

1 **Discrimination of human and dog faces and inversion responses in**
2 **domestic dogs (*Canis familiaris*)**

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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

41 **Introduction**

42 Faces convey visual information about an individual's gender, age, familiarity, intention
43 and mental state, and so it is not surprising that the ability to recognize these cues and to
44 respond accordingly plays an important role in social communication, at least in humans
45 (Bruce and Young 1998). Numerous studies have demonstrated our superior efficiency
46 in differentiating and recognizing faces compared with non-face objects, and have
47 suggested a face-specific cognitive and neural mechanism involved in face processing
48 (e.g. Farah et al. 1998; McKone et al. 2006; see also Tarr and Cheng 2003). For
49 instance, neuropsychological studies have reported selective impairments of face and
50 object recognition in neurological patients (prosopagnosia and visual agnosia) (Farah
51 1996; Moscovitch et al. 1997), and brain imaging studies have revealed distinct
52 neuroanatomical regions in the cerebral cortex, such as the fusiform gyrus, associated
53 with face processing (McCarthy et al. 1997; Tsao et al. 2006). Likewise,
54 behavioural/perceptual studies show that inversion (presentation of a stimulus upside-
55 down) results in a larger decrease in recognition performance for faces than for other
56 mono-oriented objects (e.g. Yin, 1969; Valentine 1988; Rossion and Gauthier 2002).
57 Although the precise cause of this so called 'face inversion effect' is still source of
58 debate (qualitative vs. quantitative difference between the processing of upright and
59 inverted faces; e.g. Sekuler et al. 2004; Rossion 2008, 2009; Riesenhuber and Wolff
60 2009; Yovel 2009); it is generally associated with a more holistic processing for faces
61 (both the shape of the local features (i.e. eyes, nose, mouth) and their spatial
62 arrangement are integrated into a single representation of the face) than other objects.
63 The face inversion effect is therefore considered as a hallmark for differentiating face
64 from object processing.

65 The capacity for differentiating individuals based on facial cues is not restricted
66 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 \pm 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 $34 \times 43^\circ$) 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 $4.0s \pm 0.6$ looking
241 at the first picture in the familiarisation phase, and $4.4s \pm 0.48$ 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 \pm 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 jewellery 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 ($92\% \pm 5$), 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 $4.1s \pm 0.7$, $4.1s \pm 0.8$
330 and $4.2s \pm 0.7$ viewing dog faces, human faces and object pictures. During the test phase,
331 they spent $4.3s \pm 0.78$, $4.2s \pm 0.8$ and $4.3s \pm 0.6$ 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

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.

429 **Acknowledgments**

430 We thank Dr. Olivier Pascalis for advice on experimental design and comments on the
431 manuscript, Fiona Williams for helping data collection, and Sylvia Sizer, Szymon
432 Burzynski and Angela Fieldsend for providing dog pictures. We also thank three
433 anonymous reviewers for their helpful comments and suggestions on the manuscript.
434 Ethical approval had been granted for the University of Lincoln (UK) and all procedures
435 complied with the ethical guidance of the International Society for Applied Ethology.

436

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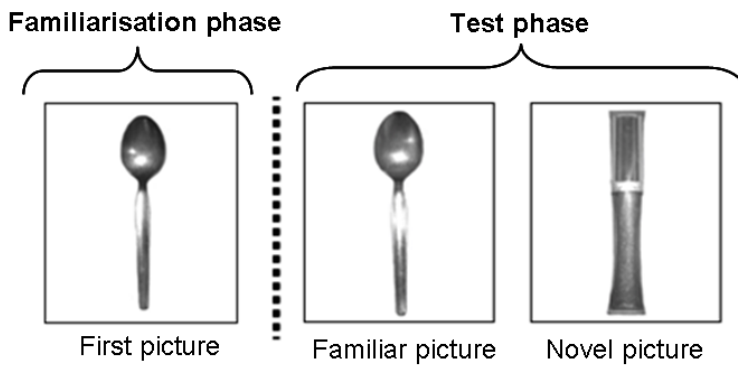
603 **Figure and Table Legends**

