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

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

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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)

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%±11.2 vs. 26.8%±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.

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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

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

15

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

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

436

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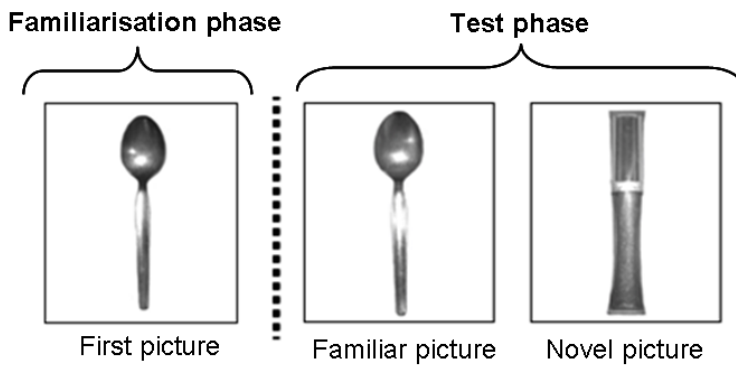599   inversion effects: A reply to Rossion (2008) Acta Psychol 132:293-299
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603   **Figure and Table Legends**

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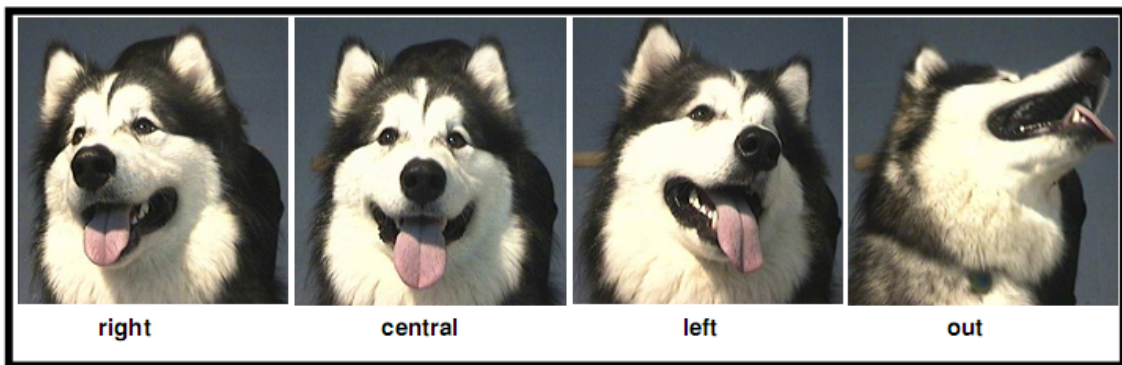607   Figure 1. Demonstration of visual stimuli used in a trial.

First picture   Familiar picture   Novel picture

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

613   presentation.

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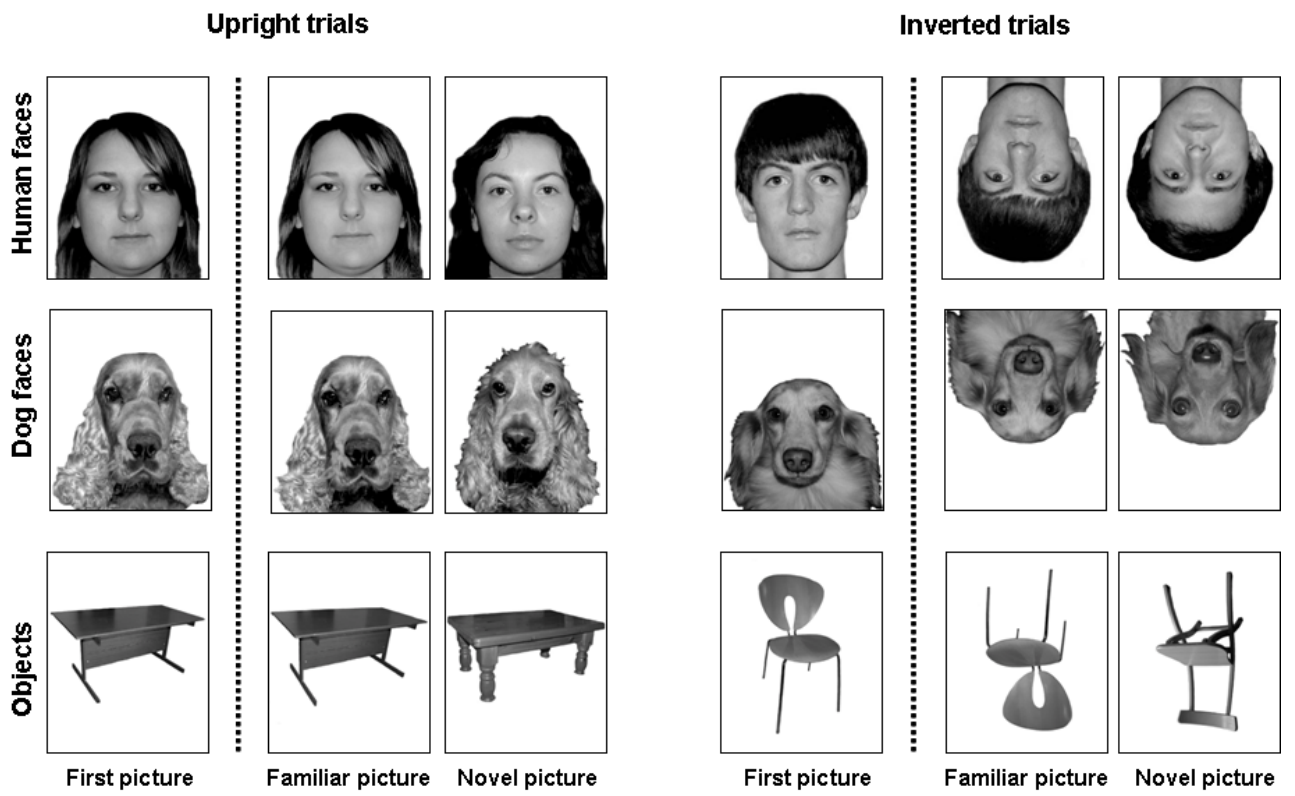
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620   Figure 3. Example of human faces, dog faces and object images used in the testing of

