspecifics, e.g., strangers with faces resembling known individuals, have not been well characterised. Using a morphing technique and preferential-looking paradigm, we address this question via the chimpanzee's facial–recognition abilities. We presented eight subjects with three types of stimuli: (1) familiar faces, (2) novel faces and (3) intermediate morphed faces that were 50% familiar and 50% novel faces of conspecifics. We found that chimpanzees spent more time looking at novel faces and scanned novel faces more extensively than familiar or intermediate faces. Interestingly, chimpanzees looked at intermediate faces in a manner similar to familiar faces with regards to the fixation duration, fixation count, and saccade length for facial scanning, even though the participant was encountering the intermediate faces for the first time. We excluded the possibility that subjects merely detected and avoided traces of morphing in the intermediate faces. These findings suggest a bias for a feeling-of-familiarity that chimpanzees perceive familiarity with an intermediate face by detecting traces of a known individual, as 50% alternation is sufficient to perceive familiarity.

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2 perception of morphed faces in chimpanzees

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16 **Summary**

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18 novel conspecifics to induce distinct behaviours for maintaining society. However, the

19 behaviours of animals when they encounter ambiguous faces of familiar yet novel conspecifics,

20 e.g., strangers with faces resembling known individuals, have not been well characterised. Using

21 a morphing technique and preferential looking paradigm, we address this question via the

22 chimpanzee's facial recognition abilities. We presented eight subjects with three types of stimuli:

23 (1) familiar faces, (2) novel faces and (3) intermediate morphed faces that were 50% familiar and

24 50% novel faces of conspecifics. We found that chimpanzees spent more time looking at novel

25 faces and scanned novel faces more extensively than familiar or intermediate faces. Interestingly,

26 chimpanzees looked at intermediate faces in a manner similar to familiar faces with regards to

27 the fixation duration, fixation count, and saccade length for facial scanning even though the

28 participant was encountering the intermediate faces for the first time. We excluded the possibility

29 that subjects merely detected and avoided traces of morphing in the intermediate faces. These

30 findings suggest a bias for a feeling of familiarity and that chimpanzees perceive familiarity with

31 an intermediate face by detecting traces of a known individual; 50% alternation is sufficient to

32   perceive familiarity.

Introduction

35 Distinction between in- and out-group members based on faces has greatly influenced the

36 evolution of society, leading to individualised relationships and cooperative networks (Hamilton,

37 1964). Notably, many social animals can distinguish between familiar and unfamiliar faces of

38 conspecifics, such as humans (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion, Schiltz,

39 & Crommelinck, 2003), chimpanzees (Boysen & Berntson, 1989; Fukushima et al., 2013; Parr,

40 Winslow, Hopkins, & de Waal, 2000), orangutans (Hanazuka, Shimahara, Tokuda, &

41 Midorikawa, 2013; Vonk & Hamilton, 2014), gorilla (Vonk & Hamilton, 2014), rhesus monkeys

42 (Gothard, Erickson, & Amaral, 2004; Murai, Tanaka, Tomonaga, & Sakagami, 2011), capuchin

43 monkeys (Pokorny & de Waal, 2009), dogs (Racca et al., 2010), sheep (Kendrick, da Costa,

44 Leigh, Hinton, & Peirce, 2001), cattle (Coulon, Deputte, Heyman, & Baudoin, 2009), pigeons

45 (Wilkinson, Specht, & Huber, 2010) and even invertebrates (Chittka & Dyer, 2012).

46 However, few studies have investigated how animals behave when they encounter

47 ambiguous faces of familiar yet novel conspecifics, e.g., strangers with faces resembling known

48 individuals. Theoretically, three behavioural outcomes are possible: animals could behave

49 towards the ambiguous faces 1) in the same manner as the familiar faces, 2) in the same manner

50   as the novel faces or 3) in a manner different from both the novel and familiar faces. A previous

51   study showed that human adults perceive familiarity towards composite faces of novel and

52   familiar (self, sibling and friend) individuals (Platek & Kemp, 2009), which supports the first

53   possible outcome among the above-mentioned possibilities. This study suggests that facial

54   resemblance acts as a cue for genetic relatedness (Daly, 1988) and increases ratings of

55   trustworthiness (DeBruine, 2002). A bias towards novelty in responses to composite faces (the

56   second possible outcome) is supported by the attention model of categorisation (Kruschke, 2003)

57   or hypodescent (Halberstadt, Sherman, & Sherman, 2011): attention is strongly tuned towards

58   the features that best distinguish between in- and out-group members while ignoring shared

59   features, i.e., the assignment of ambiguous faces to out-group members. We previously showed

60   that human infants have a lower preference for composite faces, which include aspects of

61   familiar and novel individuals, than original faces (Matsuda, Okamoto, Ida, Okanoya, & Myowa-

62   Yamakoshi, 2012) (the third possibility discussed above). This study suggests that a negative

63   feeling (or avoidant response) occurs because the composite faces elicit the concept of

64   'familiarity' but fail to satisfy it (e.g., (Mori, 1970);(Steckenfinger & Ghazanfar, 2009). It

65   remains unknown whether other primates exhibit familiarity-biased responses, novelty-biased

66   responses or negative responses when they encounter ambiguous faces. Answering this question

67   may aid our understanding of the evolutionary and developmental profiles of facial recognition

68   in detecting the category boundary between in- and out-group members.

