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## COMPARATIVE BRAIN IMAGING REVEALS ANALOGOUS AND DIVERGENT PATTERNS OF SPECIES- AND FACE-SENSITIVITY IN HUMANS AND DOGS

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8 **COMPARATIVE BRAIN IMAGING REVEALS ANALOGOUS AND DIVERGENT**  
 9 **PATTERNS OF SPECIES- AND FACE-SENSITIVITY IN HUMANS AND DOGS**

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52

**Abstract**

53 Conspecific-preference in social perception is evident for multiple sensory modalities and in  
54 many species. There is also a dedicated neural network for face processing in primates. Yet,  
55 the evolutionary origin and the relative role of neural species-sensitivity and face-sensitivity  
56 in visuo-social processing are largely unknown. In this comparative study, species- and face-  
57 sensitivity to identical visual stimuli (videos of human and dog faces and occiputs) were  
58 examined using functional magnetic resonance imaging in dogs ( $n=20$ ; 45% female) and  
59 humans ( $n=30$ ; 50% female). In dogs, the bilateral mid suprasylvian gyrus showed  
60 conspecific-preference, no regions exhibited face-preference, and the majority of the visually-  
61 responsive cortex showed greater conspecific- than face-preference. In humans, conspecific-  
62 preferring regions (the right amygdala/hippocampus and the posterior superior temporal  
63 sulcus) also showed face-preference, and much of the visually-responsive cortex showed  
64 greater face- than conspecific-preference. Multivariate pattern analyses identified species-  
65 sensitive regions in both species, but face-sensitive regions only in humans. Across-species  
66 representational similarity analyses revealed stronger correspondence between dog and  
67 human response patterns for distinguishing con- from heterospecific faces than other  
68 contrasts. Results unveil functional analogies in dog and human visuo-social processing of  
69 conspecificity but suggest that cortical specialization for face perception may not be  
70 ubiquitous across mammals.

71 *Keywords:* comparative neuroscience, face-sensitivity, conspecific-preference,  
72 functional magnetic resonance imaging (fMRI), visuo-social processing, across-species  
73 representational similarity analysis (RSA)

74

**Significance statement**

75 To explore the evolutionary origins of human face-preference and its relationship to  
76 conspecific-preference, we conducted the first comparative and noninvasive visual  
77 neuroimaging study of a non-primate and a primate species, dogs and humans. Conspecific-  
78 preferring brain regions were observed in both species, but face-preferring brain regions were  
79 observed only in humans. In dogs, an overwhelming majority of visually-responsive cortex  
80 exhibited greater conspecific- than face-preference whereas in humans, much of the visually-  
81 responsive cortex showed greater face- than conspecific-preference. Together, these findings  
82 unveil functional analogies and differences in the organizing principles of visuo-social  
83 processing across two phylogenetically distant mammal species.

84 Tuning to relevant classes of social stimuli is evidenced by both behavioral and neural  
85 processing preferences, but whether such preferences are due to comparable neural  
86 mechanisms across mammals remains equivocal. Conspecific-preference is reported in many  
87 species and across sensory modalities. Con- relative to heterospecific smells (Boulet,  
88 Charpentier, & Drea, 2009; Guo et al., 2018) and vocalizations (Andics, Gácsi, Faragó, Kis,  
89 & Miklósi, 2014; Belin, Zatorre, Lafaille, Ahad, & Pike, 2000; Dooling, Brown, Klump, &  
90 Okanoya, 1992; Petkov et al., 2008) elicit stronger behavioral and neural responses in  
91 multiple species. Visual conspecific-preference is also well-documented across mammals  
92 behaviorally (Da Costa, Leigh, Man, & Kendrick, 2004; Dufour, Pascalis, & Petit, 2006;  
93 Pascalis & Bachevalier, 1998) but only in primates neurally (Anzellotti & Caramazza, 2014;  
94 Blonder et al., 2004; Kriegeskorte, Mur, Ruff, et al., 2008; Minxha et al., 2017).