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



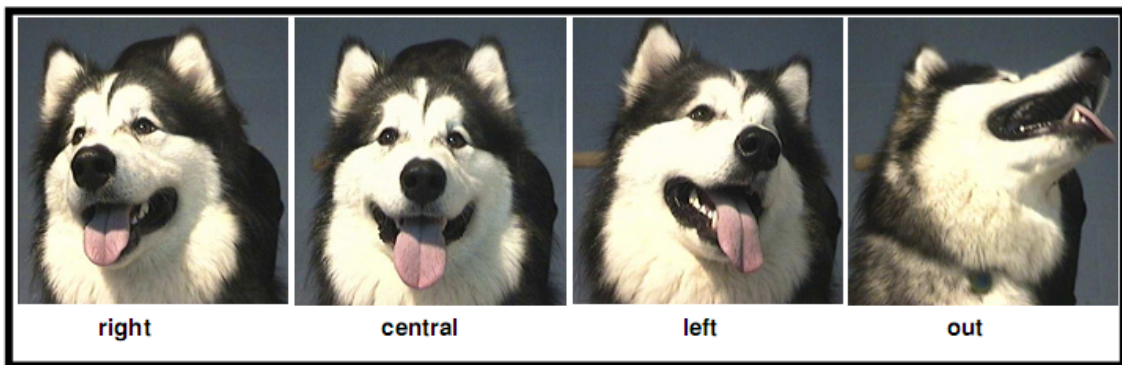
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612 Figure 2. Example of gaze direction sampled from a dog while viewing the visual
613 presentation.



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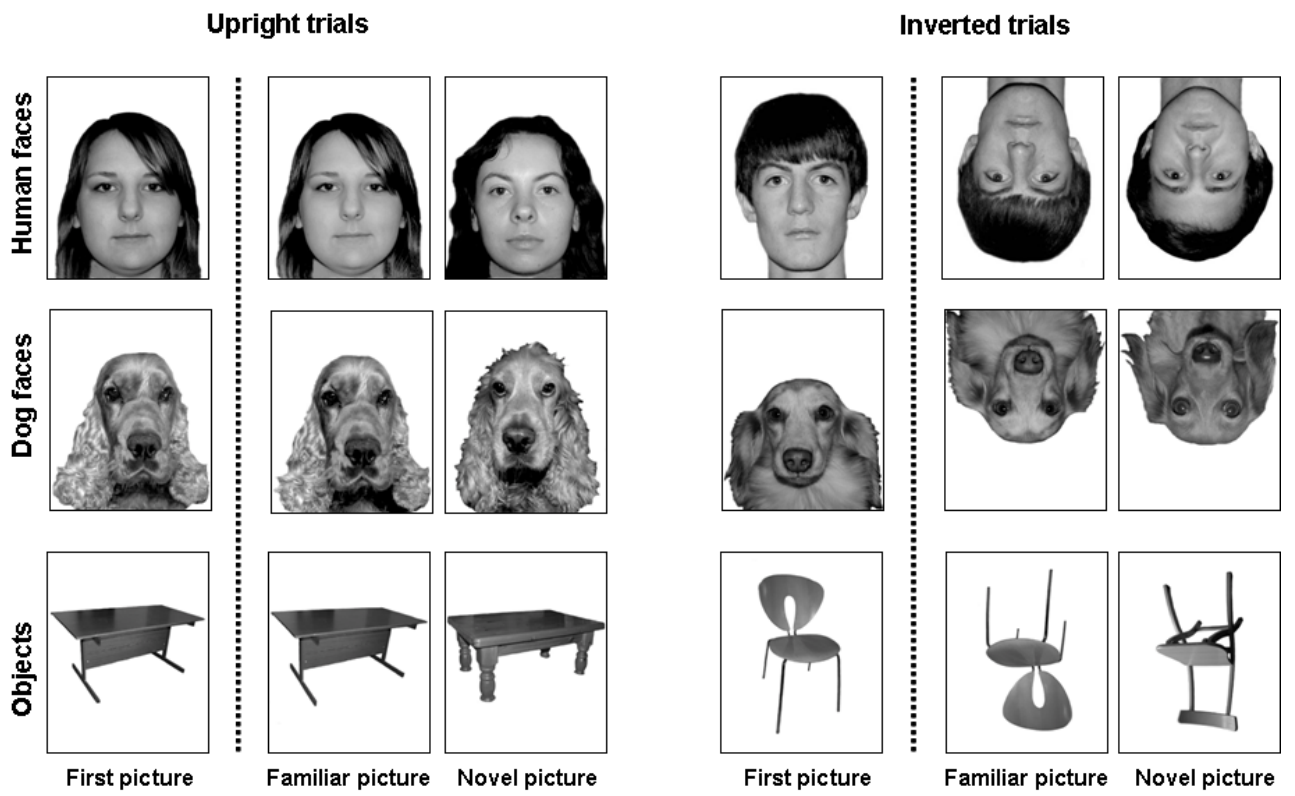
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620 Figure 3. Example of human faces, dog faces and object images used in the testing of
621 face discrimination and inversion performance in dogs.



