# Mirror experience modifies bonobos' perception of themselves

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## Abstract

12    The question of whether animals have some sort of self-awareness is a topic of great interest and

13    subject of continued debate. A necessary precondition for self-awareness is the ability to visually

14    discriminate the self from others, which has traditionally been investigating through mirror self-

15    recognition. Although great apes generally pass mirror self recognition tasks, the interpretation

16    of these results has remained controversial. The aim of this study was to investigate how

17    bonobos (*Pan paniscus*) respond to different types of images of themselves and others. In the

18    first part of the experiment, we presented mirror-naive subjects with three representations of

19    themselves (contingent mirror image, contingent video footage, non-contingent video footage)

20    and two representations of others (video footage of known and unknown conspecifics). We

21    compared responses using a 'looking-time' paradigm, based on the finding that primates

22    generally prefer to look at novel social stimuli. We found that subjects paid little attention to

23    contingent images of themselves and while interest in footage of known individuals was a little

24    higher, subjects were most interested in non-contingent images of themselves and of unfamiliar

25    individuals. In the second part of the experiment, we provided subjects with three months of *ad*

26    *libitum* mirror access, after which subjects were retested with the same non-contingent video

27    footage of themselves and of unknown conspecifics. We found that extensive experience with

28    their own mirror-image significantly reduced interest in the non-contingent footage of self, but

29    not in the footage of unknown individuals. We concluded that, when provided with extended

30    mirror experience, bonobos may form stable visual mental representations of themselves, which

31    enable them to recognise themselves in non-contingent video footage. We discuss the

32    implications of these findings in relation to the on-going debate on self-recognition in animals.

## Introduction

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

36 animals have something akin to human self-awareness, that is, whether they can recognise

37 themselves as separate from others and the environment and whether they have some

38 understanding of their own mental states. It is generally accepted that any form of self-awareness

39 arguably presupposes self-recognition, which is empirically easier to address. Since the 1970s

40 mirrors have been used as the main method of testing self-recognition, with two basic types of

41 data collected. These studies have relied either on both the spontaneous and sequential

42 appearance of social, exploratory, contingent and self-directed behaviours (Swartz, Sarauw &

43 Evans, 1999) and the self-directed behaviour in response to inconspicuous marking of a body

44 part, not visible without the aid of a mirror (the mirror-mark test; Gallup (1970)) or on one or the

45 other.

46

47 Gallup's (1970) research on chimpanzees and macaques was pioneering, and has been followed

48 by studies on a range of other primate species, including humans (Amsterdam, 1972),

49 chimpanzees (Gallup, 1970; Lethmate & Dücker, 1973; Suárez & Gallup, 1981; Calhoun &

50 Thompson, 1988; Swartz & Evans, 1991; Lin, Bard & Anderson, 1992; Povinelli et al., 1993),

51 bonobos (Hyatt & Hopkins, 1994; Westergaard & Hyatt, 1994; Walraven, Van Elsacker &

52 Verheyen, 1995), gorillas (Suárez & Gallup, 1981; Ledbetter & Basen, 1982; Posada & Colell,

53 2007), orang-utans (Lethmate & Dücker, 1973; Suárez & Gallup, 1981), lesser apes (Lethmate &

54 Dücker, 1973; Inoue-Nakamura, 1997; Suddendorf & Collier-Baker, 2009), monkeys (Lethmate

55 & Dücker, 1973; Inoue-Nakamura, 1997), and prosimians (Inoue-Nakamura, 1997) (see

56 Anderson, 1984 for review in primates).

57

58 Within the non-human primates, all great apes appear to be capable of mirror self-recognition

59 (see Swartz, Sarauw & Evans, 1999 for review). In bonobos, for example, there is evidence of

60 spontaneous self-recognition in mirrors (Hyatt & Hopkins, 1994; Westergaard & Hyatt, 1994;

61 Walraven, Van Elsacker & Verheyen, 1995), due to mirror-guided self-directed behaviour (e.g.

62 picking the teeth or eyes), in some instances from first exposure (Walraven, Van Elsacker &

63 Verheyen, 1995), although we are not aware of any reports of studies using the 'mirror-mark'

64 test on bonobos. In contrast, lesser apes (*Hylobates lar, H moloch, H agilis, Nomascus*

65 *leucogenys* and *Symphalangus syndactylus*) and monkeys (*Macaca silenus, Mandrillus sphinx,*

66 *Papio hamadryas, Ateles sp, Cebus apella*) have consistently failed the 'mirror-mark' test

67 (Lethmate & Dücker, 1973; Suddendorf & Collier-Baker, 2009). This conclusion is further

68 corroborated by the absence of spontaneous self-directed behaviours in non-ape primates

69 (*Hylobytes lar*; *Macaca spp., Cebus apella, Saimiri sciureu*s, *Saguinus oedipus*, *Lemur catta*;

70 (Inoue-Nakamura, 1997; but see Heschl & Fuchsbichler for tentative evidence of mirror self-

71 recognition in a lesser ape).

