Mirror experience modifies bonobos' perception of themselves

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The question of whether animals have some sort of self-awareness is a topic of continued debate. A necessary precondition for self-awareness is the ability to visually discriminate the self from others, which has traditionally been investigated through mirror self-recognition experiments. Although great apes generally pass such experiments, interpretations of results have remained controversial. The aim of this study was to investigate how bonobos (*Pan paniscus*) respond to different types of images of themselves and others, both before and after prolonged mirror exposure. We first presented mirror-naive subjects with representations of themselves in three different ways (mirror image, contingent and non-contingent video footage) as well as representations of others (video footage of known and unknown conspecifics). We found that subjects paid significantly less attention to contingent images of themselves (mirror, video footage) than to non-contingent images of themselves and unfamiliar individuals, suggesting they perceived the non-contingent self-image as novel. We then provided subjects with three months of access to a large mirror centrally positioned in the enclosure. Following this manipulation, subjects showed significantly reduced interest in the non-contingent self-images, while interest in unknown individuals remained unchanged, suggesting that the mirror experience has led to a fuller understanding of their own self. We discuss implications of these findings for the on-going debate on self-awareness in animals.

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9 **Abstract**

10 The question of whether animals have some sort of self-awareness is a topic of continued debate.

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12 others, which has traditionally been investigated through mirror self-recognition experiments.

13 Although great apes generally pass such experiments, interpretations of results have remained

14 controversial. The aim of this study was to investigate how bonobos (*Pan paniscus*) respond to

15 different types of images of themselves and others, both before and after prolonged mirror

16 exposure. We first presented mirror-naive subjects with representations of themselves in three

17 different ways (mirror image, contingent and non-contingent video footage) as well as

18 representations of others (video footage of known and unknown conspecifics). We found that

19 subjects paid significantly less attention to contingent images of themselves (mirror, video

20 footage) than to non-contingent images of themselves and unfamiliar individuals, suggesting

21 they perceived the non-contingent self-image as novel. We then provided subjects with three

22 months of access to a large mirror centrally positioned in the enclosure. Following this

23 manipulation, subjects showed significantly reduced interest in the non-contingent self-images,

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25 experience has led to a fuller understanding of their own self. We discuss implications of these

26 findings for the on-going debate on self-awareness in animals.

28 **Introduction**

29 A fundamental question in comparative cognition is whether, or to what degree, non-human

30 animals have something akin to self-awareness, that is, whether they can recognise themselves as

31 separate from others and the environment. Related to this is the question of whether animals,

32 other than humans, have some understanding of their own mental states. It is generally accepted

33 that self-awareness presupposes self-recognition of the body, such as its visual appearance,

34 which is empirically easier to address than mentalistic notions of the self. Since the 1970s

35 mirrors have been used as the main tool to investigate self-recognition in the visual domain.

36 Evidence for self-recognition is either in the form of spontaneous, self-directed, exploratory

37 behaviours to the mirror image (Swartz, Sarauw & Evans, 1999) or subjects targeting visual

38 markings administered to a body part that is not visible without the aid of a mirror (the "mirror-

39 mark" test; Gallup, 1970).

40

41 Gallup's (1970) research on chimpanzees and macaques was pioneering, followed by studies on

42 a range of other primate species, including humans (Amsterdam, 1972), chimpanzees (Lethmate

43 & Dücker, 1973; Suárez & Gallup, 1981; Calhoun & Thompson, 1988; Swartz & Evans, 1991;

44 Lin, Bard & Anderson, 1992; Povinelli et al., 1993), bonobos (Hyatt & Hopkins, 1994;

45 Westergaard & Hyatt, 1994; Walraven, Van Elsacker & Verheyen, 1995), gorillas (Suárez &

46 Gallup, 1981; Ledbetter & Basen, 1982; Posada & Colell, 2007), orang-utans (Lethmate &

47 Dücker, 1973; Suárez & Gallup, 1981), gibbons and siamangs (Lethmate & Dücker, 1973;

48 Inoue-Nakamura, 1997; Suddendorf & Collier-Baker, 2009), monkeys (Lethmate & Dücker,

49 1973; Inoue-Nakamura, 1997) and prosimians (Inoue-Nakamura, 1997) (see Anderson, 1984 for

50 review in primates).

51 Within the non-human primates, great apes generally appear to be capable of mirror self-

52 recognition (see Swartz, Sarauw & Evans, 1999 for review), although there are also multiple

53 reports of failure (e.g., gorillas: Shillito et al., 1999). In bonobos, evidence for mirror self-

54 recognition is in terms of mirror-guided, self-directed behaviours, e.g., subjects picking the teeth

55 or eyes (Hyatt & Hopkins, 1994; Westergaard & Hyatt, 1994), in some instances from first

56 exposure (Walraven, Van Elsacker & Verheyen, 1995). Monkeys (*Macaca silenus, Mandrillus*

57 *sphinx, Papio hamadryas, Ateles sp., Cebus apella*) generally fail the 'mirror-mark' test

58 (Lethmate & Dücker, 1973; Ujhelyi et al., 2000; Heschl & Fuchsbichler, 2009; Suddendorf &

59 Collier-Baker, 2009) and we are not aware of any positive evidence for spontaneous, self-

60 directed behaviours in front of mirrors (Inoue-Nakamura, 1997). In one study, Hauser et al.