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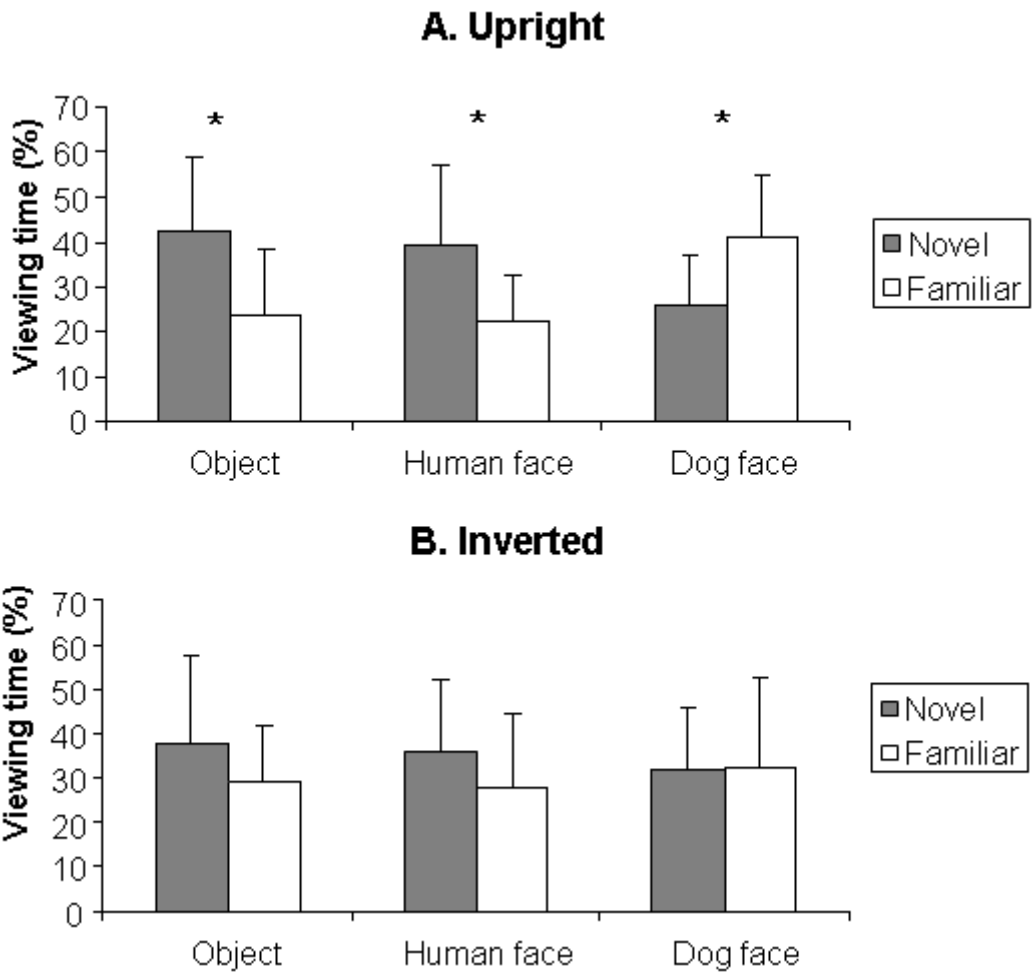
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635 Figure 4. Mean percentage and standard deviation of time spent looking at the novel
636 and the familiar picture in experiment 2 for each image category (object,
637 human faces and dog faces) in **A** upright trials and **B** inverted trials.
638 *Significant difference between the novel and the familiar picture (two tailed
639 paired t-test, $P < 0.05$).



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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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