1 **Discrimination of human and dog faces and inversion responses in**

2 **domestic dogs** *(Canis familiaris)*

3

4 Anaïs Racca[1,2], Eleonora Amadei[1,3], Séverine Ligout[1], Kun Guo[2],

5 Kerstin Meints[2], Daniel Mills[1]

6

7 [1]Department of Biological Sciences, University of Lincoln, UK

8 [2]Department of Psychology, University of Lincoln, UK

9 [3]Dipartimento di Morfofisiologia Veterinaria e Produzioni Animali, Università degli

10 Studi di Bologna, Italy

11

12

13 Corresponding author:

14 Anaïs Racca

15 aracca@lincoln.ac.uk

16 +44(0)1522 895453

17

18    **Abstract**

19        Although domestic dogs can respond to many facial cues displayed by other

20    dogs and humans, it remains unclear whether they can differentiate individual dogs or

21    humans based on facial cues alone and, if so, whether they would demonstrate the face

22    inversion effect, a behavioural hallmark commonly used in primates to differentiate face

23    processing from object processing. In this study we first established the applicability of

24    the Visual Paired Comparison (VPC or preferential looking) procedure for dogs using a

25    simple object discrimination task with 2D pictures. The animals demonstrated a clear

26    looking preference for novel objects when simultaneously presented with prior-exposed

27    familiar objects. We then adopted this VPC procedure to assess their face discrimination

28    and inversion responses. Dogs showed a deviation from random behaviour, indicating

29    discrimination capability when inspecting upright dog faces, human faces and object

30    images; but the pattern of viewing preference was dependent upon image category.

31    They directed longer viewing time at novel (vs. familiar) human faces and objects, but

32    not at dog faces, instead, a longer viewing time at familiar (vs. novel) dog faces was

33    observed. No significant looking preference was detected for inverted images regardless

34    of image category. Our results indicate that domestic dogs can use facial cues alone to

35    differentiate individual dogs and humans, and that they exhibit a non-specific inversion

36    response. In addition, the discrimination response by dogs of human and dog faces

37    appears to differ with the type of face involved.

38

39    *Keywords:* Preferential looking, Visual paired comparison, Face discrimination,

40    Inversion effect, Dogs

**Introduction**

Faces convey visual information about an individual's gender, age, familiarity, intention and mental state, and so it is not surprising that the ability to recognize these cues and to respond accordingly plays an important role in social communication, at least in humans (Bruce and Young 1998). Numerous studies have demonstrated our superior efficiency in differentiating and recognizing faces compared with non-face objects, and have suggested a face-specific cognitive and neural mechanism involved in face processing (e.g. Farah et al. 1998; McKone et al. 2006; see also Tarr and Cheng 2003). For instance, neuropsychological studies have reported selective impairments of face and object recognition in neurological patients (prosopagnosia and visual agnosia) (Farah 1996; Moscovitch et al. 1997), and brain imaging studies have revealed distinct neuroanatomical regions in the cerebral cortex, such as the fusiform gyrus, associated with face processing (McCarthy et al. 1997; Tsao et al. 2006). Likewise, behavioural/perceptual studies show that inversion (presentation of a stimulus upside-down) results in a larger decrease in recognition performance for faces than for other mono-oriented objects (e.g. Yin, 1969; Valentine 1988; Rossion and Gauthier 2002). Although the precise cause of this so called 'face inversion effect' is still source of debate (qualitative vs. quantitative difference between the processing of upright and inverted faces; e.g. Sekuler et al. 2004; Rossion 2008, 2009; Riesenhuber and Wolff 2009; Yovel 2009); it is generally associated with a more holistic processing for faces (both the shape of the local features (i.e. eyes, nose, mouth) and their spatial arrangement are integrated into a single representation of the face) than other objects. The face inversion effect is therefore considered as a hallmark for differentiating face from object processing.

The capacity for differentiating individuals based on facial cues is not restricted to humans. Using match-to-sample or visual paired comparison tasks, previous studies

67 have found that non-human primates (e.g. chimpanzees (*Pan troglodytes*): Parr et al.

68 1998, 2000, 2006; and monkeys (*Macaca mulatta, Macaca tonkeana, Cebus apella*):

69 Pascalis and Bachevalier 1998; Parr et al. 2000, 2008; Gothard et al. 2003, 2009;

70 Dufour et al. 2006; Parr and Heinz 2008) other mammals (e.g. sheep (*Ovis aries*):

71 Kendricks et al. 1996; heifers (*Bos Taurus*): Coulon et al. 2009)), birds (e.g. budgerigars

72 (*Melopsittacus undulatus*): Brown and Dooling, 1992), and even insects (e.g. paper

73 wasps (*Poliste fuscatus*): Tibbetts 2002) could discriminate the faces of their own

74 species (conspecifics), based on visual cues. Although it is not clear whether face

75 processing in non-human animals share a similar neural mechanism as that in humans,

76 some behavioural studies have noticed a face inversion effect, at least towards

77 conspecific faces in chimpanzees (e.g. Parr et al. 1998), monkeys (e.g. Parr et al. 2008;

78 Parr and Heinz 2008; Neiworth 2007; see also Parr et al. 1999) and sheep (Kendrick et

79 al. 1996), suggesting that a similar holistic process may be used for face perception by

80 these species.

81      Many studies have suggested that the development of a face-specific cognitive

82 process relies heavily on the animal's extensive experience with certain type of faces.

83 For instance, human adults have difficulties at recognizing faces from a different ethnic

84 group and demonstrate weaker holistic processing towards these faces (O'Toole et al.

85 1994; Tanaka et al. 2004). This so called 'other-race effect' can decrease and even

86 reverse by experiencing another ethnic face type (e.g. Elliott et al. 1973; Brigham et al.

87 1982; Sangrigoli et al. 2004). Furthermore, humans and some non-human primates

88 present abilities of discrimination and/or an inversion effect toward faces of other

89 species, provided that they have been frequently exposed to them (generally tested with

90 other-primate species) (Parr et al. 1998, 1999; Martin-Malivel and Fagot 2001; Pascalis

91 et al. 2005; Martin-Malivel and Okada 2007; Neiworth et al. 2007; Parr and Heinz

92    2008; Sugita 2008). Finally, human performances in simple human-face identification

93    task are known to depend primarily on the amount of preceding practice (Hussain et al.

94    2009). Taken together, exposure seems to be an important determinant for holistic face

95    processing.

96          Given their long history of domestication (estimated at 12,000-100,000 years

97    ago, Davis and Valla 1978; Vilà et al. 1997) and intensive daily interaction with humans,

98    pet domestic dogs could be a unique animal model for the comparative study of face

99    processing. Despite their extraordinary capacity for discriminating olfactory cues (e.g.