61 (1995) used a modified 'mirror-mark' test by colour-dying cotton-top tamarins' (*Saguinus*

62 *oedipus*) head hair and reported that individuals touched their heads more often and looked in the

63 mirror longer than controls. However, the study was criticized because results were not based on

64 blind video scoring (Anderson & Gallup, 1997). In a follow-up study, Hauser (2001) then failed

65 to replicate the original findings but argued that subjects had witnesses other group members

66 with colour-dyed hair, suggesting that this may have lowered their interest.

67

68 Mirror experiments have also been conducted with non-primate species with positive evidence in

69 bottlenose dolphins (Marten & Psarakos, 1994; Reiss & Marino, 2001), Asian elephants (Plotnik,

70 de Waal & Reiss, 2006) and even manta rays, the biggest brained of all fish (Ari & D'Agostino,

71 2016). At the same time, small-brained species, such as great tits, (Kraft et al., 2017) or cichlid

72 fish (Hotta, Komiyama & Kohda, 2018), typically fail mirror self-recognition tasks, suggesting

73 that mirror self-recognition may be a property of large brains, regardless of phylogeny (but see

74   Gallup & Anderson, 2018). However, there are claims of mirror-self recognition in Clark's

75   nutcrackers (Clary & Kelly, 2016), Eurasian magpies (Prior, Schwarz & Güntürkün, 2008; but

76   see Anderson & Gallup, 2015) and cleaner wrasse (Kohda et al., 2019) but not in giant pandas

77   (Ma et al., 2015), suggesting that the complexity of a species' social life may also play a role

78   (Gallup, 1998; Prior, Schwarz & Güntürkün, 2008).

79

80   In humans and great apes, the capacity to recognise one's self in a mirror emerges gradually and

81   with experience, usually starting with social behaviours directed at the mirror (e.g., threatening

82   or vocalising; Gallup, 1970), followed by spatial exploration (e.g., reaching or looking behind

83   the mirror), contingency exploration (movements of mirror-image relative to subject's body) and

84   self-exploration (teeth, eyes or genital regions; Swartz, Sarauw & Evans, 1999). In Western

85   human cultures, self-directed behaviours usually appear from 15-18 months of age and become

86   fully expressed by 24 months, while photo self-recognition occurs later (e.g., Courage et al 2004;

87   Amsterdam, 1972; Lewis & Brooks-Gunn, 1979; but see Keller et al., 2004, 2005; Kärtner et al.,

88   2012 for non-western cultures). In chimpanzees, early reactions to mirrors are similar in kind but

89   do not emerge before 24 months (Lin, Bard & Anderson, 1992). Also, there are large individual

90   differences with either much delayed onset (around 60 months: Swartz, Sarauw & Evans, 1999)

91   or no onset at all (e.g., Swartz & Evans, 1991; Povinelli et al., 1993; Walraven, Van Elsacker &

92   Verheyen, 1995).

93

94   Mirror self-recognition studies have caused much debate on how such data should be interpreted.

95   On one end of the spectrum is the interpretation that positive evidence is an indicator of self-

96   awareness (Inoue-Nakamura, 1997; Gallup, 1998; Swartz, Sarauw & Evans, 1999; Plotnik, de

97 Waal & Reiss, 2006) or a self-concept ("…a sense of continuity, a sense of personal agency and

98 a sense of identity"; Gallup 1998, p. 240). At the other end, reactions towards administered

99 marks have been interpreted as mere artefacts of experimental manipulations and that mirror

100 experiments reveal nothing about cognitive capacities (Heyes, 1994, 1995, 1996). More

101 intermediate positions are that such behaviour qualifies as evidence for self-perception, that is,

102 recognising one's own visual appearance (Nielsen, Suddendorf & Slaughter, 2006) and perhaps

103 even that one's own body is a separate entity from the surrounding world (a 'body concept'). The

104 'body-concept' hypothesis has been investigated in developing children, with the conclusion that

105 such awareness emerges in the second year of life, correlated with passing the 'mirror-mark' test

106 (Moore et al., 2007). The notion of a 'body concept' is also key to an alternative hypothesis to

107 self-recognition: kinaesthetic-visual matching. Here, the idea is that subjects act on the

108 contingency between the kinaesthetic sensations (caused by their body movements) and the

109 corresponding movements of the image in the mirror (Mitchell, 1993, 1997). Mirror self-

110 recognition, however, does not predict perpetual kinaesthetic-visual matching; subjects may

111 simply look at the mirror and know that what they see is them (Mitchell 1993).