69   We investigated this question in our closest living relative, the chimpanzee, using the

70   morphing technique and a preferential looking paradigm. As is the case with human species,

71   chimpanzees are known to possess a well-developed ability to readily individualise faces (Dahl,

72   Rasch, Tomonaga, & Adachi, 2013; Hirata, Fuwa, Sugama, Kusunoki, & Fujita, 2010; Kano &

73   Tomonaga, 2009; Tomonaga, 2007) and distinguish between familiar versus novel conspecifics

74   (Fukushima et al., 2013) even when shown only static two-dimensional images that are absent

75   any other cues (e.g., olfaction). They also have the ability to identify individuals in terms of

76   kinship detection via phenotypic matching (Parr & de Waal, 1999; Parr, Heintz, Lonsdorf, &

77   Wroblewski, 2010). Furthermore, chimpanzees show categorical perception in face recognition;

78   that is, they detect a category boundary on a spectrum-ranging morphed continuum that

79   comprises two different faces, and their sensitivity for categorisation is affected by exposure to

80   conspecific/non-conspecific faces during development (Martin-Malivel & Okada, 2007). The

81   morphing technique has the advantage of creating composite portraits between two faces with

82 physical accuracy in blend ratios, which enables us to manipulate and quantify the degrees of

83 similarity between different faces (DeBruine, Jones, Little, & Perrett, 2008; Matsuda et al., 2012;

84 Myowa-Yamakoshi, Yamaguchi, Tomonaga, Tanaka, & Matsuzawa, 2005; Parr, Taubert, Little,

85 & Hancock, 2012).

86   In contrast to the discrimination paradigm, the preferential looking paradigm with free

87 viewing has the advantage of investigating intrinsic gazing behaviours such as preference,

88 attention or processing costs by minimising training effects and testing beyond the limits of a

89 match-to-sample task, as we reported previously in adult and infant chimpanzees (Hirata et al.,

90 2010). The aim of our study was to quantify the degree of similarity between faces that

91 chimpanzees perceive as belonging to familiar conspecifics. We investigated the gazing

92 behaviour of chimpanzees when presented with composite faces representing morphs between

93 familiar and novel conspecifics. First, we presented 'intermediate faces' (50% familiar and 50%

94 novel faces) to chimpanzees and examined whether they preferred these intermediate conspecific

95 faces to the original faces. We identified the faces preferred by the chimpanzee when presented

96 with three pairs of faces: familiar versus novel faces, familiar versus intermediate faces and

97 novel versus intermediate faces.

98   Given that novel faces (i.e., potential threats) should elicit more of a response from the

99   chimpanzees than familiar faces (Pascalis & Bachevalier, 1998), we measured the time (fixation

100   duration) spent looking at a face, the frequency (fixation count) with which the chimpanzee

101   looked at the face, and the saccade length for how extensively they scan the face; these indices

102   were used to measure the attentional and processing demand/efficacy (i.e., informativeness)

103   (Antes, 1974; Henderson, 2003; Henderson & Smith, 2009; Loftus & Mackworth, 1978;

104   McCamy, Otero-Millan, Di Stasi, Macknik, & Martinez-Conde, 2014; Unema, Pannasch, Joos,

105   & Velichkovsky, 2005) during facial recognition and to differentiate gazing behaviours

106   associated with viewing familiar and novel faces.

Methods

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109  This research was conducted in accordance with the *Guide for the Care and Use of*

110 *Laboratory Animals* of Hayashibara Biochemical Laboratories, Inc. and the Weatherall Report,

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

112 Welfare and Animal Care Committee of the Hayashibara Great Ape Research Institute (GARI-

113 051101).

114

115 **Participants**

116  Eight chimpanzees (*Pan troglodytes*, two males and six females, 4-17 years old)

117 participated in this study. The names, ages, and sexes of the chimpanzees were shown in the

118 table 1. The subjects were members of a captive group at the Great Ape Research Institute

119 (Hayashibara Biomedical Laboratories, Inc.). Relative dominances and kinship structures were

120 shown in the tables S1 and S2. Loi, Zamba, Tsubaki, and Mizuki came to the institute from other

121 locations when they were 3, 3, 3, and 2 years old, respectively, and since arriving have spent

122 their time together in the same group. Misaki was added to the group when she was 3 years old.