621   face discrimination and inversion performance in dogs.

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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
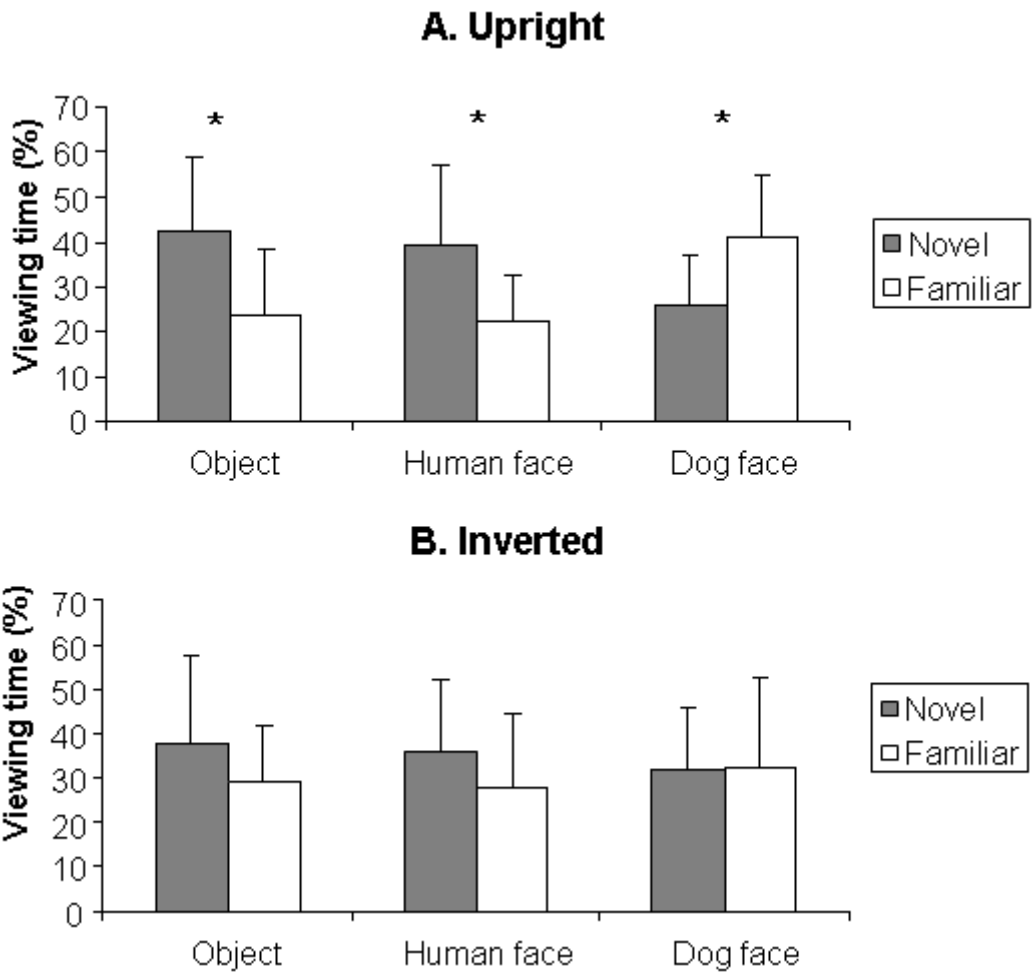
B. Inverted

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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

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