112

113 Another way of testing self-recognition is by presenting non-contingent images, usually delayed

114 videos or simply photographs. Infants as young as 5 months appear to discriminate between

115 video images of themselves and those of peers or objects (Legerstee, Anderson & Schaffer,

116 1998) and from 18-24 months they start to show the tell-tale spontaneous behaviours, such as

117 exploration of visually inaccessible body parts, in the absence of contingency cues (Lewis &

118 Brooks-Gunn, 1979). Between 24 and 48 months the emergence of self-recognition from non-

119 contingent images becomes fully established, suggesting that the task is more difficult than self-

120   recognition in a mirror (Povinelli, Landau & Perilloux, 1996). In particular, 24-36 month-old

121   children had more difficulties to infer the presence of a sticker on their heads from watching

122   delayed video image of themselves than 36-48 month-old children. In a more recent study, Hirata

123   et al. (2017) used a similar variant of the 'mark-test' to test five subadult chimpanzees with

124   extensive mirror experience (3 of 5 recognised themselves in mirrors). Here, subjects were tested

125   with live video feedback, short-delayed video feedback (i.e., 1-4 seconds) and long-delayed

126   video footage of themselves (one week). Among the control conditions, the authors used video

127   footage of humans but not of conspecifics. The finding was that the three subjects capable of

128   mirror self-recognition removed stickers placed on their heads more effectively and exhibited

129   more self-directed behaviours than the other two individuals, when shown live and short-delayed

130   video feedback but not when shown long-delayed video footage or other control conditions. In

131   sum, self-recognition from delayed, non-contingent self-images may thus be the most stringent

132   test that an individual (human or non-human) possesses a visual mental representation of their

133   own appearance, and this appears to require prior experience with mirrors.

134

135   In this study, we investigated whether bonobos had a generalised understanding of their own

136   physical appearance and whether this was dependent of experience with mirrors. To address this,

137   we tested how subjects responded to different visual images of themselves and others, including

138   when contingency cues were absent, and how mirror exposure influenced their performance. We

139   hypothesised that mirror-naïve individuals did not have a full understanding of their own visual

140   appearance, but that prolonged mirror experience could provide subjects with crucial experience.

141   To address this, we tested mirror-naïve subjects with different visual representations of

142   themselves and others, including non-contingent video footage of themselves. Two years later,

143   following a 3-month period of *ad libitum* access to a mirror, we retested the same subjects again

144   with the two critical conditions, i.e., non-contingent representations of themselves and others.

145   We assessed subjects' interest in the different stimuli by comparing looking times, based on the

146   fact that both human and nonhuman primates spend more time looking at novel than familiar

147   faces and other stimuli (e.g., patterns: (Fantz, 1964; Gunderson & Sackett, 1984; Gunderson &

148   Swartz, 1985); objects: (Bachevalier, Brickson & Hagger, 1993; Pascalis & Bachevalier, 1998);

149   conspecific faces: (Pascalis & Bachevalier, 1998; Gothard, Erickson & Amaral, 2004; Gothard,

150   Brooks & Peterson, 2009; but see Winters, Dubuc & Higham, 2015 for criticism). We predicted

151   that stimuli perceived as unfamiliar should cause longer looking times than stimuli perceived as

152   familiar (Pascalis & de Schonen, 1994).

153   **Methods**

154   **Study site & subjects**

155   The study was carried out at La Vallée des Singes Primate Park in Romagne (France) with a

156   group of bonobos (2014: N=17; 2016: N=20; table 1) housed in an indoor enclosure (400m^2)

157   with access to two outdoor wooded islands (11,500m^2). Experiments were carried out from

158   January to July 2014 and from February to July 2016. Eight subjects (table 1) participated in all

159   trials, which involved a 'looking-time' bias task with sequential stimulus presentation, a

160   paradigm originally developed in the late 1950s for research with pre-verbal human infants (e.g.,

161   Fantz, 1963; Winters, Dubuc & Higham, 2015).

162

163   Prior to testing, individuals were exposed to the equipment during one week to minimise any

164   potential effects of novelty. Videos stimuli were then presented by means of an APPLE iPad

165 (screen size approx. 15 x 20 cm) placed behind a transparent Acrylic panel (Fig. 1a) to which a

166 PANASONIC HC-V100 full HD camera was mounted to record the subjects' reactions face-on.

167 The mirror stimulus was presented by means of a one-way mirror (25 x 30 cm), attached behind

168 the same panel (Fig. 1b and c).

169

170 **Part 1 - Before mirror exposure**

171 The first part of the experiment was carried out in 2014 with N=8 subjects (4 males, 4 females,

172 age range 9–34 years), none of whom had any known experience with mirrors. The experiment

173 comprised five experimental conditions presented to all subjects in the following order: (1)

174 contingent video footage of self (live feedback of self, visible on an iPad: *C self*); (2) contingent

175 mirror image of self (live depiction of self, visible in a one-way mirror: *mirror*); (3) non-

176 contingent video footage of self (previously recorded video footage of self, visible on an iPad:

177 *NC self*); (4) non-contingent video footage of known group member (previously recorded video

178 footage of other group member visible on an iPad: *known*); (5) non-contingent video footage of

179 unknown conspecific (previously recorded video footage of unfamiliar conspecific visible on an

180 iPad: *unknown*) (see ESM 1 and 2).

181

182 Footage for *'NC self'* and *'known'* were recorded during the *'mirror'* and *'C self'* conditions.

183 Footage for *'unknown'* (N=2 males; N=1 female) were recorded at the 'Lola ya Bonobo'

184 Sanctuary in the Democratic Republic of the Congo (see ESM 3 and 4 for sample footage). In

185 both the *'known'* and *'unknown'* conditions, the footage showed generally inactive individuals

186 also glancing at the camera from time to time. Footage for stimulus presentation was selected at

187 random, resulting in N=6 same-sex pairs and N=2 opposite-sex pairs for the *'known'* condition

188 and N=4 same-sex and N=4 opposite-sex pairs for the *'unknown'* condition. An alternative

189 design would have been to control for sex (i.e., to compare same-sex and different-sex footage)

190 or to simply use same-sex footage. As this would have created sample size issues we opted for

191 randomly assigning footage of *'known'* and *'unknown'* individuals to our eight subjects.