123 Since then, she has spent her time with the above-mentioned individuals in the same enclosure,

124 with few exceptions (described below). Natsuki was born to Tsubaki, and Iroha was born to

125 Mizuki. These offspring grew up in the same group with their mothers and other group members.

126 Hatsuka is a daughter of Misaki but was neglected between the ages of 40 days and 2.5 years.

127 During this period, human caretakers nursed Hatsuka, but she spent 10 minutes to 3 hours of

128 nearly every day with all of the other chimpanzees in the same space. Misaki spent all of her

129 time with the other chimpanzees (except her daughter) during this period. After the age of 2.5

130 years, Hatsuka spent all of her time with Misaki (her mother), and the two of them were

131 separated from the other members in an adjacent enclosure. However, they maintained visual

132 contact with the other members in the neighbouring enclosure through wire mesh or transparent

133 panels. In short, the adult participants (Loi, Zamba, Tsubaki, Mizuki, and Misaki) had known

134 each other since they were 2-3 years old, for approximately 10 years or more, and the adolescent

135 (Natsuki) and infant (Hatsuka and Iroha) individuals were born into this group and had known

136 each other and the other group members since they were born.

137   Three individuals, whose faces were presented to the subjects as familiar-face stimuli,

138 also participated in the study (Loi, Misaki and Zamba). Although these three individuals saw

139 their   own   faces   on   a   screen   in   the   experiment,   our   previous   study   using   the

140   electroencephalography (EEG) recording showed that no significant difference was observed

141   between self- and familiar-face recognition (Fukushima et al., 2013). This finding may be caused

142   by past experiences with informal tests of mirror self-recognition and recognition of self-images

143   on TV monitors (Hirata, Fuwa, & Myowa-Yamakoshi, in preparation). Thus, we presented self-

144   face stimuli as 'familiar' faces to the three individuals. This is consistent with a previous study

145   that showed animals failed to treat self images any differently than other familiar faces, which

146   suggests that the subjects found self images to be familiar given the glass and other reflective

147   surfaces present in their outdoor habitats (Vonk & Hamilton, 2014).

148   The relative dominances and kinship structures between each subject and familiar-face

149   stimuli were tabulated (Table S1-2).

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152   **Experimental apparatus**

153   The subjects sat in an experimental room (3 m × 2 m × 2.5 m, L × W × H) and viewed

154   the images on a 17-inch LCD screen (1024 × 768 pixels) at a distance of 60 cm. The eye

155   movements of the chimpanzees were recorded using a table-mounted eye tracker (Tobii T60,

156   Stockholm, Sweden) (Hirata et al., 2010).

157

158   **Stimuli description**

159   Prior to the experiments, coloured and frontal-orientation photographs of familiar (in-

160   group) chimpanzees and novel chimpanzees (from an out-group housed at the Kumamoto

161   Sanctuary, Wildlife Research Centre, Kyoto University) were taken. Each photograph was

162   rotated in-plane to horizontally align the interpupil distance and was then resized to 512 × 680

163   pixels (at a distance of 60 cm with approximately 13.3 × 17.4 degrees of visual angle). Using

164   computer morphing software (Sqirlz Morph 2.1: Xiberpix, Solihull, UK, www.xiberpix.com),

165   approximately 350 points were positioned on each chimpanzee face (approximately 100 points

166   for facial contour and 250 for facial parts) to delineate specific facial landmarks (e.g., distinctive

167   wrinkles under the eyes, across the muzzle, and in the ear region) (DeBruine et al., 2008; Parr et

168   al., 2012). To create intermediate faces, a familiar face and a novel face were morphed together

169   using the software (Sqirlz Morph 2.1) to produce a new face incorporating 50% of the familiar

170   face and 50% of the novel face by calculating the mean shape and colour of the constituents

171   (Figure 1) (Matsuda et al., 2012). A previous study showed that chimpanzees could detect facial

172   similarities between mothers and sons but not between mothers and daughters (Parr & de Waal,

173   1999), which suggests that chimpanzees are better at detecting facial similarities among males;

174   consequently, we morphed two photographs of male chimpanzees to create an intermediate face.

175   Intermediate faces were created from photographs of different chimpanzees than those used as

176   the familiar face and novel face stimuli; this step was taken to prevent an adaptation effect that

177   could occur when the chimpanzees were repeatedly presented with images of the same faces

178   (even though the morphs bore only partial resemblance to the original faces).