95 A visual processing preference that has received considerable empirical attention is  
96 face-sensitivity. In primates, behavioral data implicate highly developed and specialized  
97 visual skills in facial information processing (Cassia, Turati, & Simion, 2004; Dufour et al.,  
98 2006; Kanwisher, McDermott, & Chun, 1997; Morton & Johnson, 1991; Valenza, Simion,  
99 Cassia, & Umiltà, 1996). Imaging findings suggest that face processing in nonhuman  
100 primates (Tsao, Freiwald, Knutsen, Mandeville, & Tootell, 2003) and in humans (Duchaine  
101 & Yovel, 2015; Kanwisher et al., 1997) is supported by dedicated cortical patches/regions.  
102 The presence of non-conspecific-preferring face-sensitive regions in humans (Blonder et al.,  
103 2004; Tong, Nakayama, Moscovitch, Weinrib, & Kanwisher, 2000) and non-conspecific-  
104 preferring face-sensitive neurons in macaques (Minxha et al., 2017) is further support of the  
105 potential centrality of faceness – in addition to or even beyond conspecificity – as an  
106 organizing principle for primate visual social perception.

107 In non-primate mammals, the role of faces in visuo-social perception is largely  
108 unknown. For navigating the environment, relative to primates, many non-primates rely less

109 on vision, or rely more on non-facial visual cues (Leopold & Rhodes, 2010). Although to  
110 various non-primates faces are attractive stimuli, direct behavioral evidence for strictly-  
111 defined face sensitivity is scarce (Leopold & Rhodes, 2010). Up until most recently, neural  
112 face sensitivity has only been reported in sheep (Kendrick & Baldwin, 1987; Peirce, Leigh,  
113 Dacosta, & Kendrick, 2001).

114 Domestic dogs are an ideal test case for comparative investigations of non-primate  
115 face processing. Due to social proximity to humans, dogs have been a species of choice in  
116 comparative studies of social perception and, with recent advances in awake dog fMRI  
117 (Bunford, Andics, Kis, Miklósi, & Gácsi, 2017), neural mechanisms thereof. Similarly to  
118 humans, dogs can differentiate conspecific from heterospecific visual stimuli (Racca et al.,  
119 2010). Furthermore, evidence indicates that dogs also rely on faces as an important source of  
120 information that is socially relevant (Gácsi, Miklósi, Varga, Topál, & Csányi, 2004) and that  
121 dogs are attracted to human faces and can differentiate familiar from novel human faces  
122 (Huber, Racca, Scaf, Virányi, & Range, 2013). Although prior data suggest that specific  
123 canine temporal regions respond more strongly to (human) faces than objects (Cuaya,  
124 Hernández-Pérez, & Concha, 2016; Dilks et al., 2015), the designs of these small-sample  
125 fMRI studies do not allow for inferences about whether the observed sensitivity to (human)  
126 faces is driven by sensitivity to animacy or bodily stimuli in general, or to faceness in  
127 particular. Recent data show that some canine temporal regions respond more strongly to dog  
128 than human faces (Thompkins et al., 2018), but whether this conspecific-preference is face-  
129 specific, remains untested. Others did not find any dog brain regions to respond more  
130 strongly to faces than scrambled images (Dilks et al., 2015; Szabó et al., 2020).

131 To comparatively assess the role of conspecificity and faceness in visuo-social  
132 perception beyond the primate order, here, we performed the same fMRI experiment in  
133 humans and dogs, using identical stimuli for both species: videos of human and dog faces and

134 occiputs (i.e., back of the head – stringent comparison stimuli that are similar to faces in  
135 terms of animacy, familiarity [of the species to the viewer], intactness, and shape). We  
136 hypothesized that (1) as in the auditory modality (Andics et al., 2014), conspecific-preference  
137 is a relevant organizing principle of visuo-social perception in both dog and human brains,  
138 and (2) face-preference is less central, relative to conspecific-preference, in dogs than in  
139 humans. To test these hypotheses, we conducted whole brain univariate and multivariate  
140 analyses, directly contrasted processing preferences in visually-responsive cortices of both  
141 species, and performed across-species representational similarity analyses.