100   Schoon 1997; Furton and Myers 2001), domestic dogs also process visual inputs

101   efficiently. Although they could have less binocular overlap, less range of

102   accommodation and colour sensitivity, and lower visual acuity (20/50 to 20/100 with

103   the Snellen chart) compared with humans, they in general have a larger visual field and

104   higher sensitivity to motion signals (for a review see Miller and Murphy 1995).

105   Growing evidence has revealed that they can rely on facial cues for social

106   communication. They can display a range of facial expressions and these are believed to

107   be important in intraspecific communication (e.g. Feddersen-Petersen 2005). They also

108   attend to and use human facial cues. For instance, they attend to human faces to assess

109   their attentional state (Call et al. 2003; Gácsi et al. 2004; Viranyi et al. 2004) or in

110   problem solving situations (Topál et al. 1997; Miklósi et al. 2003). They are particularly

111   efficient at reading and understanding some human directional communicative cues,

112   such as following human eye/head direction to find hidden food (e.g. Miklósi et al.

113   1998; Soproni et al. 2001), and even exceed the ability of some non-human primates in

114   such tasks (e.g. Povinelli et al. 1999; Soproni et al. 2001; Hare et al. 2002). In a recent

115   study, Marinelli and colleagues (2009) observed the apparent attention of dogs while

116   looking at their owner and a stranger entering and leaving a room. They showed that the

117    dogs' attention towards their owner decreased if both the owner and the stranger were

118    wearing hoods covering their heads. This could suggest that dogs use the face as a cue

119    to recognize their owners. Moreover, another study suggests dogs may even have an

120    internal representation of their owner's face, and can correlate visual inputs (i.e.

121    owner's face) with auditory inputs (i.e. owner's voice) (Adachi et al. 2007). Finally, our

122    recent behavioural study (Guo et al. 2009) revealed that when exploring faces of

123    different species, domestic dogs demonstrated a human-like left gaze bias (i.e. the right

124    side of the viewer's face is inspected first and for longer periods) towards human faces

125    but not towards monkey or dog faces, suggesting that they may use a human-like gaze

126    strategy for the processing of human facial information but not conspecifics.

127         In this study, we examined whether domestic dogs (*Canis familiaris*) could

128    discriminate faces based on visual cues alone, whether they demonstrate a face

129    inversion effect, and to what extent these behaviour responses were influenced by the

130    species viewed (i.e. human faces vs. dog faces), given their high level of natural

131    exposure to both species.

132

133    **Experiment 1: Object discrimination in domestic dogs measured by a visual**

134    **paired comparison task**

135         Compared with other methodologies such as match-to-sample task, the visual

136    paired comparison (VPC or preferential looking) task does not involve intensive

137    training, is rapid to perform and is naturalistic. Consequently, it is commonly used in

138    the study of visual discrimination performance in human infants (e.g. Fantz 1964; Fagan

139    1973; Pascalis et al. 2002) and non-human primates (e.g. Pascalis and Bachevalier

140    1998; Gothard et al. 2003, 2009; Dufour et al. 2006). It is based on behavioural changes

141    stemming from biases in attention towards novelty. In this task, a single stimulus is

142 presented to the participant in a first presentation phase (familiarisation phase), followed

143 by the simultaneous presentation of the same stimulus and a novel stimulus in the

144 second presentation phase (test phase). It is assumed that if the individual can

145 discriminate between the familiar and the novel stimulus, there will be increased

146 attention shown towards the novel stimulus, which is evident from a longer viewing

147 time.

148 To our knowledge, the VPC task has not been applied in the controlled testing of

149 the perceptual ability of domestic dogs. Therefore, in the first experiment, we employed

150 an object discrimination task to establish whether the domestic dog could fulfil the

151 necessary criteria for using the VPC task in such studies.

152

153 **Method**

154 *Animals*

155 Seven adult domestic pet dogs (*Canis familiaris*, 5.6±2.8 (mean±SD) years old;

156 1 miniature Dachshund, 2 Lurchers, and 4 cross-breeds; 2 males and 5 females) were

157 recruited from university staff and students for this experiment. The study was carried

158 out at the University of Lincoln (UK) from May to June 2008.

159 *Visual stimuli*

160 Eighteen gray-scale digitized common object pictures (subtending a visual angle

161 of 34×43°) were used in this experiment. The pictures were taken using a Nikon D70

162 digital camera and further processed in Adobe Photoshop. Specifically, a single object

163 was cropped from the original picture and was then resized (to ensure a similar height

164 between objects) and overlapped with a homogenous white background to create object

165 image used in the study. The object pictures were then paired according to similarity of

166 their general shape, and each trial contained two different images of the same object

167 (first picture and familiar picture) and one image of a different object (novel picture)

7

168    (see Fig.1 for an example).  All visual stimuli were back-projected on the centre of a

169    'dark' projection screen using customized presentation software (Meints and Woodford

170    2008).

171          To reduce the chance of discriminating objects using a low level cognitive

172    process, such as detecting differences in contrast or brightness, two precautions were

173    taken: (1) for each trial the first and familiar images were two different images of the

174    same object with a slight difference in the perspective to avoid repetition of the contrast

175    and brightness distribution in the pictures; (2) the contrast and brightness of the three

176    pictures forming each trial were visually adjusted to appear as similar as possible.

177    Therefore, the dogs could not rely on the immediate change of contrast or brightness to

178    differentiate the familiar and novel stimulus presented simultaneously in the test phase.

179    *Experimental protocol*

180          During the experiment, the dog was familiarised with a quiet, dim-lit test room

181    and then sat about 60cm in front of the projection screen. A researcher stood behind the

182    dog, put her hands on the shoulders or under the head of the dog but did not interfere

183    with it during the image presentation or force it to watch the screen. The small dogs

184    were sat on the lap of the researcher. A CCTV camera (SONY SSC-M388CE,

185    resolution: 380 horizontal lines) placed in front of the dog was used to monitor and

186    record the dog's eye and head movements. Once the dog's attention had been attracted

187    towards the screen using a sound stimulus behind it (e.g. a call to the dog, tap on the

188    screen), the trial was started with a small yellow fixation point (FP) presented in the

189    centre of the screen at the dog's eye level (also the centre of the project stimulus). The

190    diameter of the FP was changed dynamically by expanding and contracting (ranging

191    between 2.8 and 6.6°) to attract and maintain the dog's attention. The dog's head and

192    eye positions were monitored on-line by a second researcher, in an annexe room,

193    through CCTV. Once the dog's gaze was oriented towards the FP a visual stimulus was

194 then presented. During the presentation, the dog passively viewed the images. No

195 reinforcement was given during this procedure, neither were the dogs trained on any

196 other task with these stimuli.