179   We used movie clips of dynamic facial expressions as visual stimuli because primates

180   and humans are more responsive to moving faces than to static faces (Shepherd, Steckenfinger,

181   Hasson, & Ghazanfar, 2010). We created moving stimuli of mouth-opening chimpanzee faces

182   that were familiar, novel or intermediate; these stimuli are known as *dynamic facial expressions*

183   or *dynamic faces* (Kilts, Egan, Gideon, Ely, & Hoffman, 2003; LaBar, Crupain, Voyvodic, &

184   McCarthy, 2003). Moving stimuli were created in the following manner: first, two coloured

185   photographs (mouth-closing and mouth-opening faces) of each individual chimpanzee were

186   taken prior to the main experiment. Next, for each participant, ten intermediate images with

187   expressions situated between the close-mouthed and open-mouthed expressions were created in

188 9% steps using the computer-morphing techniques. Then, to create a moving clip, the 12 images

189 (one mouth-closing image, 10 intermediate images and the final mouth-opening image) were

190 presented in succession. Each image was presented for 40 ms, and the final image was presented

191 for an additional 760 ms; thus, each animation clip lasted 1,200 ms. Each clip was shown five

192 times (i.e., totalling a six-second duration) in both the main and control experiments (see video

193 clips of examples in the electronic supplementary materials; *familiar-face.avi*, *intermediate-*

194 *face.avi* and *novel-face.avi*). A human expert viewed the images to confirm that the presentation

195 speed sufficiently reflected the natural changes in the dynamic facial expressions of

196 chimpanzees.

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198

199 **Experimental procedure and data analysis**

200   Each chimpanzee's gaze was calibrated on the eye tracker prior to the experiment.

201 Two-point automated calibration was conducted by presenting a movie clip on each reference

202 point. A relatively small number of reference points was adopted for the chimpanzees because

203 they tended to view these reference points only briefly and no training procedure was adopted for

204   them. However, we checked the accuracy after the initial calibration and repeated the calibration

205   if necessary. Our validation session confirmed the comparable accuracy between chimpanzees

206   and humans (see (Hirata et al., 2010; Kano, Hirata, Call, & Tomonaga, 2011); the calibration

207   errors were 0.2-1 degree in both chimpanzees and humans). Then, the chimpanzees were

208   presented with the following four pairs of stimuli: (1) familiar versus novel faces, (2) familiar

209   versus intermediate faces, (3) novel versus intermediate faces and (4) novel versus morphed

210   faces of two novel chimpanzees. In each of the four trials, a pair of faces was presented side-by-

211   side on an eye tracker screen for six seconds. Each novel chimpanzee face was presented only

212   once to prevent an adaptation effect. Each trial was preceded by a stimulus intended to attract the

213   participant's visual attention to the centre of the screen. The order of the four test trials and the

214   side on which a given face appeared was random and counterbalanced across participants.

215   In the data analysis, entire faces of presented stimuli were chosen as areas of interest

216   rather than specific facial parts because we used movie stimuli of dynamic facial expressions as

217   mentioned above. We measured the total looking durations, counts and saccade lengths for each

218   face. The saccade length was measured as a sum of the looking path length during the face

219   scanning for each face. We averaged the same types of facial stimuli for each participant to

220   minimise the variations in looking behaviours that occasionally appear during free viewing. The

221   data were normalised to calculate proportions between three types of facial stimuli (familiar,

222   intermediate and novel faces for Figure 1) and between two types of facial stimuli (novel and

223   morphed faces of two novel faces for Figure 2) (Matsuda et al., 2012). We omitted data if the

224   chimpanzee (participant) looked at only one side of a pair of stimulus faces (strong side bias; see

225   chimpanzee #4 eye tracking data in the supplementary information for Figure 2).

227 Results

228 Figure 1a depicts an example of the three different types of stimuli: a familiar face, an

229 intermediate face and a novel face. The fixation duration, fixation count and saccade length for

230 each image are shown in Figure 1b, 1c and 1d, respectively. The non-parametric Friedman test

231 for all participants (N = 8) revealed significant overall effects for the fixation duration (χ^2(2) =

232 6.25, $N = 8$, $p = 0.04$; Figure 1b), for the fixation count (χ^2(2) = 7.47, $N = 8$, $p = 0.02$; Figure 1c)

233 and for the saccade length (χ^2(2) = 9.25, $N = 8$, $p = 0.01$; Figure 1d). The non-parametric

234 Wilcoxon signed-rank test (two-tailed) showed that the fixation count and saccade length were

235 significantly different between the familiar and novel faces ($Z = -2.24$, $N = 8$, $p = 0.02$ for the

236 fixation count and $Z = -2.52$, $N = 8$, $p = 0.01$ for the saccade length), whereas the fixation

237 duration was similar ($Z = -1.68$, $N = 8$, $p = 0.11$); all indices were significantly different for the

238 intermediate and novel faces ($Z = -2.52$, $N = 8$, $p < 0.01$ for the fixation duration; $Z = -2.24$, $N =$

239 8, $p < 0.03$ for the fixation count; $Z = -2.38$, $N = 8$, $p < 0.02$ for the saccade length). No

240 significant differences in these indices were found for the familiar and intermediate faces ($Z =$

241 0.70, $N = 8$, $p = 0.55$ for the fixation duration; $Z = -0.35$, $N = 8$, $p = 0.78$ for the fixation count; Z

242 = 0.14, $N = 8$, $p = 0.95$ for the saccade length). These results suggest that novel faces elicit a

243   greater response than familiar or intermediate faces.