192

193 Each subject was presented with each of the five conditions once and in the same sequential

194 order over an eight-month period (see Table S2). Stimuli were presented only very briefly, for a

195 total of 30s, starting with the first glance from the subject towards the stimulus. A trial was

196 terminated after 30s or as soon as a subject left. We are aware of the fact that fixed order

197 stimulus presentation designs carry the disadvantage of potentially creating cross-condition

198 dependencies. A completely randomised design might have been preferable but not practical due

199 to the low number of subjects available for testing. In particular, we regarded it as essential that

200 all subjects entered part 2 of the experiment with the exact same stimulus history. We also

201 considered it unlikely that dependencies across conditions played a role because stimulus

202 exposure was very short (30s) and intervals between subsequent presentations were long (median

203 = 38.5 days, range: 0-95 days).

204

205 Trials were carried out only when a subject was alone and inactive (i.e., resting or observing) in

206 one of the indoor cages and at a suitable orientation and distance from the corridor (0.3-2.0 m).

207 The subject was exposed to one of two portable devices, an iPad or a one-way mirror, each with

208 a camera mounted to record looking responses (Fig. 1).

209

210 We measured looking-time during stimulus presentation. Looking time as a proxy for familiarity

211 is not uncontroversial (e.g. Winters, Dubuc & Higham 2015) but appears to be a reliable variable

212 in face recognition tasks in which primates generally look longer to unfamiliar than familiar

213 (conspecific) faces (Pascalis & de Schonen, 1994; Pascalis & Bachevalier, 1998; Gothard,

214 Erickson & Amaral, 2004; Gothard, Brooks & Peterson, 2009; Fujita, 1987; Demaria & Thierry,

215 1988). Looking-time was coded post-hoc from the video recordings. Coding was blind insofar as

216 all videos were randomly labelled so that the rater (GS) was unable to infer the experimental

217 condition. Videos were analysed frame-by-frame with MPEG Streamclip 1.9.2. Looking time

218 was determined by measuring the duration between the first glance towards the stimulus and the

219 beginning of gaze aversion. If multiple gazes occurred over the 30s stimulus presentation, we

220 added them up. All clips were coded independently and blindly by a second rater (EG), which

221 did not reveal any reliability issues (Pearson's correlation coefficient, $r = 0.93$, N=56).

222

223 Eight of 17 adult group members were tested and analysed in this study (see Table 1). Regarding

224 the remaining individuals (N=9): One adult male (BO) participated in all experimental conditions

225 but had to be excluded due to poor video quality that prevented accurate coding. Two further

226 individuals (NK and LUE) also had to be excluded because they were too close to the camera,

227 which prevented reliable coding of looking time. One adult female (LY) had to be excluded

228 because she only participated in two conditions. Finally, we were unable to test the remaining

229 two adult females (DNL and UK) due to their lack of interest and participation. The dependent

230 infants and juveniles (LO, MO and KLS) were not tested.

231

232 **Part 2 - After mirror exposure**

233 Fifteen months after the first part of the experiment, subjects were provided with prolonged

234 access to a large mirror (45 x 115 cm) to gain extended experience with mirror reflections of

235 themselves. The mirror was placed in front of a resting platform in the indoor enclosure allowing

236 extensive *ad libitum* access to all individuals over a period of three months (i.e., from Nov 2015

237 to Feb 2016; approx. 2,000 hours). At this time of year, the group was kept inside due to cold

238 weather conditions and the park was closed to the public. Although we did not quantify the

239 amount of time and manner by which subjects interacted with the mirror, all subjects had

240 countless opportunities to familiarise themselves with their own mirror reflections. Anecdotal

241 reports from the keepers suggested that subjects did not spend noticeable amounts of time in

242 front of the mirror to inspect themselves but, in hindsight, it would have been interesting to

243 collect systematic data on how subjects behaved in front of the mirror, both quantitatively and

244 qualitatively.

245

246 We were mainly interested in the effect of mirror experience on subjects' perception of their own

247 and others' non-contingent images. To this end, we retested all individuals that had participated

248 in part 1 (N=8) with the two critical conditions from part 1, i.e., non-contingent video footage of

249 themselves and of unknown conspecifics. Stimulus presentation began 10 - 20 days after removal

250 of the mirror. All aspects of presentation were identical to part 1, including the video footage.