197 In total, 6 trials were tested in a random order for each dog, and 3 pre-test trials

198 were used to familiarise the dog with the general procedure. A typical trial consisted of

199 two presentations (or phases). The first familiarisation phase had a single first picture

200 presented at the centre of the screen for 5 seconds, and the second test phase had the

201 familiar and novel pictures presented also for 5 seconds side-by-side with a 35° spatial

202 gap between them (distance between the inner edges of two simultaneously presented

203 pictures). The side location (left or right) of the novel picture was randomised and

204 counterbalanced. The time between the familiarisation phase and the test phase (inter-

205 phase interval) varied between 1 and 4 seconds, depending on the time needed to re-

206 attract the attention of the dog towards the FP. A trial was aborted if the dog spent less

207 than 1 second exploring the first picture during the familiarisation phase or if the

208 researcher failed to re-attract dog's attention towards the FP within a maximum of 4

209 seconds during the inter-phase interval. The dogs were allowed short breaks when

210 needed and were given treats during the breaks. All of the dogs tested successfully

211 completed at least 67% of the trials (81%±11). Two dogs needed an extra session to

212 retest missed trials to reach this criterion.

213 The dog's eyes and head movements were recorded and then digitised with a

214 sampling frequency of 60 Hz. The image was replayed off-line frame by frame for

215 accurate analysis by one researcher and the direction of the dog's gaze toward the

216 screen was manually classified as 'left', 'right', 'central' and 'out' looking accordingly

217 (see Fig. 2 for an example). The coding of each trial was started with a "central" gaze

218 (direct gaze towards the central FP) which was used as a reference position for the

219 entire trial. The gaze direction was then coded as 'left' or 'right' once the dog's eye

220 deviated from this reference position, assessed by a change of pupil position. The

221 movement of head and/or eyebrows were also used to facilitate the coding. Establishing

222 if a subject was looking 'out' was accomplished by training the observers. This

223 involved repeatedly presenting them with video sequences in which a human subject

224 oscillated her gaze between the outer edge of the image and beyond. The 'out' looking

225 was always chosen when in doubt.

226 The researcher was blind about the side location of the pictures on the screen

227 during the test phase for each trial when performing off-line data analysis.

228 *Data analysis and statistics*

229 For each trial, the viewing time of gaze direction classified as 'left', 'right', 'central'

230 and 'out' was calculated separately. As the amount of time spent looking at the pictures

231 varied widely between subjects we calculated the proportion of 'left' and 'right'

232 viewing time as a proportion of cumulative viewing time allocated within the screen

233 (i.e. right+left+central) in order to normalize our data. The data were then unblinded so

234 that the proportion of 'left' and 'right' viewing time could be contextualised according

235 to the position of the familiar and novel pictures, and was averaged across trials for each

236 dog. A two-tailed paired *t*-test was used to compare viewing time between two pictures

237 for all the tested dogs.

238

239 **Results and Discussion**

240 Within a 5-second presentation time, the dogs spent on average 4.0s±0.6 looking

241 at the first picture in the familiarisation phase, and 4.4s±0.48 looking at the familiar and

242 novel pictures in the test phase. The two tailed paired *t*-test showed that the novel

243 picture attracted a significantly longer viewing time than the familiar picture

244 ($41.1\% \pm 11.2$ vs. $26.8\% \pm 7.2$, $t_6=4.83$, $P=0.003$), suggesting that the dogs demonstrated a

245 clear preference for novelty and could differentiate two objects presented

246   simultaneously in the test phase. The VPC task, therefore, can be used for investigating

247   face discrimination and inversion performance in domestic dogs. We should, however,

248   acknowledge that the researcher stood behind the dog during the study was not blind

249   towards the stimuli presented. As subtle unconscious cues may have been transmitted to

250   the dogs by the experimenter, this potential factor was eliminated in our second

251   experiment.

252

253   **Experiment 2: Face discrimination and inversion performance in the viewing of**

254   **human and dog faces**

255        In the second experiment, we employed VPC tasks to examine (1) whether

256   domestic dogs could discriminate individual faces based on visual cues alone; (2)

257   whether they show a face inversion effect as seen in human and non-human primates;

258   and (3) to what extent their face discrimination and inversion performance were

259   influenced by the species of viewed faces (i.e. human faces vs. dog faces).

260

261   **Method**

262        Twenty-six adult domestic pet dogs were recruited from university staff and

263   students for this experiment, with fifteen of them successfully completing the

264   experiment. The reasons for failure to complete were mainly due to a lack of attention,

265   restlessness or distress. One of the fifteen dogs was also excluded from the data analysis

266   because of producing scores above 2.5 standard deviations from the mean, and so was

267   rejected as an outlier. The final sample contained fourteen dogs (4.3±3.2 (mean±SD)

268   years old; 1 Alaskan Malamute, 1 miniature Dachshund, 2 Jack Russells, 2 Labradors, 3

269   Lurchers and 5 cross-breeds; 6 males and 8 females). Four of them had also participated

270   in the first experiment. All dogs were well socialised to humans and other dogs. The

271   study took place at the University of Lincoln (UK) from October to December 2008.

272     A total of seventy-two gray scale digitized unfamiliar human face, unfamiliar

273     dog face and common object images (24 images per category; 36×45 cm) were used in

274     this experiment (see Fig.3 for examples). The human faces were taken from Caucasian

275     students at the University of Lincoln (aged between 19 and 26 years old; 8 women and

276     8 men) who did not present any distinctive facial marks, facial jewelleries and make-up.

277     The faces of adult dogs (aged between 2 and 7 years old; 8 males and 8 females) were

278     obtained from pedigree dog breeders (Poodle, miniature Dachshund, Spaniel and Border

279     Terrier). All face images were judged to have neutral facial expressions with a straight

280     gaze. The common object images contained pictures of generally seen upright items:

281     table, lamp, chair and car.

282     Eight trials were used for each image category to test discrimination

283     performance (24 trials in total for each dog). Four of them were upright trials where all

284     the pictures were presented in an upright orientation. The other 4 trials were inverted

285     trials where the first picture was presented upright during the familiarisation phase but

286     the familiar and the novel pictures were presented upside-down (180° rotation) during

287     the test phase. For a given trial, the stimuli used as familiar or novel items were

288     randomly determined. The human faces were paired by gender and age, the dog faces

289     were paired by gender, age and breed, and the object pictures were paired by category

290     type. The gender of human faces, the breed of dog faces and the type of objects were

291     balanced between upright and inverted trials. Each pair of human and dog faces was

292     also assessed as more similar or different based on hair/fur colour and facial marking,

293     and was then balanced between upright and inverted trials. Furthermore, all the pictures

294     presented within a given trial were digitally processed in the same way as described in

295     Experiment 1 to control for some low-level image properties (i.e. background colour,

296     size, contrast and brightness of the stimuli); the overall brightness (stimulus +

297 background) of the first picture presented in the familiarisation phase was also set as the

298 mean brightness of the novel and familiar pictures presented in the test phase. The dogs,

299 therefore, had to rely on differences in the face/object contained in the picture, rather

300 than differences in overall picture brightness, to differentiate familiar and novel

301 pictures.