## 142 **Materials and Methods**

### 143 **Participants**

144 Data were collected in the context of a two-site (Hungary: Eötvös Loránd University and  
145 Mexico: Universidad Nacional Autónoma de México) project. Participants were 20 family  
146 dogs ( $M_{age}=5.37$  years,  $SD=2.91$ , range=2.5-11 years; 5 intact males, 4 intact females, 6  
147 neutered males, 5 spayed females) and 30 humans ( $M_{age}=32.3$  years,  $SD=7.5$ , range=21-50  
148 years; 50% female). Fourteen dogs were recruited from the Hungarian site and 6 were  
149 recruited from the Mexican site and all 30 humans were recruited from the Hungarian site. In  
150 Hungary, dog owners and humans were recruited through the Department of Ethology  
151 participant pool and website, popular social networking sites, and via snowball sampling and  
152 in Mexico, dog owners were recruited by research staff in dog parks and via snowball  
153 sampling. All procedures involving dogs met national and international guidelines for animal  
154 care and were approved by the appropriate ethics committees (the Food Chain Safety and  
155 Animal Health Directorate Government Office [Hungary] and the Bioethics Committee of the  
156 Institute of Neurobiology, Universidad Nacional Autónoma de México [Mexico]). All  
157 procedures involving humans were approved by the appropriate ethics committee (Committee  
158 of Scientific and Research Ethics [ETT-TUKEB], Budapest, Hungary) and were in

159 accordance with the 1964 Helsinki declaration and its later amendments. All humans  
160 participated voluntarily and provided written informed consent.

161 Dogs had an average age of 5.37 years ( $SD=2.91$ , range=2.5 to 11 years) and were all  
162 family dogs. Independent samples  $t$ -tests indicated no cross-site differences in dogs' age or  
163 average number of scanning sessions needed ( $ps>.211$ ). Humans had an average age of 32.3  
164 years ( $SD=7.5$ , range=21-50 years). Most completed a master's degree or equivalent (47%),  
165 followed by bachelor's degree (37%), and high school degree (16%). Seven women and four  
166 men currently owned a dog and 12 women and 14 men had ever owned a dog. All  
167 participants had intact or corrected-to-intact vision and were free of major medical or  
168 neurologic illness as indicated by self-report. Exclusion criteria were contraindications to  
169 magnetic resonance imaging (e.g., claustrophobia, pregnancy, non-removable ferrous  
170 objects). No participants reported having experienced a traumatic experience with dogs.

### 171 **Experimental Design and Procedure**

172 Experimental and stimulus design were identical for dogs and humans. The experiment  
173 comprised six runs, each run containing 12 blocks, each block comprised of 4, 2-s long  
174 stimuli representing one of four conditions: dog face (DF), dog occiput (DO), human face  
175 (HF), and human occiput (HO). Each block was preceded by a 10 s window during which a  
176 fixation cross was presented and, during the pre-block windows, participants were presented  
177 with a brief alerting sound via headphones. Stimulus order within blocks and block order  
178 within runs was pseudo-randomized so that within blocks 1-4, 5-8, or 9-12, there was not  
179 more than one block of the same condition, and so that across the 12 blocks, blocks of the  
180 same condition did not immediately follow one another. Participants received one of six  
181 randomizations. The total length of a run was 226 s. Stimuli were presented ~155cm in front  
182 of participants' eyes and controlled using Matlab (version R2016a) Psychophysics Toolbox  
183 Version 3. Dogs were trained to lay motionless during scanning (Andics et al., 2016, 2014)



184 and to look at the stimuli. Dogs viewed the presentation screen directly (on an MR  
185 compatible LCD Monitor NordicNeuroLab AS in Hungary, and via back-projected onto a  
186 white screen using an Epson x14+ projector in Mexico), while maintaining a sphinx position  
187 with their heads supported by a chinrest (Berns, Brooks, & Spivak, 2013; Cuaya et al., 2016)  
188 and humans viewed the screen through a mirror attached to the head coil.

189 Dogs were tested in one run per session, with no more than four sessions per day and  
190 humans were tested in a single session. Sessions with dogs were continued until six  
191 functional runs (average number of days needed was 3.15, range 2-6) were obtained.

192 Sessions were continuously monitored (for dogs closing their eyes, or not being  
193 fixated at the stimuli for longer than 4 secs) on a monitor by experimenters responsible for  
194 scanning participants (the first four authors). No scans had to be discarded for these reasons.  
195 Humans were instructed to passively view the stimuli.

#### 196 **fMRI Stimuli**

197 Stimuli consisted of color videos (with an approximate size of faces/occiputs from lowest  
198 point of the chin to highest point on top of the head=28 cm) of unknown human and dog  
199 faces and human and dog occiputs (36 images of each), depicted in front of a uniform blue  
200 background (see Movie 1).