251 The time lapse between the first and second stimulus presentation for a given subject and

252 condition was held constant for each subject and averaged at approximately 22 months (see

253 Table S2).

254

255 **Statistical analyses**

256 In a first analysis, prior to the 3-month mirror exposure, we modelled looking time as the

257 response variable, experimental condition as the main predictor variable and subject ID as the

258 random intercept in a linear mixed model (LMM). We added age as a control predictor to

259 account for the possibility that younger individuals might show more interest than older

260 individuals (Westergaard & Hyatt, 1994; Walraven, Van Elsacker & Verheyen, 1995). Looking

261 time and age were square root transformed to achieve homogenous and approximately normally

262 distributed residuals. We tested this full model against an informed null model (Forstmeier &

263 Schielzeth, 2011), which only included age as predictor and subject ID as random intercept. We

264 tested the difference between the full and null model with a likelihood ratio test (LRT, Dobson,

265 2002). Note that this comparison is equivalent to testing of 'experimental condition' (models

266 with vs. without experimental condition as variable). Post hoc diagnostics were implemented in

267 order to test the stability of the model. This entailed running the full model eight times, each time

268 removing data of one of the eight individuals and permitted us to verify whether one of the

269 individuals was influential with respect to the interpretation of our model results. Results of this

270 procedure indicated stable model results, that is, exclusion of any one individual did not change

271 the conclusions of our analysis.

272

273 In a second analysis, we tested how looking time was affected by the interaction between

274 stimulus type (self vs. unknown, i.e., self Y/N) and mirror exposure (non-exposed vs. exposed,

275 i.e., exposed Y/N), again with a Linear Mixed Model. Once again, we controlled for age, which

276 was included in the respective null model, and implemented post-hoc diagnostics to test the

277 stability of the model, which returned stable model results.

278

279   Statistical analyses were carried out with R v. 3.1.2 and lme4 v. 1.1-11 (R Core Team, 2014;

280   Bates et al., 2015). Data are available in the electronic supplementary material (ESM 5).

281   **Compliance with ethical standards**

282   All applicable international, national and institutional guidelines for the care and use of animals

283   were followed. The study was authorised and given ethical approval by the "La Vallée des

284   Singes" scientific coordinator and zoological director. Trials were carried out opportunistically

285   when and where subjects felt so inclined. The study was in line with the ARRIVE guidelines and

286   recommendations from the EAZA and the AFdPZ code of ethics.

287   **Results**

288   The first part of the experiment consisted of exposing subjects to different motion images of

289   themselves, of other group members and of unfamiliar conspecifics (see Table S2). The results of

290   the model indicated that looking time was affected by experimental condition (LRT, $\chi^2 = 25.87$,

291   d.f. = 4, P<0.001; Fig. 2; Table 2), with short looking times in the '*C self*' and '*mirror*'

292   conditions (<5.0 of 30s) and three-fold longer looking times in the '*NC self*' and '*unknown*'

293   conditions, whereas looking times to '*known*' individuals were intermediate (Fig. 2: model

294   estimates, Table 3: descriptive data). In sum, subjects showed most interest in images of

295   strangers and non-contingent images of themselves and least interest in contingent images of

296   themselves (video clips and mirror reflections), suggesting that non-contingent self-images were

297   perceived in the same way as unknown individuals.

298

299   We then provided subjects with three months of *ad libitum* mirror access. Following this

300   manipulation and almost two years after the previous trials, subjects were retested with non-

301   contingent footage of themselves (*NC self*) and strangers (*unknown*), the two conditions that

302   elicited most interest before (Fig. 2).

303

304   When comparing interest across the two time periods, the full model was significantly different

305   from the null model (LRT, χ^2=18.06, d.f.=3, P<0.001; Fig. 3, Table 4), indicating that looking

306   time differed as a function of mirror-exposure, stimulus identity, and their interaction. The

307   interaction effect was close to significance (LRT, χ^2=3.61, df=1, P=0.057), indicating that

308   interest, as measured by looking time, was substantially lower in the '*NC self*' condition after the

309   three-month mirror-exposure than before, which was not the case for the '*unknown*' condition

310   (see fig 3 for model prediction means and SDs). These results suggest that prolonged mirror

311   exposure decreased subject interest in their non-contingent self-images, while interest in stranger

312   individuals remained similar.

313   **Discussion**

314   In this study, we were interested in how prolonged mirror-exposure influenced the response to

315   visual representations of the self. The underlying rationale was that, during human development,

316   recognition of non-contingent footage of the self is cognitively most challenging, suggesting that

317   bonobos may struggle more with such stimuli, compared to contingent depictions of themselves.

318   To address this, we carried out a two-part experiment during which subjects watched motion

319   images depicting either themselves or another individual.

320

321   In the first part, subject responses to three types of self-images (mirror reflection, contingent

322   video footage and non-contingent video footage) were compared with responses to video footage

323   of familiar and unfamiliar conspecifics. Results revealed low interest in the mirror and in

324   contingent self-footage, but high interest in the non-contingent self-footage condition, similar to

325   interest in unfamiliar individuals.

326

327   A first parsimonious explanation of this result might be that bonobos did not recognise

328   themselves in any of the three conditions (mirror, contingent, non-contingent), but that non-

329   contingent movement was simply more interesting than contingent movement. However, this

330   interpretation is at odds with the fact that the '*known*' condition caused less interest than '*non-*

331   *contingent self*' and '*unknown*' conditions, all of which moved in asynchronous ways, so we

332   consider this explanation as unlikely.