302 The experimental procedure and data analysis were identical to those described

303 in Experiment 1. An additional precaution was, however, used here: the researcher

304 behind the dog was instructed not to look at the pictures by keeping her head down

305 during the trial to avoid potential influence on the dog's viewing behaviour. The 15

306 dogs tested successfully completed at least 75% of the trials (92%±5), and needed extra

307 sessions to retest missed trials to reach this criterion (the dogs did not miss more trials

308 with regards to one stimulus category than another, ANOVA, P>0.05). Two researchers

309 coded the direction of the dog's gaze in the same way as in experiment 1, and without

310 prior knowledge about the side location of the familiar and novel pictures presented.

311 The inter-rater reliability measures yielded correlations of 0.94 between the two

312 researchers after coding data independently.

313 *Data analysis and statistics*

314 As in experiment 1, the cumulative viewing time directed at the 'left', 'right', 'central'

315 and 'out' of the screen was calculated separately for each trial. We then calculated the

316 proportion of 'left' and 'right' viewing time as a proportion of cumulative viewing time

317 allocated within the screen in order to normalize our data. The proportion of 'left' and

318 'right' viewing time was then referenced to the viewing time directed at the familiar and

319 novel pictures and averaged between trials and across image categories for each dog.

320 Data were checked for normality using a Kolmogorov-Smirnov test ($P>0.05$), therefore,

321 analyses of variance with repeated measures were conducted on the proportion of

322 viewing time at the stimuli considering the following factors: Stimulus Type (dog face

323 vs. human face vs. object), Orientation (upright vs. inverted) and Image novelty (novel

324 vs. familiar assessed by gaze direction). We then used *planned comparisons*, run within

325 the ANOVA, to determine if there was a significant attraction towards the novel

326 stimulus in the different type of stimuli and in the different orientation.

327

328 **Results and Discussion**

329 During the familiarisation phase, the dogs spent on average 4.1s±0.7, 4.1s±0.8

330 and 4.2s±0.7 viewing dog faces, human faces and object pictures. During the test phase,

331 they spent 4.3s±0.78, 4.2s±0.8 and 4.3s±0.6 looking at the familiar and novel images of

332 dog faces, human faces and objects. We did not observe a significant difference in

333 viewing time across image categories or presented orientations (ANOVA, P>0.05). The

334 averaged cumulative viewing time, in milliseconds, directed at the novel picture

335 (looking 'left' or 'right' depending on the side location of the stimuli), 'familiar' picture

336 (looking 'right' or 'left'), 'central' and 'out' of the screen are presented in Table 1.

337 Our ANOVA analysis conducted on the proportion of viewing time allocated to

338 the stimuli revealed no significant effect for Image novelty ($F_{1,13}$=3.84; $P$=0.0717) but a

339 significant interaction between Stimulus Type and Image novelty ($F_{2,26}$=5.98;

340 $P$=0.0073). *Planned comparisons* show that during the test phase with the upright

341 images, the novel object and novel human face picture attracted a significantly longer

342 viewing time than the familiar object and familiar human face (object: $F_1$=8.15,

343 $P$=0.0135; human face: $F_1$=7.09, $P$=0.0195), and that the familiar dog face attracted a

344 significantly longer viewing time than the novel dog face ($F_1$=5.43, $P$=0.037) (Figure

345 4.A). For inverted stimuli, the novel and familiar pictures in the test phase resulted in no

346 significant difference in the viewing time for each image category (object: $F_1$=1.08,

347 $P$=0.32; human face: $F_1$=1.13, $P$=0.31; dog face: $F_1$=0.005, $P$=0.94) suggesting that the

14

348 dogs did not reliably differentiate between the two inverted pictures presented

349 simultaneously (Fig 4.B).

350     The absence of an interaction between Stimulus Type and Orientation suggests

351 that the observed inversion effect was neither face-specific nor species-specific.

352

353 **General Discussion**

354     In this study we first demonstrated that the Visual Paired Comparison (VPC)

355 procedure can be successfully applied to domestic dogs for the study of visual

356 discrimination. To the authors' knowledge, this is the first report of the use of VPC in

357 non-primate animals.

358     Using a VPC task, we observed a clear difference between the proportion of

359 viewing time directed at a simultaneously presented novel image and prior-exposed

360 familiar image, suggesting the dogs could make a within-category discrimination

361 between upright dog faces, human faces and object images. Therefore, the capacity for

362 differentiating individual faces based on visual cues alone, which is evident in humans

363 and non-human primates (e.g. Bruce and Young 1998; Pascalis and Bachevalier 1998;

364 Parr et al. 2000; Dufour et al. 2006), extends to domestic dogs. Interestingly, their

365 viewing preferences seemed to differ for the processing of faces of different species.

366 The dogs demonstrated a preference for the novel face when presented with human

367 faces, but a preference for the familiar face when presented with dog faces. This

368 discrepancy may reflect different cognitive processes in the initial perception of dog and

369 human faces.

370     When applying a VPC task in infant studies, a preference for novelty has been

371 reported frequently and used as the criterion for determining discrimination abilities

372 (e.g. Fantz 1964; Fagan 1973; Pascalis et al. 2002). However, cases of preference for

373 familiarity have also been observed (for a review see Pascalis and de Haan 2003). The

374  completeness of the encoding has been identified as a major factor influencing

375  children's viewing preferences. In general, a well-encoded stimulus will tend to result in

376  a preference for novelty and an incomplete encoding of a stimulus will tend to result in

377  a preference for familiarity in order to complete the encoding of the stimulus (e.g.