72

73 Mirror experiments have also been conducted with non-primate species bringing to light

74 somewhat controversial evidence (see Gallup & Anderson, 2018 for a critical view) in bottlenose

75 dolphins (Marten & Psarakos, 1994; Reiss & Marino, 2001), Asian elephants (Plotnik, De Waal

76 & Reiss, 2006), and even manta rays, the biggest brained of all fish (Ari & D'Agostino, 2016),

77 suggesting that mirror self-recognition may have more to do with large brains in general,

78 regardless of phylogenetic relatedness. Meanwhile, small-brained species typically fail mirror

79 self-recognition tasks (e.g. great tits, (Kraft et al., 2017); cichlid fish (Hotta, Komiyama &

80   Kohda, 2018), although, there is positive evidence from Eurasian magpies (Prior, Schwarz &

81   Güntürkün, 2008; but see Anderson & Gallup, 2015 for a critical view of these results) and

82   Clark's nutcrackers (Clary & Kelly, 2016). However, the giant panda's failure of mirror self-

83   recognition (Ma et al., 2015) seems to suggest that large brains alone might not be enough

84   suggesting that mirror self-recognition might further be linked to social variables (Gallup, 1998;

85   Prior, Schwarz & Güntürkün, 2008).

86

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

88   appropriate experience. In western human cultures, the capacity to carry out self directed

89   behaviours in front of a mirror usually appears from 15-18 months of age and is fully expressed

90   by 24 months (e.g. Amsterdam, 1972; Lewis & Brooks-Gunn, 1979; but see Keller et al., 2004,

91   2005; Kärtner et al., 2012 for evidence of delayed mirror self-recognition emergence in other

92   cultures). In chimpanzees, early reactions to mirrors are similar in kind and latency to those

93   observed in human children, but the behaviour does not emerge before 24 months (Lin, Bard &

94   Anderson, 1992) and is robustly present only from around 5 years (Swartz, Sarauw & Evans,

95   1999) with some individuals never developing the capacity (e.g. Swartz & Evans, 1991;

96   Povinelli et al., 1993; Walraven, Van Elsacker & Verheyen, 1995). Behaviours typically

97   observed by mirror-naïve animals are, first, social behaviours directed at the mirror (e.g.

98   threatening, vocalising etc. (Gallup, 1970)), followed by exploratory behaviours (e.g. reaching or

99   looking behind the mirror), exploration of the contingency between the mirror-image and the

100  subject's body, and, finally, exploration of body parts that are usually visually inaccessible, such

101  as the teeth, eyes or genital regions (Swartz, Sarauw & Evans, 1999).

102

103    There is much controversy around how evidence of mirror self-recognition should be interpreted.

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

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

106    Waal & Reiss, 2006) or even for a self-concept, defined by Gallup (1998, p. 240) as "…a sense

107    of continuity, a sense of personal agency and a sense of identity". At the other end, reactions

108    towards administered marks have been interpreted as mere artefacts of experimental

109    manipulations (Heyes, 1994, 1995, 1996). More intermediate position state that such behaviour

110    qualifies as evidence for self-perception, that is, recognising one's own appearance (Nielsen,

111    Suddendorf & Slaughter, 2006) or a basic understanding of one's own body as a separate entity

112    from the surrounding world ('body concept'). The 'body-concept' hypothesis has been

113    investigated in developing children, with the conclusion that objective self-awareness emerges in

114    the second year of life, correlated with passing the mirror-mark test, which suggests that the two

115    capacities are linked (Moore et al., 2007). The notion of a 'body concept' is also key to an

116    alternative hypothesis to self-recognition, which is that subjects simply engage in some form of

117    kinaesthetic-visual matching as they identify the contingency between the kinaesthetic sense of

118    their body and its movements and the objective visual image as provided by the mirror (Mitchell,

119    1993, 1997).

120

121    Several studies on children have tested the effect of contingency cues on self-recognition by

122    presenting non-contingent cues, usually delayed videos or simply photographs. While some

123    claim that children are able to identify themselves by ages 18-24 months, regardless of

124    contingency cues (Lewis & Brooks-Gunn, 1979), others have shown not only a clear

125    developmental trend of self-recognition from non-contingent images between the ages of two

126    and four, but also a significant delay compared to the emergence of mirror self-recognition

127    (Povinelli, Landau & Perilloux, 1996). Of course, self-recognition from delayed, non-contingent

128    self-images presupposes that individuals, human or non-human, acquire sufficient mirror-

129    exposure to derive and develop a visual mental representation of their own appearance. As

130    previously mentioned, in non-human animals the fist response to their mirror-image is to treat it

131    as another conspecific (Swartz, Sarauw & Evans, 1999).

132

133    Given their phylogenetic closeness to both humans and chimpanzees and based on their capacity

134    for mirror self-recognition (Hyatt & Hopkins, 1994; Westergaard & Hyatt, 1994; Walraven, Van

135    Elsacker & Verheyen, 1995) (demonstrating their ability to form a self-image based on

136    kinaesthetic-visual matching) it is reasonable to suppose that, with extended mirror experience,

137    bonobos might be capable of developing full visual self-images, with an understanding of their

138    physical appearance. If this is the case, a visual mental representation may be formed from

139    exposure to one's mirror image and potentially stored in memory. The aim of this study was to

140    address how bonobos respond to different visual images of self and others and to investigate how

141    mirror exposure influenced perception of self-images when contingency cues are absent. We

142    exposed subjects to different visual representations of themselves and known and unknown

143    others and considered subjects' differing responses between conditions. We hypothesised that

144    bonobos may not have an a-priori ability to recognise themselves, particularly in the absence of

145    kinaesthetic-visual matching opportunities, but that they have the ability to develop a visual

146    mental representation of self, if given sufficient visual experience. To this end, we first exposed

147    subjects to different depictions of the self and others. Two years later, following a 3-month

148    period of *ad libitum* access to a mirror we exposed the same subjects again to key depictions of

149    the self and others. We hypothesized that prolonged mirror-exposure would provide subjects

150    with crucial perceptual experience regarding their own physical appearance, which subjects

151    might use to develop a visual mental representation of self, enabling them to recognise non-

152    contingent representations of themselves, without the help of kinaesthetic feedback.