333

334   A second explanation for the high interest in the '*non-contingent self*' condition might be that

335   subjects did not recognise themselves and responded as if it were an unfamiliar individuals (fig

336   2) whereas they did recognise themselves in the contingent footage and mirror images. But if

337   they recognised themselves, why did they not engage in the usual tell-tale behaviours of self-

338   recognition, such as exploration of visually inaccessible body parts and contingency testing?

339   One explanation for this curious absence is that stimulus exposure was too short (30s),

340   effectively preventing subjects from engaging in self-exploration. However, it must be stated that

341   during the subsequent prolonged mirror exposure, neither the keepers nor the researchers ever

342   noted self-exploration by subjects. The fact that subjects showed little interest in the contingent

343   stimuli suggests that they were already familiar with their own reflections (from windows, water

344   surfaces or their own shadows), but that this was not be enough to develop a full sense of how

345   one looks.

346

347   In the second part of the experiment, we provided subjects with extended experience of self-

348   reflections by giving them uninterrupted access to a mirror for three consecutive months. We

349   predicted that this experience should enable subjects to familiarise themselves with a wider range

350   of visual depictions of themselves, which would allow them to generalise and form a mental

351   representation of their own visual appearance. When retesting subjects with the two critical

352   stimuli (non-contingent footage of self and unknown individuals), 10-20 days after the mirror

353   was removed, we found that interest in the non-contingent footage significantly decreased, while

354   interest in strangers remained similar (fig. 3), in line with our predictions. In hindsight, an

355   interesting point of comparison would have been to also rerun the '*known*' condition, as a further

356   control. Based on the fact that the subjects had extensive opportunities to observe each other

357   daily, we would not have predicted any change in interest in this condition after the mirror-

358   exposure.

359

360   Could results be explained by low-level stimulus habituation to differences in background? We

361   find this an unlikely scenario since stimulus presentations were exceedingly short (30s) and

362   presented only twice over a period of 22 months, rendering perceptual habituation an implausible

363   scenario. Moreover, responses to non-contingent self and known individuals were different,

364   despite similar backgrounds, while responses to non-contingent self and strangers were similar,

365   despite different backgrounds. Also, it may have been difficult for subjects to pay attention to the

366 backgrounds given the short presentation periods. Explanations based on background, in other

367 words, requires complex and non-parsimonious argumentations that we find uncompelling.

368

369 At the very least, therefore, subjects must have managed to familiarise themselves with all

370 aspects of their visual appearance, allowing them to categorise the '*non-contingent self*' footage

371 as more familiar compared to the stranger footage. But whether or not subjects really proceeded

372 to form a true mental concept of their own visual appearance ("that's me"), as opposed to some

373 lower level sense of familiarity, will have to be addressed by future research.

374 **Conclusion**

375 Our data suggest that, given sufficient mirror exposure, bonobos acquire the ability to use mirror-

376 reflections of themselves to learn about their own physical appearance. In contrast to other

377 research our results suggest that this level of awareness is detached from the here and now and

378 can include visual non-contingent representations of the self. Whether or not these findings

379 qualify as evidence of self-recognition cannot be decided with our data, due the alternative

380 interpretations outlined before. Much remains to be elucidated regarding the mechanisms and the

381 implications of great apes' capacity of self-recognition, such as the amount of mirror exposure

382 minimally necessary or the stability of the resulting self-recognition over time (see Calhoun &

383 Thompson (1988) de Veer et al. (2003).

384

385 A philosophically and theoretically interesting problem concerns the implications of self-

386 recognition data for questions about self-awareness and awareness of others. As mentioned,

387 mirror self-recognition has also been demonstrated in non-primate species, particularly dolphins

388 and elephants, which has led to interesting claims, such as them having "…complex social

389 understanding and empathic behaviour" (Prior, Schwarz & Güntürkün, 2008, p.1642) and

390 suggestions that complex cognition emerges through convergent evolution (Plotnik, de Waal &

391 Reiss, 2006; Mitchell, 2012). In this view, self-recognition is to be found in any organism

392 capable of complex cognition, together with empathy, social awareness and theory of mind (e.g.,

393 Gallup, 1991; Gergely, 1994; Suddendorf & Collier-Baker, 2009; Anderson & Gallup, 2015;

394 Dale & Plotnik, 2017) rather than a specifically evolved cognitive specialisation.

395

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402

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582

Figure 1

Portable acrylic panel for stimulus presentation.

(A) Video camera and iPad displaying a non-contingent video stimulus. (B) Video camera and one-way mirror (front). (C) Video camera and one-way mirror (back). Photos by G.Shorland.

Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.