378  Wagner and Sakovits 1986; Hunter and Ames 1988). Incomplete encoding is generally

379  due to a lack of familiarisation time compared to the complexity of the stimulus (the

380  more complex the stimulus is, the more familiarisation time is needed). In our study, 5

381  seconds were given to the dogs as a familiarisation time and, in average, dogs paid

382  attention to the stimuli for 4.1 seconds, whatever the stimulus type. A possible

383  explanation of our results could therefore be that dog faces are more complex than

384  human faces to encode for dog observers. Alternatively, our results could also be due to

385  our methodology. Indeed, some cases of preference for familiarity in children have been

386  observed when the familiar stimulus was similar, but not identical to the stimulus

387  previously seen (Gibson and Walker 1984). In our study, the first stimulus presented in

388  the familiarisation phase and the familiar stimulus presented in the test phase were not

389  identical (same face/object but different picture) in order to avoid a discrimination based

390  simply on contrast/brightness similarities. Thus, it could be possible that dogs detected

391  the difference between the first and the familiar stimulus for dog faces but not for

392  human faces. Finally, the discrepancy of dog preferences between dog and human faces

393  could also correspond to a different social response towards conspecifics versus humans

394  in dogs or to differential exposure to conspecifics and humans. These possibilities

395  warrant future research in the area.

396      In this study we also observed that the dogs did not make reliable within-

397  category discriminations once the images were inverted. The inversion of dog faces,

398  human faces and object images had a similar deteriorative effect on their discriminative

399  responses. If we apply the same arguments as have been used in human studies, then we

400    might be tempted to conclude that there is a similar cognitive strategy in processing of

401    dog faces, human faces and common objects in domestic dogs. However, our previous

402    study suggests this is not the case as dogs seem to present a different gaze strategy

403    while viewing human faces (left gaze bias) compared to dog faces and objects (no bias)

404    (Guo et al. 2009). Using both face and non-face stimuli, a face-specific inversion effect

405    has been observed in some non-human primates, such as chimpanzees (e.g. Parr et al.

406    1998), rhesus monkeys (Parr et al. 2008; Parr and Heinz 2008) and cotton-top tamarins

407    (Neiworth et al. 2007), but other studies have failed to observe this effect in rhesus

408    monkeys (Parr et al. 1999). In this latter experiment, Parr and her colleagues found a

409    non-face-specific inversion effect: i.e. monkeys demonstrated an inversion effect

410    towards faces of different species (rhesus monkey and capuchin) and objects

411    (automobile). Our study produces similar results for domestic dogs, i.e. a more general

412    inversion effect toward faces and objects. However, it should be noted that our

413    methodology for assessing the inversion effect was very conservative. As the first

414    picture in the familiarisation phase was presented upright to show normal configuration,

415    a mental rotation was needed to compare the inverted familiar picture with the encoded

416    upright first picture during the test phase. If dogs have a poor capacity for mental

417    rotation, then they would treat both the inverted familiar picture and inverted novel

418    picture as new pictures, and not present any gaze preference. It would be worthwhile to

419    revisit this face inversion response with different methodologies (e.g. present inverted

420    stimuli in both the familiarisation and test phases) in future research.

421

422    In conclusion, a Visual Paired Comparison (VPC) procedure can be used successfully to

423    study discrimination abilities of dogs and thus can provide an effective tool to study

424    canine cognition. Furthermore, we found no evidence that domestic dogs show a face-

425    specific inversion response, but they do have the ability to discriminate both individual

426    human and dog faces using 2-dimensional visual information only. These images do not

appear to be processed equivalently, with the looking response differing according to the type of face involved.

**Acknowledgments**

**References**

Adachi I, Kuwahata H, Fujita K (2007) Dogs recall their owner's face upon hearing the owner's voice. Anim Cogn 10:17-21

Brigham JC, Maass A, Snyder LD, Spaulding K (1982) Accuracy of eyewitness identifications in a field setting. J Personal Soc Psychol 42:673-681

Brown SD, Dooling RJ (1992) Perception of conspecific faces by budgerigars (*Melopsittacus undulatus*): I. Natural faces. J Comp Psychol 106:203-216

Bruce V, Young AW (1998) In the Eye of the Beholder: The Science of Face Perception. University Press, Oxford.

Call J, Brauer J, Kaminski J, Tomasello M (2003) Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans. J Comp Psychol 117:257-263

Coulon M, Deputte BL, Baudoin C (2009) Individual Recognition in Domestic Cattle (*Bos taurus*): Evidence from 2D-Images of Heads from Different Breeds. PLoS ONE 4: e4441

Davis SJM, Valla FR (1978) Evidence for domestication of the dog 12,000 years ago in the Natufian of Israel. Nature 276:608-610

Dufour V, Pascalis O, Petit O (2006) Face processing limitation to own species in primates: A comparative study in brown capuchins, Tonkean macaques and humans. Behav Process 73:107-113

Elliott ES, Wills EJ, Goldstein AG (1973) The effects of discrimination training on the recognition of white and oriental faces. Bull Psychon Soc 2:71-73

Fagan JF (1973) Infants' delayed recognition memory and forgetting. J Exp Child Psychol 16:424-450

460    Fantz RL (1964) Visual Experience in Infants: Decreased Attention to Familiar Patterns
461        Relative to Novel Ones. Science 146:668-670

462    Farah MJ (1996) Is face recognition 'special'? Evidence from neuropsychology. Behav
463        Brain Res 76:181-189

464    Farah MJ, Wilson KD, Drain M, Tanaka JN (1998) What Is" Special" About Face
465        Perception? Psychol Rev 105:482-498

466    Feddersen-Petersen DU (2005) Communication in Wolves and Dogs. In: Bekoff M (ed)
467        Encyclopedia of Animal Behavior, Vol. I, Greenwood Publishing Group, Inc.,
468        Westport, pp 385-394

469    Furton KG, Myers LJ (2001) The scientific foundation and efficacy of the use of
470        canines as chemical detectors for explosives. Talanta 54: 487-500

471    Gácsi M, Miklósi Á, Varga O, Topál J, Csányi V (2004) Are readers of our face readers
472        of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of
473        human's attention. Anim Cogn 7:144-153

474    Gibson EJ, Walker AS (1984) Development of knowledge of visual-tactual affordances
475        of substance. Child Dev 55: 453-60

476    Gothard KM, Erickson CA, Amaral DG (2004) How do rhesus monkeys (*Macaca
477        mulatta*) scan faces in a visual paired comparison task? Anim Cogn 7:25-36

478    Gothard KM, Brooks KN, Peterson MA (2009) Multiple percetual strategies used by
479        macaque monkeys for face recognition. Anim Cogn 12:155-167

480    Guo K, Meints K, Hall C, Hall S, Mills D (2009) Left gaze bias in humans, rhesus
481        monkeys and domestic dogs. Anim Cogn 12:409-418

482    Hare B, Brown M, Williamson C, Tomasello M (2002) The Domestication of Social
483        Cognition in Dogs. Science 298:1634-1636

484    Harris A, Aguirre GK (2008) The representation of parts and wholes in face-selective
485        cortex. J Cogn Neurosci 20:863-878

486    Hunter MA, Ames EW (1988) A multifactor model of infant preferences for novel and
487        familiar stimuli. Adv Infancy Res 5:69-95

488    Hussain Z, Sekuler AB, Bennett PJ (2009) How much practice is needed to produce
489        perceptual learning ? Vis Res 21:2624-2634

490    Kendrick KM, Atkins K, Hinton MR, Heavens P, Keverne B (1996) Are faces special
491        for sheep? Evidence from facial and object discrimination learning tests showing
492        effects of inversion and social familiarity. Behav Process 38:19-35.