153

154    We assessed interest in the different stimuli by comparing differences in looking times. This is

155    based on the more general finding that both human and nonhuman primates generally spend

156    more time looking at novel than familiar stimuli (e.g. patterns: (Fantz, 1964; Gunderson &

157    Sackett, 1984; Gunderson & Swartz, 1985); objects: (Bachevalier, Brickson & Hagger, 1993;

158    Pascalis & Bachevalier, 1998); conspecific faces: (Pascalis & Bachevalier, 1998; Gothard,

159    Erickson & Amaral, 2004; Gothard, Brooks & Peterson, 2009).)  As a general pattern, in tasks

160    relating to face recognition of conspecifics, all species tested show a visual bias for novelty

161    (Pascalis & de Schonen, 1994; Pascalis & Bachevalier, 1998; Gothard, Erickson & Amaral,

162    2004; Gothard, Brooks & Peterson, 2009; but see Winters, Dubuc & Higham, 2015 for an

163    overview of issues and controversy around the looking-time paradigm.), while a visual bias for

164    familiar stimuli has only been observed in studies comparing conspecific vs. (novel) hetero-

165    specific faces (Fujita, 1987; Demaria & Thierry, 1988). Familiar stimuli were also preferred in a

166    reaching paradigm for familiar vs. novel hidden objects (Shinskey & Munakata, 2005).

167    Furthermore, during visual processing and formation of mental representations in human infants

168    a bias for a familiar stimulus precedes an inevitable and consistent bias for a novel stimulus

169    (Roder, Bushnell & Sasseville, 2000).

170

171    We hypothesize that if bonobos show more interest (i.e., look longer) in novel than familiar

172    stimuli, similarly to other tested primates (Gunderson & Sackett, 1984; Bachevalier, Brickson &

173    Hagger, 1993; Pascalis & de Schonen, 1994), then any footage perceived as unfamiliar should

174    cause longer looking times than footage perceived as familiar. In particular, if subjects failed to

175    recognise visual representations of themselves, then these should cause longer looking time than,

176    for instance, footage of familiar group members.

177

## Methods

### Study site & subjects

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

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

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

183    January to July 2014 and February to July 2016.

184

185    Eight subjects (4 males; 4 females see Table 1) participated in all trials, which involved a visual

186    bias task with sequential stimulus presentation, a paradigm originally developed in the late 1950s

187    for research with pre-verbal human infants (e.g. Fantz, 1963; Winters, Dubuc & Higham, 2015).

188

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

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

191    placed behind a transparent Acrylic panel (Fig. 1a) to which a PANASONIC HC-V100 full HD

192    camera was fixed in order to record the subject's reaction face-on. The mirror stimulus was

193     presented by means of a one-way mirror (25 x 30 cm) attached behind the same panel (Fig. 1b

194     and c).

195

## Part 1 - Before mirror exposure

197     The first part of the experiment was carried out in 2014 with N=8 subjects who had no known

198     prior experience with mirrors. The experiment comprised five experimental conditions presented

199     to all subjects in the following order: (1) contingent video footage of self (live feedback of self

200     visible on iPad: *C self*); (2) contingent mirror image of self (live depiction of self visible on one-

201     way mirror: *mirror*); (3) non-contingent video footage of self (previously recorded video footage

202     of self visible on iPad: *NC self*); (4) footage of known group member (previously recorded video

203     footage of other group member visible on iPad: *known*); (5) footage of unknown conspecific

204     (previously recorded video footage of unfamiliar conspecific visible on iPad: *unknown*) (see

205     Tables S1 and S2). Footage for *'NC self'* and *'known'* were recorded during the *'mirror'* and *'C*

206     *self'* conditions. Footage for *'unknown'* (N=2 males; N=1 female) were recorded at the 'Lola ya

207     Bonobo' Sanctuary in the Democratic Republic of the Congo (see ESM 2 and 3 for sample

208     footage). In both the *'known'* and *'unknown'* conditions, the footage showed generally inactive

209     individuals glancing at the camera from time to time. Footage for stimulus presentation was

210     selected at random, resulting in N=6 same-sex pairs and N=2 opposite-sex pairs for the *'known'*

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

212

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

214     order over an eight-month period (see Table S2). All video stimuli were presented very briefly,

215    for total of 30 seconds, starting with the first glance from the subject towards the stimulus. A

216    trial was terminated after 30s or as soon as a subject upped and left.

217

218    We are aware of the fact that fixed order stimulus presentation designs carry the disadvantage of

219    potentially creating systematic cross-condition dependencies. Any eventual differences in

220    behavioural responses could therefore be explained in terms of behavioural

221    habituation/sensitisation to some unknown aspects of the experiment (e.g. iPad) rather than

222    stimulus properties per se. Despite this well-known disadvantage, we opted for fixed order

223    stimulus presentation because we were interested in eventual changes of attention due to

224    prolonged exposure to a mirror. It was therefore essential that all subjects entered the experiment

225    with the exact same stimulus history before and after mirror exposure. We consider it unlikely

226    that this design could explain differences across conditions, mainly because stimulus exposure

227    was very short (30s) and time lapse across presentations was generally very large (Mean = 43.3

228    days / Median = 38.5 days RANGE: 0-95).