244   Although intermediate faces were less preferred than novel faces, it is possible that the

245   chimpanzees detected traces of morphing (e.g., a blur in wrinkles) and subsequently avoided the

246   unnatural-looking intermediate faces. In this case, the chimpanzees should show a lower

247   preference for the morphed faces *per se*, irrespective of constituent individuals or whether a

248   familiar or novel face was shown. To exclude this possibility, we presented the subjects with an

249   image of a novel chimpanzee and an image of a morphed face between two different novel

250   chimpanzees. The duration spent looking at the two faces and the frequency with which the faces

251   were observed did not differ significantly, nor did the saccade length for facial scanning

252   (Wilcoxon signed-rank test (two-tailed), $Z = 1.52$, $N = 7$, $p = 0.16$ for the fixation duration,

253   Figure 2a; $Z = 1.18$, $N = 7$, $p = 0.30$ for the fixation count, Figure 2b; $Z = 0.68$, $N = 7$, $p = 0.58$

254   for the saccade length, Figure 2c). This result indicates that the participants neither detected nor

255   avoided the morphed faces; instead, they showed a lower preference for the intermediate faces

256   than the novel faces because of constituent familiar faces.

257   We found systematic differences for participants in the perception of facial parts and

258   body (the eyes, mouth and body of stimuli were defined as areas of interest); the non-parametric

259   Friedman test for all participants revealed significant overall effects for the fixation duration

260   ($\chi^2(2) = 14.25$, $N = 8$, $p = 0.0008$). The non-parametric Wilcoxon signed-rank test (two-tailed)

261   showed that the fixation duration was significantly different between the eyes and mouth ($Z = $ -

262   2.52, $N = 8$, $p = 0.008$) and between the mouth and body ($Z = 2.52$, $N = 8$, $p = 0.008$) but not

263   between the eyes and body ($Z = 1.40$, $N = 8$, $p = 0.20$). Larger attention to the mouth part of

264   facial stimuli may result from the presentation of movie stimuli of mouth-opening faces.

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Discussion

270   In contrast with our previous human study (Matsuda et al., 2012), chimpanzees did not exhibit

271   negative/ avoidant responses to intermediate faces (i.e., 50-50% composite faces between

272   familiar and novel conspecifics). This difference occurred largely because the chimpanzees paid

273   less attention to the familiar faces and preferred the novel faces. This novelty preference for

274   familiar faces appeared as early as approximately 200 ms after stimulus presentation (Figure S1

275   in the supplementary information), which is consistent with our previous EEG study that showed

276   that different neural responses to familiar and novel faces have a latency of approximately 200

277   ms (Fukushima et al., 2013).

278   Furthermore, the chimpanzees appeared to avoid looking at the familiar and

279   intermediate faces to a similar extent. One possible reason for this outcome was that morphing

280   made a face more similar to the prototype and, therefore, made the face more attractive (Langlois

281   & Roggman, 1990); however, this was not the case. Rather, the results indicate that the

282   chimpanzees detected the resemblance between the intermediate face and the familiar face and

283   thus responded to these faces in a similar manner. In other words, the category boundary

284   between familiar (i.e., in-group) and novel (i.e., out-group) faces is more closely situated towards

285   novel faces on a spectrum ranging from the familiar to the novel. This claim is consistent with a

286   previous study of morphed-face recognition in humans that showed a bias in favour of a feeling

287   of familiarity when one encounters intermediate faces (50-50%) of self-, sibling- and friend-

288   stranger morphing (Platek & Kemp, 2009).

289   The ability to detect facial resemblance may play a key role in kinship recognition.

290   Previous studies illustrated that chimpanzees are capable of visually recognising kin from

291   pictures of novel individuals (Parr & de Waal, 1999; Parr et al., 2010). These previous studies,

292   however, used a matching-to-sample paradigm, and the chimpanzees went through basic training

293   of the match-to-sample task for familiar related individuals; thus, they may have simply learned

294   to detect individuals with facial resemblances (Parr & de Waal, 1999; Parr et al., 2010). Using a

295   free-viewing paradigm, we demonstrated that chimpanzees voluntarily detect individuals with

296   facial resemblances.

297   We previously showed that human infants have a lower preference for intermediate

298   faces (i.e., morphs between familiar (mother) and novel (stranger) faces) than for original faces

299   (Matsuda et al., 2012), which is different from the results of the chimpanzees in the present study.