493    Marinelli L, Mongillo P, Zebele A, Bono G (2009) Measuring social attention skills in
494        pet dogs. J Veterinary Behavior: Clin Appl Res, 4: 46-47

495 Martin-Malivel J, Fagot J (2001) Perception of pictorial human faces by baboons:
496   Effects of stimulus orientation on discrimination performance. Anim Learn Behav
497   29:10-20

498 Martin-Malivel J, Okada K (2007) Human and Chimpanzee Face Recognition in
499   Chimpanzees (*Pan troglodytes*): Role of Exposure and Impact on Categorical
500   Perception. Behav Neurosci 121:1145-1155

501 Maurer D, Grand RL, Mondloch CJ (2002) The many faces of configural processing.
502   Trends Cogn Sci 6:255-260

503 McCarthy G, Puce A, Gore JC, Allison T (1997) Face-Specific Processing in the
504   Human Fusiform Gyrus. J Cogn Neurosci 9:605-610

505 McKone E, Kanwisher N, Duchaine BC (2006) Can generic expertise explain special
506   processing for faces? Trends Cogn Sci 11:8-15

507 Meints K, Woodford A (2008) Lincoln Infant Lab Package 2008: A new
508   programme package for IPL, Preferential Listening, Habituation and
509   Eyetracking [WWW document: Computer software & manual]. URL:
510   http://www.lincoln.ac.uk/psychology/babylab.htm.

511 Michel C, Rossion B, Han J, Chung CS, Caldara R (2006) Holistic processing is finely
512   tuned for faces of one's own race. Psychol Sci 17:608-615

513 Miklósi Á, Kubinyi E, Topál J, Gácsi M, Virányi Z, Csányi V (2003) A Simple Reason
514   for a Big Difference Wolves Do Not Look Back at Humans, but Dogs Do. Curr
515   Biol 13:763-766

516 Miklósi Á, Polgárdi R, Topál J, Csányi V. (1998) Use of experimenter-given cues in
517   dogs. Anim Cogn 1:113-121

518 Miller PE, Murphy CJ (1995) Vision in dogs. J Am Vet Med Assoc 207:1623-34

519 Moscovitch M (1997) What Is Special about Face Recognition?: Nineteen Experiments
520   on a Person with Visual Object Agnosia and Dyslexia but Normal Face
521   Recognition. J Cogn Neurosci 9:555-604

522 Neiworth JJ, Hassett JM, Sylvester CJ (2007) Face processing in humans and new
523   world monkeys: the influence of experiential and ecological factors. Anim Cogn
524   10:125-134

525 O'Toole AJ, Deffenbacher KA, Valentin D, Abdi H (1994) Structural aspects of face
526   recognition and the other-race effect. Mem Cogn 22:208-224

527 Overman WH, Doty RW (1982) Hemispheric specialization displayed by man but not
528   macaques for analysis of faces. Neuropsychologia 20:113-128

529 Parr LA, Dove T, Hopkins WD (1998) Why Faces May Be Special: Evidence of the
530   Inversion Effect in Chimpanzees. J Cogn Neurosci 10 615-622

531    Parr LA, Heintz M, Akamagwuna U (2006) Three studies on configural face processing
532        by chimpanzees. Brain Cogn 62:30-42

533    Parr LA, Winslow JT, Hopkins WD (1999) Is the inversion effect in rhesus monkeys
534        face-specific? Anim Cogn 2:123-129

535    Parr LA, Winslow JT, Hopkins WD, de Waal FBM (2000) Recognizing Facial Cues:
536        Individual Discrimination by Chimpanzees (*Pan troglodytes*) and Rhesus Monkeys
537        (*Macaca mulatta*). J Comp Psychol 114:47-60

538    Parr LA, Heintz M, Pradhan G (2008) Rhesus monkeys (*Macaca mulatta*) lack
539        expertise in face processing. J Comp Psychol 122:390-402

540    Parr LA, Heintz M (2008) Discrimination of faces and houses by rhesus monkeys: the
541        role of stimulus expertise and rotation angle. Anim Cogn 11:467-474

542    Pascalis O, Bachevalier J (1998) Face recognition in primates: a cross-species study.
543        Behav Process 43:87-96

544    Pascalis O, Scott LS, Kelly DJ, Shannon RW, Nicholson E, Coleman N, Nelson CA
545        (2005) Plasticity of face processing in infancy. Proc Natl Acad Sci 102:5297-5300

546    Pascalis O, de Haan M (2003) Recognition memory and novelty preference: what a
547        model? In Hayne H, Fagen J (Eds) Progress in Infancy Research, Vol3, Lawrence
548        Erlbaum Associates, New Jersey, pp 95-120

549    Pascalis O, de Haan M, Nelson CA (2002) Is Face Processing Species-Specific During
550        the First Year of Life? Science 296:1321-1323

551    Povinelli DJ, Bierschwale DT, Cech CG (1999) Comprehension of seeing as a
552        referential act in young children, but not juvenile chimpanzees. Br J Dev Psychol
553        17:37-60

554    Riesenhuber M, Wolff BF (2009) Task effects, performance levels, features,
555        configurations, and holistic face processing: A reply to Rossion. Acta Psychol
556        102:286-292

557    Rossion B, Gauthier I (2002) How Does the Brain Process Upright and Inverted Faces?
558        Behav Cogn Neurosci Rev 1:62-74

559    Rossion B (2008) Picture-plane inversion leads to qualitative changes of face
560        perception. Acta Psychol 128 : 274-289
561
562    Rossion B (2009) Distinguishing the cause and consequence of face inversion: The
563        perceptual field hypothesis Acta Psychol 132:300-312

564    Sangrigoli S, Pallier C, Argenti AM, Ventureyra VAG, de Schonen S (2005)
565        Reversibility of the Other-Race Effect in Face Recognition During Childhood.
566        Psychol Sci 16:440-444

567 Schoon A (1997) The performance of dogs in identifying humans by scent. Ph.D.
568     Dissertation, Rijksuniveristeit, Leiden.
569
570 Sekuler AB, Gaspar CM, Gold JM, Bennett PJ (2004) Inversion leads to quantitative,
571     not qualitative, changes in face processing. Curr Biol 14:391-396
572
573 Soproni K, Miklósi A, Topál J, Csányi V (2001) Comprehension of human
574     communicative signs in pet dogs (*Canis familiaris*). J Comp Psychol 115:122-126