229

230    Stimulus presentation was carried out whenever a subject was alone in one of the indoor cages

231    and at a suitable orientation and distance from the corridor (0.3-2.0 m). The subject was tested

232    only if inactive (resting and observing) and exposed to one of two portable devices, an iPad or a

233    one-way mirror, each with a camera mounted to record looking responses (fig. 1).

234

235    We measured looking time during stimulus presentation as a proxy for interest, coded post-hoc

236    from the video recordings. Coding was blind insofar as all videos were randomly labelled so that

237    the coder was unable to infer the experimental condition. Videos were analysed frame-by-frame

238    with MPEG Streamclip 1.9.2.

239

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

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

242    but had to be excluded due to poor video quality, which prevented accurate coding. One adult

243    female (LY) had to be excluded because she only participated in two conditions. Two individuals

244    (NK and LUE) had to be excluded because they were too close to the camera, which prevented

245    reliable coding of looking time. Finally, we were unable to test the remaining adult females

246    (DNL and UK). The dependant infants and juveniles (LO, MO and KLS) were not tested.

247

248    **Part 2 - After mirror exposure**

249    Fifteen months after the first part of the experiment was completed (i.e., from Nov 2015

250    onwards), subjects were provided with prolonged access to a mirror to gain extended experience

251    with mirror reflections of themselves. A mirror (45 x 115 cm) was placed in front of a resting

252    platform of the indoor enclosure allowing *ad libitum* access over a period of three months (i.e.,

253    from Nov 2015 to Feb 2016). At this time of year, the group was kept inside due to cold weather

254    conditions and the park was closed to the public.

255

256    In order to test the effect of mirror experience on the subjects' perception of their own non-

257    contingent image compared to footage of an unknown individual, all individuals that had

258    participated in part 1 (N=8) were retested with two identical stimuli from part 1, specifically,

259    non-contingent video footage of self (*NC self*) and video footage of unknown conspecifics

260    (*unknown*)*,* in order to draw a comparison between the results before and after mirror exposure.

261    Stimulus presentation began 10 - 20 days after removal of the mirror. All aspects of presentation

262    were identical to part 1. The time lapse between the first and second stimulus presentation for a

263    given subject and condition was held constant for each subject averaging at approximately 22

264    months (see Table S2).

265

266    **Statistical analyses**

267    In a first analysis, prior to the 3-month mirror exposure, we modelled looking time with a linear

268    mixed model (LMM), with looking time as the response variable and experimental condition as

269    the main predictor variable. We included subject ID as random intercept. We added age as

270    control predictor to account for the possibility that younger individuals might show more

271    interested than older individuals (Westergaard & Hyatt, 1994; Walraven, Van Elsacker &

272    Verheyen, 1995). Looking time and age were square root transformed to achieve homogenous

273    and approximately normally distributed residuals. We tested this full model against an informed

274    null model (which included only age as predictor and subject ID as random intercept) with a

275    likelihood ratio test (LRT, Dobson, 2002). Note that this comparison is equivalent to more

276    traditional p-value significance testing of 'experimental condition' (models with vs. without

277    experimental condition).

278

279    Post hoc diagnostics were implemented in order to test the stability of the model. This entailed

280    running the full model eight times, each time removing data of one of the eight individuals. This

281    permitted us to verify whether one of the individuals was influential with respect to the

282    interpretation of our model results. Results of this procedure indicated stable model results, such

283    that exclusion of any one individual did not change the conclusions of our analysis.

284

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

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

287    exposed, i.e., exposed Y/N) using a LMM. Once again, we controlled for age, which was

288    included in the respective null model, and we implemented post-hoc diagnostics, testing the

289    stability of the model. Again, diagnostics results indicated stable model results.

290

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

292    Bates et al., 2015). The data that support the findings of this study are available in the electronic

293    supplementary material (ESM 4).

294

295    **Compliance with ethical standards**

296    Ethical approval: All applicable international, national, and/or institutional guidelines for the

297    care and use of animals were followed. This experimental study was authorised and given ethical

298    approval by the "La Vallée des Singes" scientific coordinator and zoological director. Trials

299    were carried out opportunistically when and where subjects felt so inclined. The study was inline

300    with the ARRIVE guidelines and recommendations from the EAZA and the AFdPZ code of

301    ethics.

302

## Results

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

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

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

307 d.f. = 4, P<0.001; Fig. 2; Table 2).

308

309 The median looking time in both *C self* and *mirror* conditions was relatively low, standing just

310 under five seconds (4.6s and 4.5s, respectively, medians calculated from raw data), whereas for

311 the *NC self* and *unknown* conditions median looking time was approximately four to five times

312 higher (22.1s and 18.1s, respectively). Median looking time for the *known* condition, however,

313 lay in between (11.1s).

314

315 If we take looking time as an indicator of interest, these results indicate that subjects seemed to

316 show relatively little interest in the contingent images of themselves (both on the iPad and the

317 mirror) but showed more interest in non-contingent images of themselves and of unfamiliar

318 individuals. If we agree that individuals show more interest (as measured by looking time) in

319 novelty, then these results indicate that subjects did not treat the contingent images of themselves

320 (*C self* and *mirror*) as novel but more we would have predicted for familiar images. Subjects did,

321 however, show a lot of interest in the non-contingent images of themselves and the images

322 unfamiliar individuals. A possible explanation for this discrepancy might be quite simple. When

323 presented with the stimuli, exposure was very short (30s) and subjects did not move or interact

324 with the images but generally just looked at them, as a result the contingent images of

325 themselves (live representations) did not move either in comparison to the non-contingent

326   images of themselves, other known and unknown individuals.  They might thus have been

327   simply more interested in images of moving individuals than the relatively 'still' images.