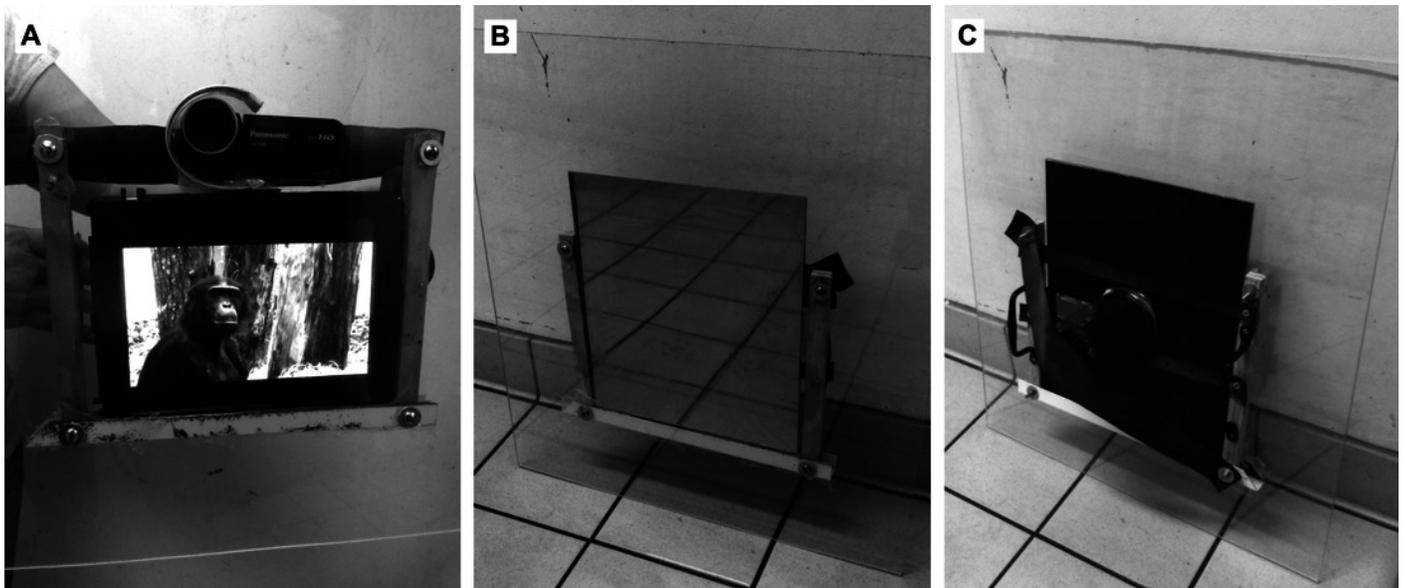



Figure 2

Subject looking time and model predictions for the five test conditions.

Subject looking time (circles) and model prediction (squares) for the five test conditions with 95% confidence interval; note that looking time was square root transformed for modeling but for presentation we back-transformed it along the y axis. Conditions are presented chronologically from left to right.

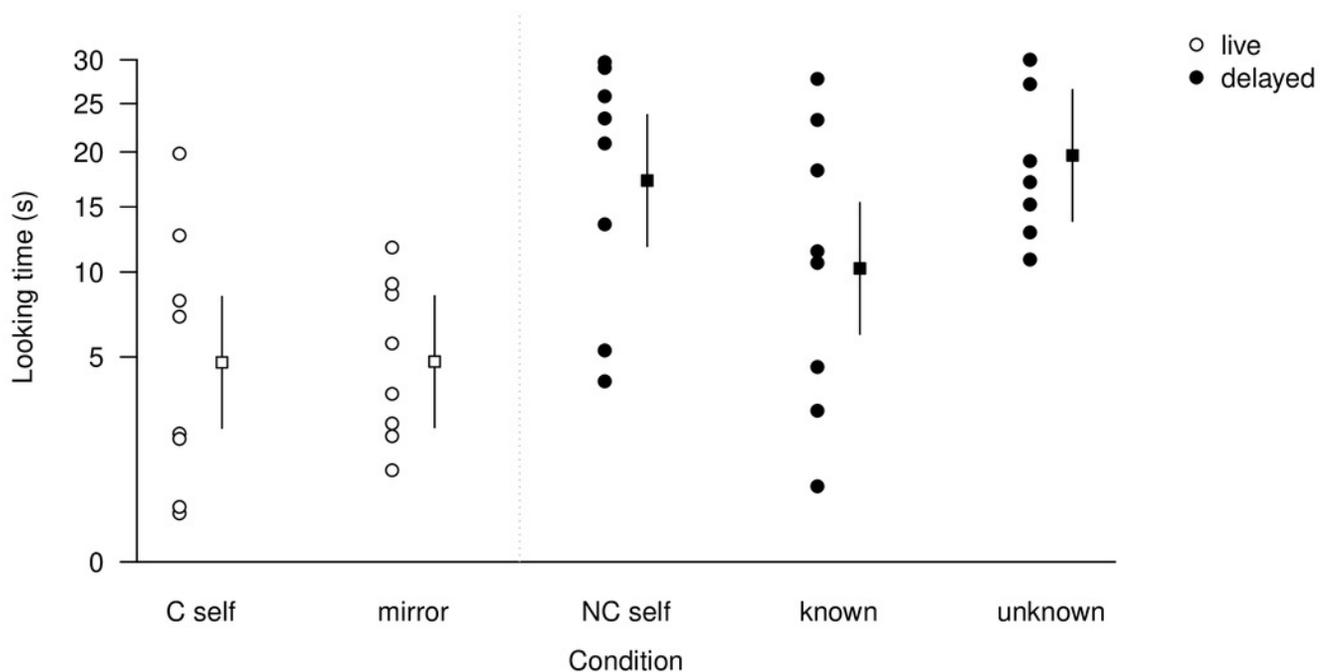
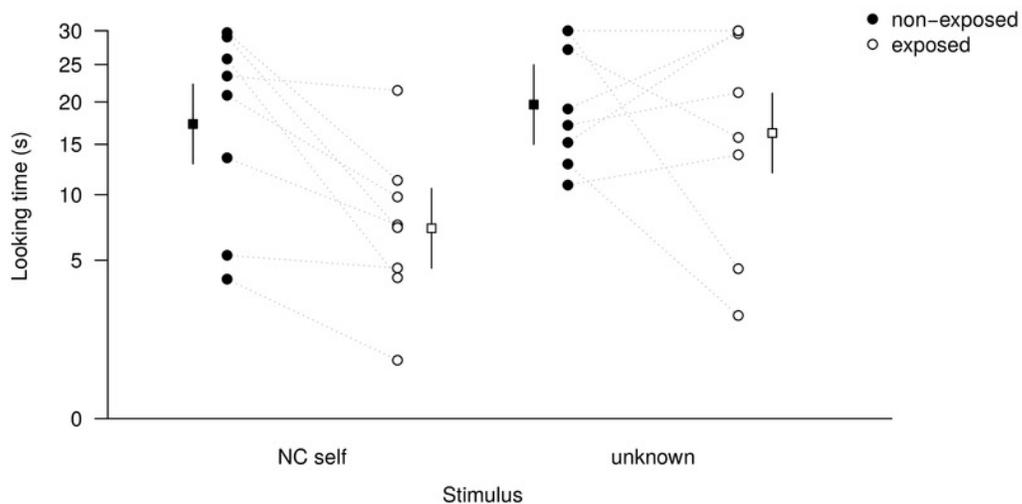