574 Sugita Y (2008) Face perception in monkeys reared with no exposure to faces. Proc
575     Natl Acad Sci 105:394-398
576
577 Tanaka JW, Farah MJ (1993) Parts and wholes in face recognition. Q J Exp Psychol
578     46:225-245

579 Tanaka JW, Kiefer M, Bukach CM (2004) A holistic account of the own-race effect in
580     face recognition: evidence from a cross-cultural study. Cogn 93:1-9

581 Tarr MJ, Cheng YD (2003) Learning to see faces and objects. Trends Cogn Sci 7:23-30

582 Tibbetts EA (2002) Visual signals of individual identity in the wasp *Polistes fuscatus*.
583     Proc R Soc Lond, Ser B: Biol Sci 269:1423-1428

584 Topál J, Miklósi Á, Csányi V (1997) Dog-Human Relationship Affects Problem-
585     Solving Behavior in the Dog. Anthrozoos 10:214-224

586 Tsao DY, Freiwald WA, Tootell RBH, Livingstone MS (2006) A Cortical Region
587     Consisting Entirely of Face-Selective Cells. Science 311:670-674

588 Valentine T (1988) Upside-down faces: a review of the effect of inversion upon face
589     recognition. Br J Psychol 79:471-491

590 Vila C, Savolainen P, Maldonado JE, Amorim IR, Rice JE, Honeycutt RL, Crandall
591     KA, Lundeberg J, Wayne RK (1997) Multiple and Ancient Origins of the Domestic
592     Dog. Science 276:1687-1689

593 Virányi Z, Topál J, Gácsi M, Miklósi Á, Csányi V (2004) Dogs respond appropriately
594     to cues of humans' attentional focus. Behav Process 66:161-172

595 Wagner SH, Sakovits LJ (1986) A process analysis of infant visual and cross-modal
596     recognition memory: Implications for an amodal code. Adv Infancy Res 4:195–217

597 Yin RK (1969) Looking at upside-down faces. J Comp Psychol 81:141-145

598 Yovel (2009) The shape of facial features and the spacing among them generate similar
599     inversion effects: A reply to Rossion (2008) Acta Psychol 132:293-299
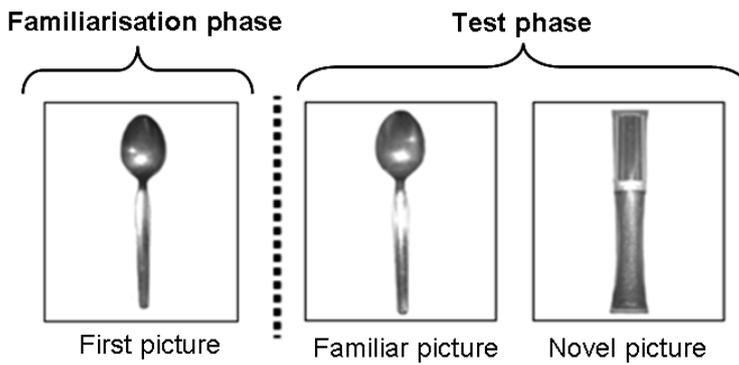600
601
602

603 **Figure and Table Legends**

604

605

606

607 Figure 1. Demonstration of visual stimuli used in a trial.
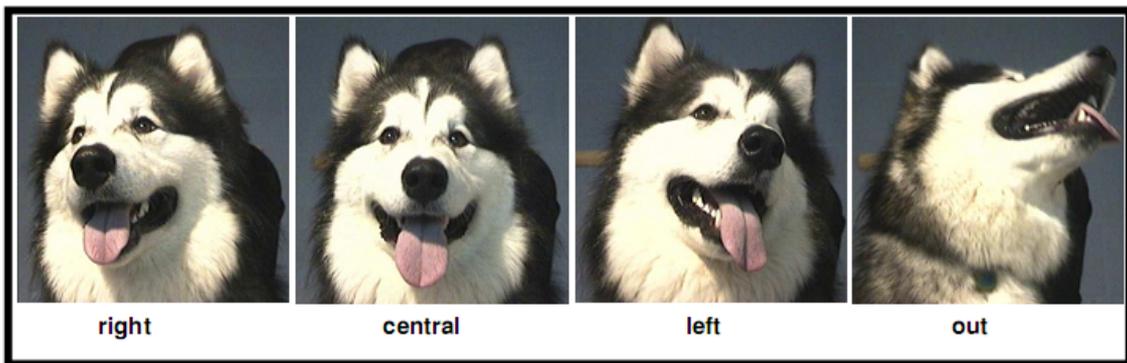


608

609

610

611

612 Figure 2. Example of gaze direction sampled from a dog while viewing the visual

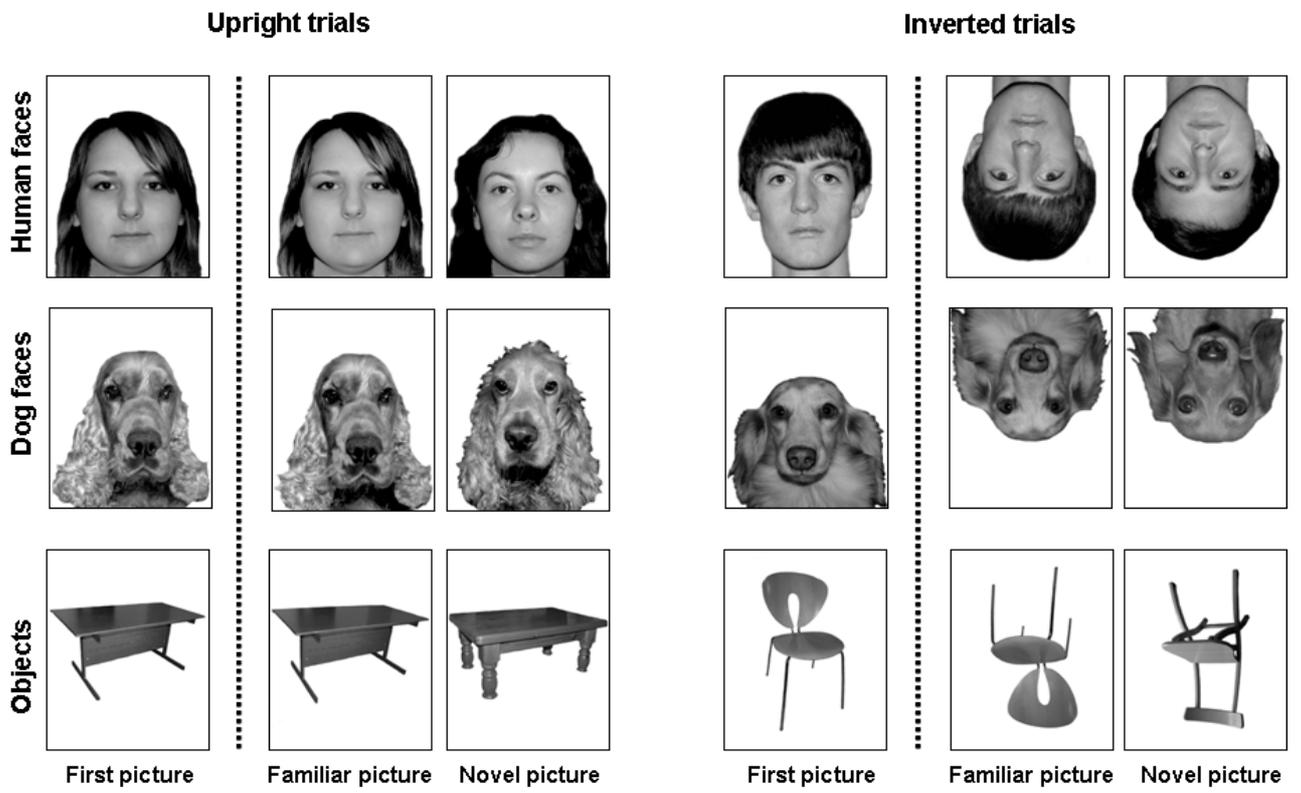613       presentation.