328

329   In a second part, we therefore provided subjects with three months of *ad libitum* mirror access to

330   test whether prolonged mirror experience with the opportunity to interact freely with their

331   mirror-image would influence the way they perceived the delayed video footage of themselves.

332   Following this treatment and almost two years after the previous trials, subjects were retested

333   with non-contingent footage of themselves (*NC self*) and of an unknown conspecific (*unknown*).

334   The full model was significantly different from the null model (LRT, $\chi^2$=18.06, d.f.=3, P<0.001;

335   Fig. 3, Table 3), indicating that looking time differed as a function of mirror-exposure, stimulus

336   identity, and their interaction. The interaction effect was close to significance (LRT, $\chi^2$=3.61,

337   df=1, P=0.057), indicating that interest as measured by looking time was substantially lower in

338   the *NC self* condition after the three-month mirror-exposure than before (median 22.1s vs. 7.4s),

339   which was not the case for the *unknown* condition (18.2s vs. 18.5s).

340

341   These results indicate that the prolonged mirror exposure modified subject interest in their non-

342   contingent self-images but not their interest in the images of unfamiliar individuals. Indeed, our

343   subjects were still very interested in the images of unfamiliar individuals but their interest in

344   their own delayed images decreased significantly. We are confident that the decrease of interest

345   for the *NC self* cannot simply be explained in terms of habituation to the stimuli given the fact

346   that the stimulus was presented once for 30s, 22 months prior to the second 30s presentation.

347   Furthermore, if that was the case then we should observe a similar pattern for the unknown

348   individual image. In conclusion, the exposure to the mirror seems to have allowed our subject to

349    learn something about their own physical appearance that in consequence led them to treat the

350    delayed image of themselves as less novel than images of unfamiliar individuals.

351    **Discussion**

352    In this study we were interested in how mirror-naive bonobos responded to different contingent

353    live and non-contingent delayed images of themselves, as well as of known and unknown

354    individuals, and how prolonged mirror-exposure influenced the response to non-contingent video

355    footage of self. To address this, we carried out a two-part experiment during which subjects

356    watched motion images of bonobos, depicting either themselves or another individual. In the first

357    part of the experiment, subject response to three types of motion self-images (mirror reflection,

358    contingent video feedback and non-contingent video footage) was compared with response to

359    video footage of familiar and unfamiliar conspecifics. Results revealed low interest (as assessed

360    by looking time) in the mirror condition and in contingent footage of the self. In contrast, interest

361    was high in both non-contingent footage of self and footage of unfamiliar individuals while

362    interest for footage if known individuals lay in between.

363

364    We draw the following tentative conclusions from these patterns. First, given that to the best of

365    our knowledge the subjects were mirror-naïve and that human and nonhuman primates generally

366    show more interest in novel than familiar stimuli, including faces (Pascalis & de Schonen, 1994;

367    Pascalis & Bachevalier, 1998; Gothard, Erickson & Amaral, 2004; Dufour, Pascalis & Petit,

368    2006; Gothard, Brooks & Peterson, 2009) we would have predicted high interest in all but the

369    *known* condition. However, this is not what was observed as subjects showed surprisingly little

370    interest in the *C self* and *mirror* conditions while, as predicted, they showed high interest in the

371    *NC self* and *unknown* conditions. Given these contrasting findings, several interpretations are

372    required. First, a reasonable interpretation regarding the high interest for the *NC self* and

373    *unknown* conditions is that the non-contingent footage of self (*NC self*) was not recognised as a

374    representation of self, but as an unfamiliar individual and hence elicited equal interest.

375    Supporting this first conclusion is the fact that subject interest in familiar conspecifics was

376    somewhat intermediate, indicating that the high interest in the *NC self* and *unknown* conditions

377    was not simply due to observing others through the novel medium of a video screen.

378

379    More difficult to explain is the low interest elicited by the two contingent self-images (*C self* and

380    *mirror*). We would have expected both to elicit high interest due to the novelty and unfamiliarity

381    of the perceived individual (self). We suggest that that it is the synchrony of the contingent

382    images that elicits little interest in comparison to the asynchrony of the non-contingent footage.

383    More explicitly, while there are few to no times when animals experience complete synchrony

384    with an image, be it of themselves or of another, the reality is that when sitting looking at the

385    synchronous image, the depicted individual is merely sitting and "looking back" whereas in a

386    non-contingent and thus non-synchronous image, the depicted individual might seem more

387    active, sitting and looking around, observing its environment, seemingly looking back at the

388    subject and perhaps moving a little while the subject itself is not.  Another suggestion, although

389    less likely in our opinion, might be that subjects were already somewhat familiar with seeing

390    their own reflection, in windows and water surfaces, providing them with sufficient contingency

391    cues to recognise themselves in such reflections. Such self-images would not, however, provide

392    such clear visual feedback as that provided by a mirror and would therefore not permit subjects

393    to observe and learn their own physical features for recognition in non-contingent self-images.