300   This variation may originate from differences in the species, the age of the chimpanzees and/or

301   the target faces. Thus, it is difficult to directly compare our results from human infants and adult

302   chimpanzees without considering species similarities and differences in their cognitive

303   development and adaptive significance. For example, a previous study showed that infant

304   chimpanzees preferentially looked at their mother's face, the most familiar face to the infants,

305   over a computer-created, average face (i.e., novel face) when they were between 4 and 8 weeks

306   of age; however, such a preference for the mother's face suddenly disappeared after 8 weeks of

307   age (Myowa-Yamakoshi et al., 2005). The developmental change in the mother/stranger

308   preference has also been observed in human infants (Gredeback, Fikke, & Melinder, 2010). This

309   may be because both chimpanzee and human infants need to recognise their caregiver during the

310   initial phase of their development (it is vital for their survival); however, infants become

311   socialised at a certain stage by engaging in interactions with individuals other than their mothers

312   (Matsuzawa, Tomonaga, & Tanaka, 2006). In short, it is natural to assume that preferences for

313   certain faces are affected by various factors, including development and the environment (Dahl

314   et al., 2013; Martin-Malivel & Okada, 2007).

315   The present study revealed a facial preference pattern in chimpanzees using familiar,

316   novel, and morphed intermediate faces as stimuli in a free viewing paradigm. Our study suggests

317   a representation bias in favour of a feeling of familiarity when one encounters intermediate faces

318   between in- and out-group conspecifics.

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436 **Table 1.** Participants' names, age and sex

437

reference number	name	age (years)	sex
chimpanzee 1	Hatsuka	4	female
chimpanzee 2	Iroha	4	female
chimpanzee 3	Loi	17	male
chimpanzee 4	Misaki	12	female
chimpanzee 5	Mizuki	15	female
chimpanzee 6	Natsuki	7	female
chimpanzee 7	Tsubaki	16	female
chimpanzee 8	Zamba	17	male

438

439 **Figure legends**

440

441 **Figure 1.** Visual preferences of chimpanzees for different types of faces. (*a*) An example of

442 three different types of stimuli: familiar face (i), intermediate face (ii) and novel face (iii). (*b*)

443 The mean-proportional fixation duration for each of the face types. (*c*) The mean-proportional

444 fixation count for each of the face types. (*d*) The mean-proportional saccade length for each of

445 the face types. Boxplots describe the responses to each type of facial stimuli. * $p < 0.05$, ** $p <$

446 0.01 (Friedman test).

447

448 **Figure 2.** Visual preferences of chimpanzees for different face types. (*a*) The mean proportional

449 fixation duration for each of the face types: a 100% novel face and a 50%-50% morphed face

450 with different novel faces. (*b*) The mean proportional fixation count for each of the face types.

451 (*c*) The mean proportional saccade length for each of the face types. Boxplots describe the

452 responses to each type of face stimuli. n.s.: no significant difference (Wilcoxon signed-rank test).