Figure 3

Subject looking time and model predictions before and after mirror exposure.

Subject looking time and model prediction before and after mirror exposure. Looking time (circles) before and after three-months *ad libitum* mirror exposure. Model predictions (squares) are given with 95% confidence intervals; note that looking time was square root transformed for modelling but for presentation we back-transformed it along the y axis.

Study subjects housed at La Vallée des Singes primate park, France.

Individuals having participated in all trials are indicated in bold (N=8). Individuals marked by an asterisk initially participated but were excluded for reasons detailed below. Age-class as defined by Kano (1984) at beginning of study.

1   **Table 1.** Study subjects housed at La Vallée des Singes primate park, France

Individual		Code	Sex	Age-Class	Year of birth
Daniela		DNL	F	Adult	1968
Lisala		**LSL**	**F**	**Adult**	**1980**
Ukela		UK	F	Adult	1985
Bondo	*	BO	M	Adult	1991
Kirembo		**KI**	**M**	**Adult**	**1992**
Ulindi		**UL**	**F**	**Adult**	**1993**
Diwani		**DW**	**M**	**Adult**	**1996**
David		**DV**	**M**	**Adult**	**2001**
Khaya		**KH**	**F**	**Adult**	**2001**
Lingala		**LNG**	**F**	**Sub-adult**	**2003**
Lucy	*	LY	F	Sub-adult	2003
Kelele		**KEL**	**M**	**Sub-adult**	**2004**
Luebo	*	LUE	M	Sub-adult	2006
Nakala	*	NK	F	Juvenile	2007
Loto		LO	M	Juvenile	2009
Moko		MO	M	Infant	2012
Khalessi		KLS	F	Infant	2012

2   Individuals having participated in all trials are indicated in bold (N=8). Individuals
3   marked by an asterisk initially participated but were excluded for reasons detailed
4   below. Age-class as defined by Kano (1984) at beginning of study.

Table 2 **(on next page)**

Result of the LMM testing the effect of condition on looking time.

1   **Table 2.** Result of the LMM testing the effect of condition on looking time

	Estimate	Standard error	*t*
Intercept	3.18	0.44	7.18
Condition (*C self*)			
- Mirror	0.01	0.49	0.02
- NC Self	1.98	0.49	4.03
- Known	1.03	0.49	2.08
- Unknown	2.26	0.49	4.58
Age	-0.12	0.03	-3.75

Descriptive results: experimental condition, mirror exposure, median looking-time and quartiles calculated from raw data.

1 **Table 3.** Descriptive results: experimental condition, mirror exposure, median looking-time and quartiles
2 calculated from raw data.

Condition	Mirror exposure	Median looking time	Quartiles
C self	non-exposed	4.6	1.4 - 9.3
mirror	non-exposed	4.5	2.2 - 8.7
NC self	non-exposed	22.1	11.5 - 26.6
known	non-exposed	11.1	4.1 - 19.5
unknown	non-exposed	18.1	14.6 - 27.9
NC self	exposed	7.4	4.4 - 10.2
Unknown	exposed	18.5	11.5 - 29.7

Result of the LMM, testing the effects of stimulus identity (self vs. unknown) and mirror-exposure (non-exposed vs. exposed) on looking time.

1 **Table 4.** Result of the LMM, testing the effects of stimulus identity (self vs. unknown) and mirror-
2 exposure (non-exposed vs. exposed) on looking time.

	Estimate	Standard error	t
Intercept	5.85	0.35	16.63
Mirror-exposure (non-exposed) - exposed	-0.40	0.39	-1.04
Stimulus identity (non-self) - self	-0.27	0.39	-0.71
Mirror exposure : Stimulus identity	-1.07	0.55	-1.96
Age	-0.17	0.03	-6.41