394

395    We find it unlikely that the fixed sequence had an effect on subject interest for reasons

396    previously mentioned, such as the fact that stimulus presentation was of short duration (30 s) and

397    that trials were generally spaced out over time. Furthermore, had the fixed sequence had an

398    effect we might expect a steady decrease in interest as trials progressed, due to habituation to

399    both the experimental procedure and the presentation of stimuli, but this is not what was

400    observed.

401

402    Overall, the most striking result was the high level of interest in non-contingent footage of self,

403    similar to interest in unfamiliar (but not familiar) individuals, suggesting that subjects may have

404    perceived themselves as unknown conspecifics in the non-contingent footage. To address this

405    hypothesis, we carried out the second part of the experiment, which consisted of providing

406    subjects with extended experience of self-reflections by providing them with a mirror for three

407    consecutive months. We predicted that, if bonobos are capable of self-recognition, as has been

408    previously demonstrated (Hyatt & Hopkins, 1994; Westergaard & Hyatt, 1994; Walraven, Van

409    Elsacker & Verheyen, 1995), then increased mirror experience might enable subjects to form a

410    mental representation of their morphological self, which might then pave the way for self-

411    recognition from non-contingent self-images. Following the mirror exposure phase, subjects

412    were retested with the two critical stimuli, non-contingent footage of self (*NC self*) and footage

413    of an unknown individual (*unknown*), between 10-20 days after the mirror was removed. These

414    trials were thus carried out almost two years after the corresponding trials for the first part of the

415    experiment, ruling out simple habituation effects. Considering that the video clips were only 30s

416    long and shown only once to each subject, it seems unlikely that this experience would have had

417    a major effect on performance if shown a second time 22 months later. Our findings showed that

418    after prolonged mirror exposure, subject interest in the non-contingent footage of self

419    significantly decreased, while interest levels for the footage of an unknown individual remained

420    the same. We suggest that prolonged mirror exposure may have allowed the subjects to form a

421    visual mental representation of self, which then affected their future interest in non-contingent

422    footage of themselves. The observed drop in interest might be explained as subjects perceiving

423    their own footage as "familiar" following the mirror exposure, while the footage of unknown

424    conspecifics remains novel and of high interest.

425

426    We suggest that given sufficient experience bonobos appear to acquire the ability to use the two-

427    dimensional cues, provided by a mirror-reflection of themselves, to recognise and learn about

428    their own physical characteristics and features, which then transfers and generalises to self

429    depictions detached from the here and now. This was evidenced by the fact that, when presented

430    with a non-contingent video of self after lengthy mirror exposure, interest in the stimulus was

431    significantly decreased compared to before the mirror experience, suggesting that the self-image

432    was now perceived as familiar. Crucially, in the control condition (*unknown*), no such decrease

433    in interest was observed upon stimulus presentation. Whether this is evidence of self-recognition

434    cannot be concluded here.

435

436    **Conclusion**

437    While this experimental paradigm, investigating bonobos' responses to different images of self,

438    and known and unknown conspecifics, does not permit us to draw any conclusion regarding self-

439   recognition from either a contingent video self-image or a mirror-image, we have gained some

440   insight into the bonobos capacity to form a visual mental representation of self and the ability to

441   later recognise this self-image from non-contingent video footage. If our interpretations are

442   correct then the implications of these findings may not only provide additional evidence that

443   bonobos are capable of some form of self-recognition by perceiving themselves as distinct

444   entities but also that there may be some form of continuity to the perceived self given the fact

445   that they might be able to recognise themselves from images that are not from the 'here and

446   now'. This sense of continuity has been argued to be one of several a criteria of self-concept

447   (Gallup, 1998).

448

449   Much remains to be elucidated regarding the mechanisms and the implications of the great apes'

450   capacity for the development of self-recognition. Our data suggest that three months' of mirror

451   experience is sufficient to develop and memorise a visual mental representation of self, but how

452   much mirror-exposure is necessary minimally? How does such self-recognition persist through

453   time in the absence of one's mirror image? Calhoun & Thompson (1988) found that young

454   chimpanzees were still capable of mirror self-recognition even after one year with no mirror-

455   exposure, suggesting that once developed the capacity remains perhaps indefinitely. A

456   philosophically and empirically interesting problem also concerns the implications of self-

457   recognition for questions about self-awareness and awareness of others. As mentioned, mirror

458   self-recognition has also been demonstrated in other species particularly dolphins, and elephants,

459   which has led to further claims about their cognitive capacities, such as having "…complex

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

461   Mirror self-recognition, in other words, may just be one part of a package of cognitive capacities

462    obtained from convergent evolution (Plotnik, De Waal & Reiss, 2006). Whether or not there are

463    such intrinsic links, such as suggested by Gallup (1982) in terms of connection between self-

464    recognition and empathy, or even theory of mind (e.g. Gallup, 1991; Gergely, 1994; Suddendorf

465    & Collier-Baker, 2009; Anderson & Gallup, 2015; Dale & Plotnik, 2017), needs to be addressed

466    with further research.