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Figure 1

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Figure 2

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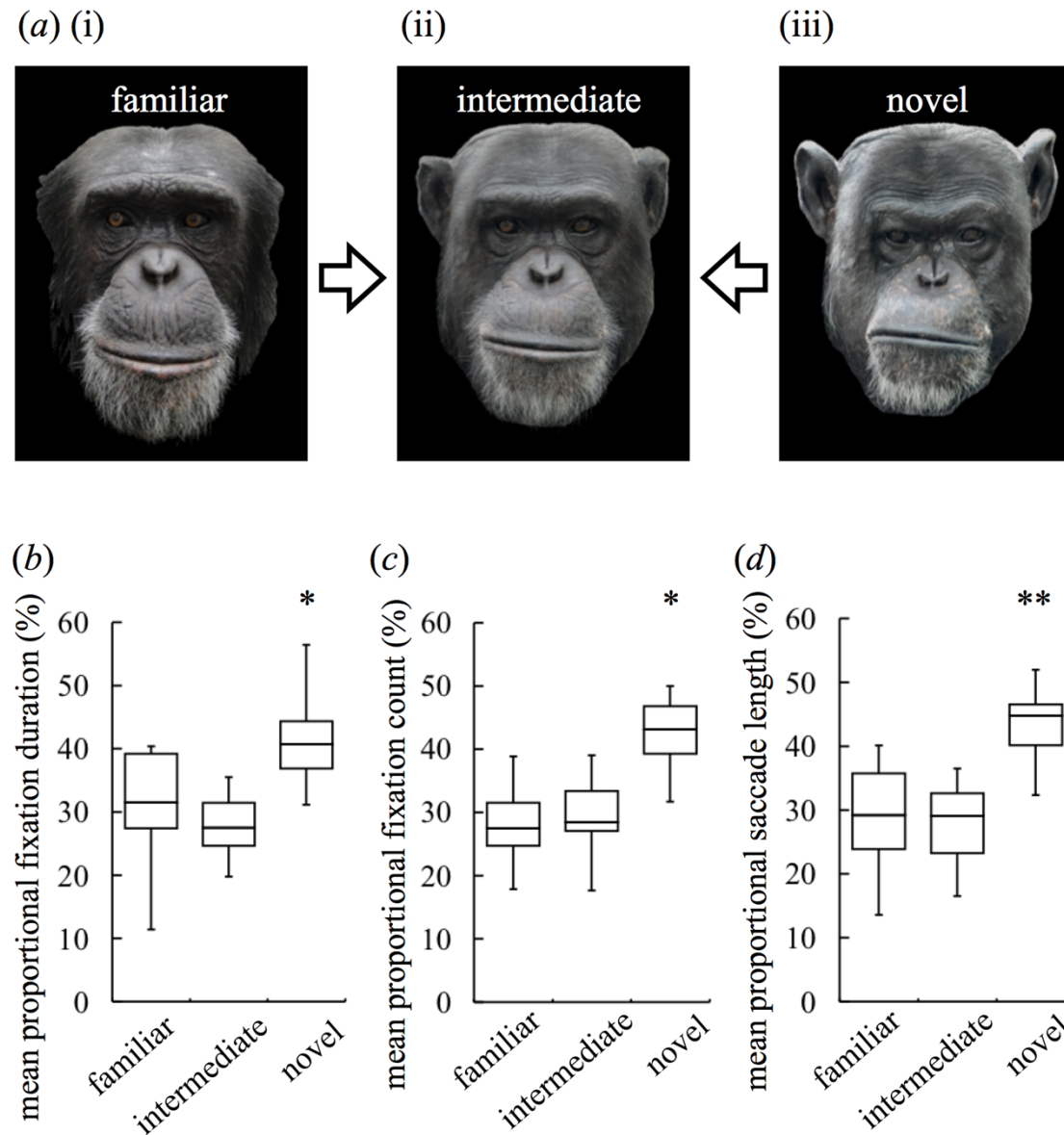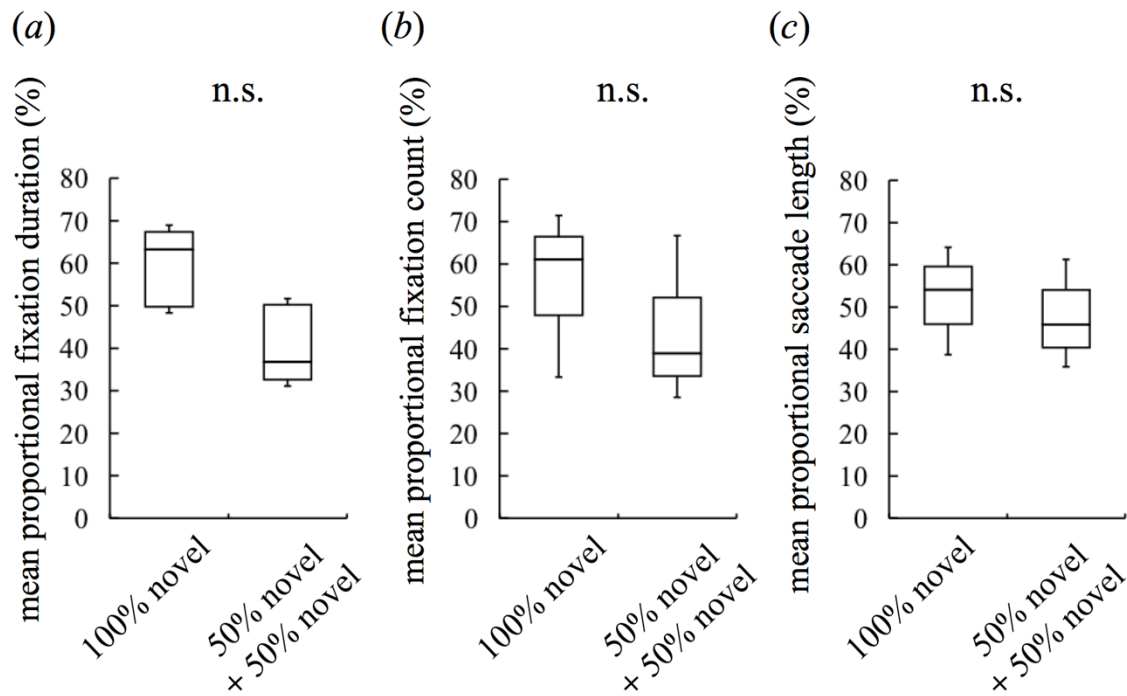
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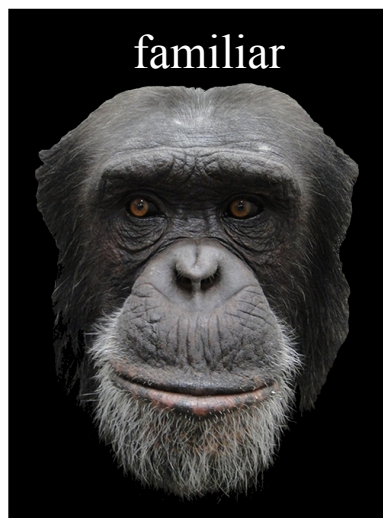
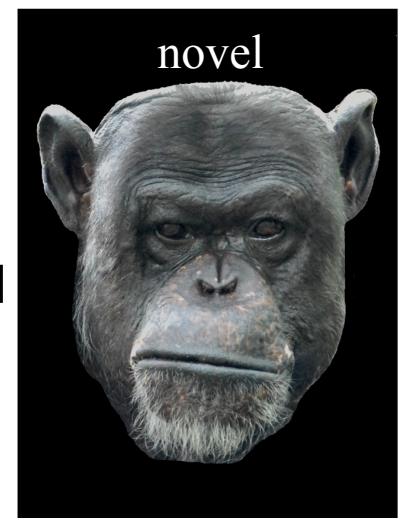
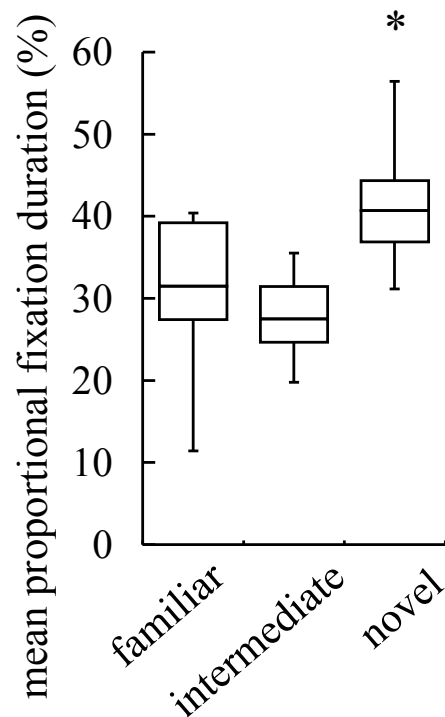
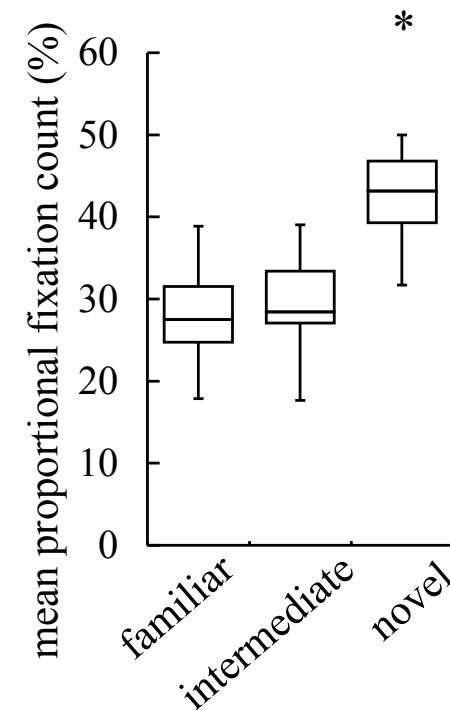
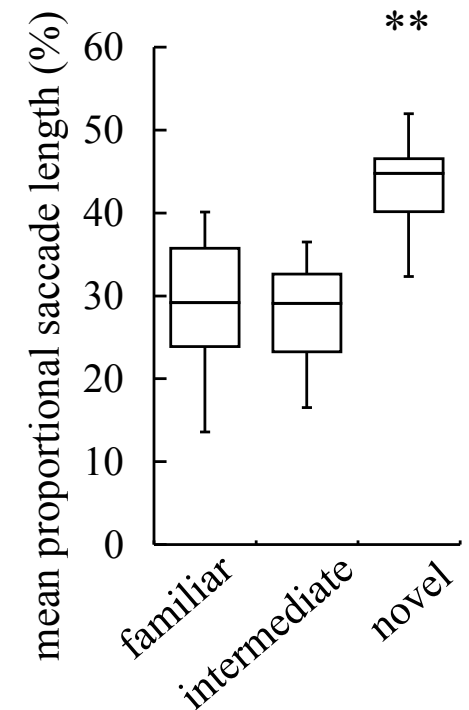
Visual preferences of chimpanzees for different types of faces.

(*a*) An example of three different types of stimuli: familiar face (i), intermediate face (ii) and novel face (iii). (*b*) The mean-proportional fixation duration for each of the face types. (*c*) The mean-proportional fixation count for each of the face types. (*d*) The mean-proportional saccade length for each of the face types. Boxplots describe the responses to each type of facial stimuli. * $p < 0.05$, ** $p < 0.01$ (Friedman test).

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