614

615

616

617

618

619

620     Figure 3.  Example of human faces, dog faces and object images used in the testing of

621          face discrimination and inversion performance in dogs.



622

623

624

625

626

627

628

629

630

631

632

633

634

635     Figure 4. Mean percentage and standard deviation of time spent looking at the novel

636         and the familiar picture in experiment 2 for each image category (object,

637         human faces and dog faces) in **A** upright trials and **B** inverted trials.

638         *Significant difference between the novel and the familiar picture (two tailed

639         paired t-test, *P<0.05*).

## A. Upright
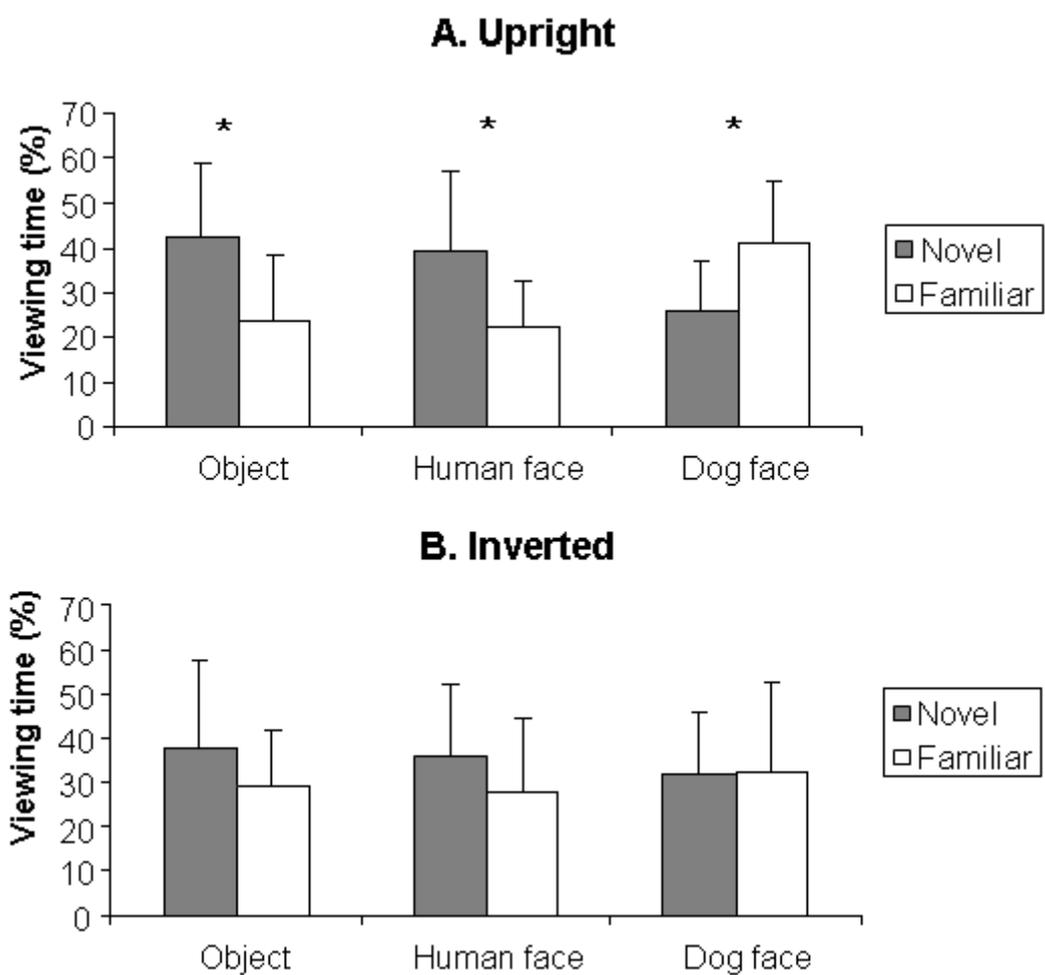


## B. Inverted



640

641

642

643

644

645

646

647   Table 1.  Mean time and standard deviation (mean±SD), in seconds, spent looking at the

648               novel picture, the familiar picture, 'central' and 'out' of the screen for each

649               image category in upright and inverted trials in experiment 2.

650

| | | Novel | Familiar | Central | Out |
|---|---|---|---|---|---|
| Object | Upright | 1.73 ± 0.64 | 1.12 ± 1.80 | 1.49 ± 0.94 | 0.92 ± 0.13 |
| | Inverted | 1.58 ± 0.90 | 1.34 ± 0.58 | 1441 ± 731 | 911 ± 0.13 |
| Human face | Upright | 1.48 ± 0.75 | 0.99 ± 0.60 | 1.55 ± 0.89 | 1.31 ± 0.15 |
| | Inverted | 1.53 ± 0.81 | 1.28 ± 0.68 | 1.62 ± 0.67 | 1.84 ± 0.15 |
| Dog face | Upright | 1.14 ± 0.55 | 1.73 ± 0.56 | 1.49 ± 0.59 | 0.74 ± 0.71 |
| | Inverted | 1.46 ± 0.77 | 1.33 ± 0.89 | 1.56 ± 0.73 | 0.87 ± 1.20 |

651

652

653

654

655

656

657

658

659

660

661