467

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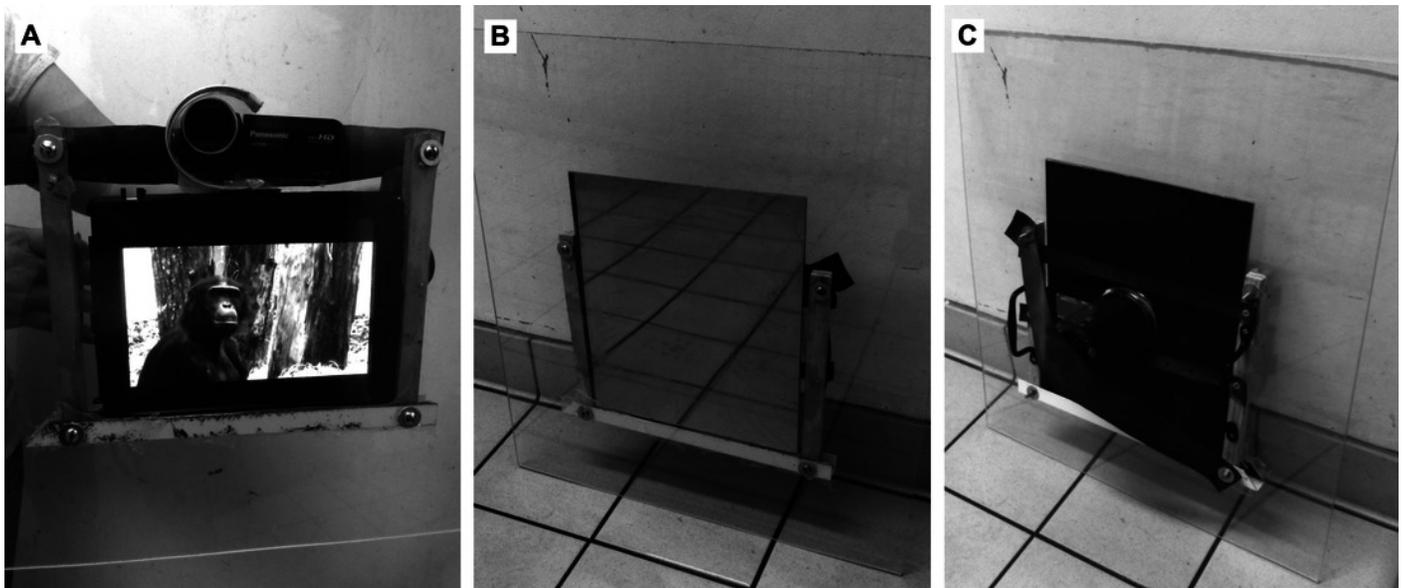
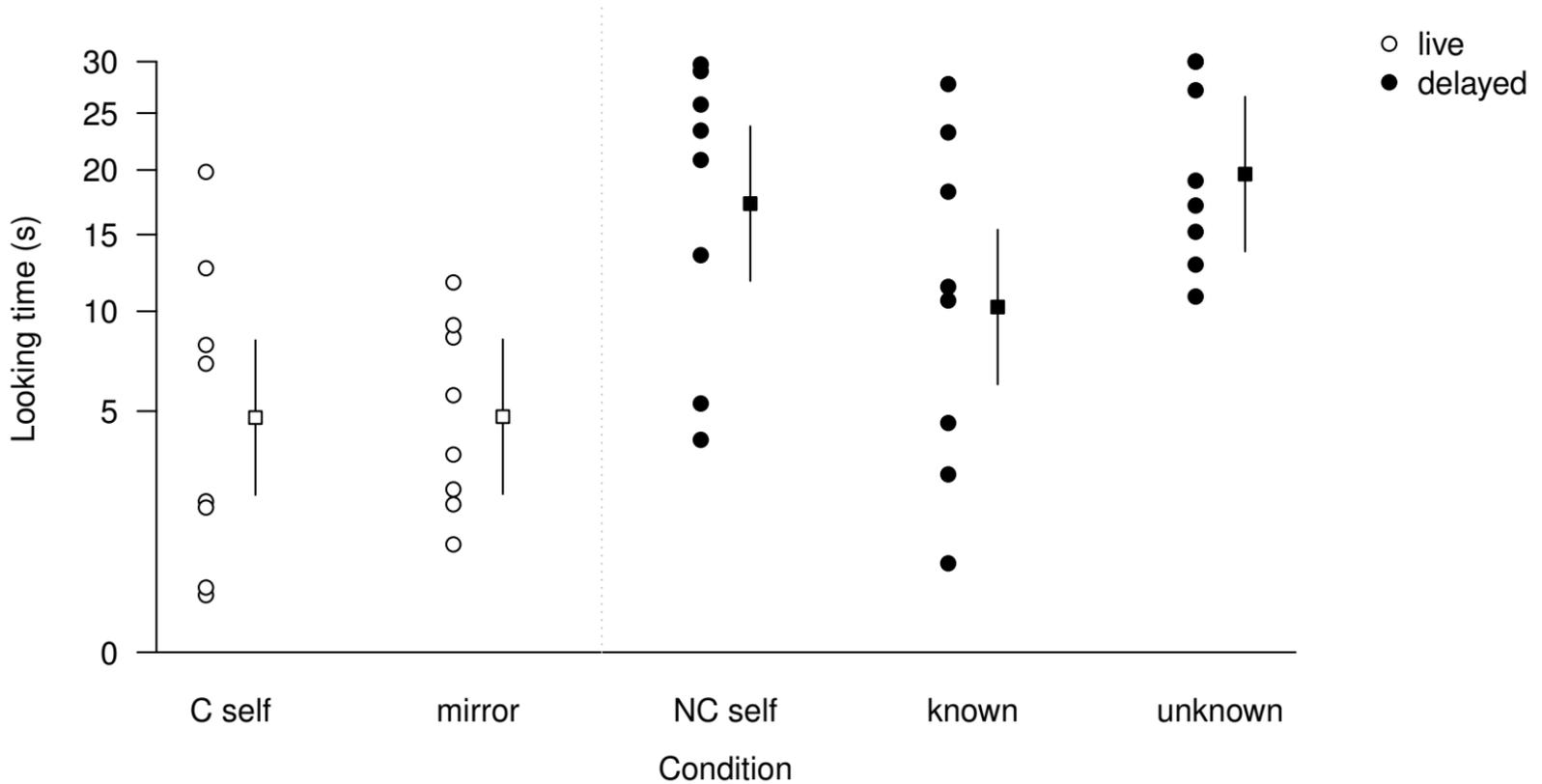
624

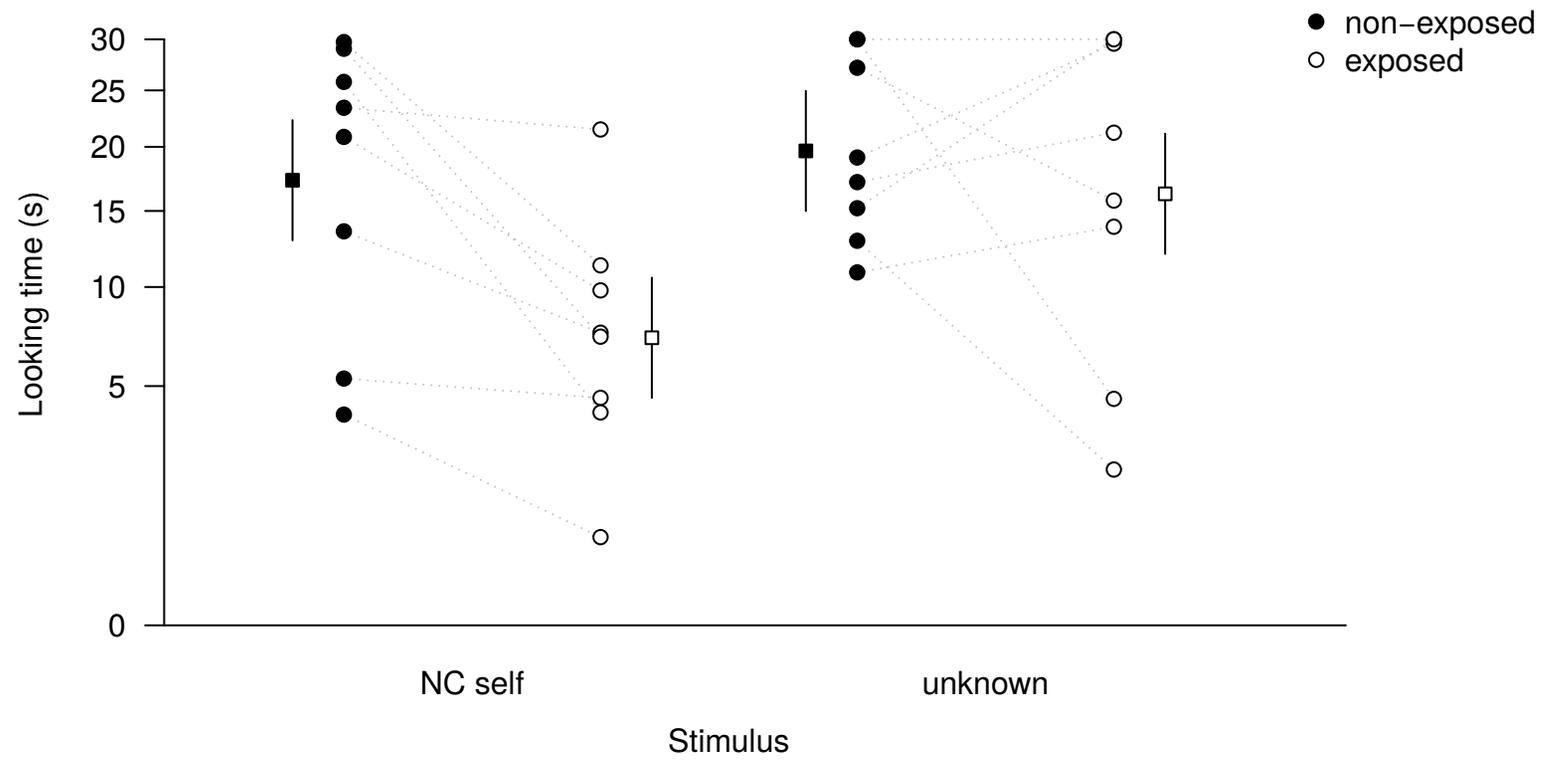
# Figure 1

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.*

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

Looking time (circles) and model predictions (squares) with 95% confidence interval; note that looking time was square root transformed for modelling. Conditions are presented chronologically from left to right.

Subject looking time and model predictions 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 modeling.

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.

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

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

|  | Estimate | Standard error | *t* |
|---|---|---|---|
| Intercept | 3.18 | 0.44 | 7.18 |
| *- 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 |

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 1.** 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 (exposed) | -0.40 | 0.39 | -1.04 |
| - Stimulus identity (Self) | -0.27 | 0.39 | -0.71 |
| Age | -0.17 | 0.03 | -6.41 |
| Exposure : Self | -1.07 | 0.55 | -1.96 |