201 Movement in the videos involved minor facial movements, such as eyeblinks or subtle  
202 change in the exact direction or location of eye gaze, or minor head movements, such as  
203 vertical movement due to inhalation/exhalation. In case of human faces, individuals posed  
204 without glasses, jewelry, or intense make-up and with as neutral expression as possible. To  
205 avoid creating stimuli that are potentially threatening for the dogs, human individuals were  
206 instructed not to look directly into the camera and similar dog footage was selected (i.e., with  
207 gaze slightly averted). In selecting our stimuli, we aimed to balance ecological validity,  
208 experimental control, and feasibility. Specifically, to enhance ecological validity and

209 feasibility, we chose natural color images as it was essential that images are engaging and  
210 easily perceivable for dogs to ensure that they look at them during scanning. To ensure  
211 experimental rigor, recording of images was done under identical settings and circumstances  
212 (e.g., with regard to lighting and time of day) and differences in visual properties (brightness,  
213 contrast, hue, saturation, motion) were considered in analyses (see below).

#### 214 **fMRI Data Acquisition and Preprocessing**

215 At both test sites, scanning was performed on a 3T MRI scanner (Ingenia 3T, Philips Medical  
216 System) using, for both dogs and humans, a BOLD-sensitive T2\*-weighted echo-planar  
217 imaging sequence (both dogs and humans: TR=3200 ms, TE=29 ms, flip angle=90°, 2.5 mm-  
218 thick slices with .5 mm gap; dogs: field of view: 300\*198\*110 mm, acquisition matrix  
219 120×79; 37 axial slices; humans: field of view: 300\*198\*132 mm, acquisition matrix  
220 120×79; 44 axial slices). Each of the six runs included 75 volumes. A high-resolution  
221 anatomical scan was also acquired at a separate session for dogs and at the end of the  
222 functional imaging session for humans, using a T1-weighted 3D TFE sequence, with 1×1×1  
223 mm resolution with 180 slices, covering the whole brain, for anatomical localization.

224 For dogs at both sites, Philips SENSE coils and for humans a Philips dStream Head  
225 32ch coil was used. The former at the Hungarian site consisted of two, 14x17 cm elliptical  
226 elements (Flex-M) and at the Mexican site of two 11 cm-diameter circular elements (Flex-S),  
227 with one placed under the dog's head and the other on top of the dog's head, fixed with  
228 plastic strips, as in previous studies (Andics et al., 2014, 2016).

229 Image preprocessing and statistical analysis were performed using SPM12  
230 ([www.fil.ion.ucl.ac.uk/spm](http://www.fil.ion.ucl.ac.uk/spm)) and followed conventional preprocessing steps (realignment,  
231 normalization to a pre-selected, individually labelled canine brain of an average-sized dog as  
232 template for dogs (Czeibert et al., 2019) and a Montreal Neurological Institute (MNI)  
233 template for humans, resampling to 2x2x2mm<sup>3</sup> voxels, and smoothing with an isotropic

234 Gaussian kernel (FWHM 4 mm for dogs, 8 mm for humans). For dogs, the longitudinal axis  
235 of the brain was established through the rostral and caudal commissures, and the origin for  
236 obtaining coordinates was set to the mid of the rostral commissure. Negative to positive x, y,  
237 and z coordinates are in mm and, as in MNI space for humans, denote left to right, posterior  
238 to anterior, and inferior to superior directions, respectively. For dogs and humans, if  
239 translation exceeded 3 mm, the scan was excluded (3 dog runs and no human runs were  
240 affected by these criteria).

241 The average of maximal movements for each translation direction was below 2.059  
242 mm for dogs (1.523 in the x, .947 in the y, and 2.059 in the z direction) and .605 mm for  
243 humans (.183 in the x, .434 in the y, and .605 in the z direction) and, for each rotation axis,  
244 was below 1.196° (.698 for pitch, 1.196 for roll, and .773 for yaw) and .571° (.571 for pitch,  
245 .199 for roll, and .231 for yaw), respectively. The average of the maximum scan-to-scan  
246 movement per dog and per translation direction was .853 mm (.730 in the x, .618 in the y,  
247 and 1.212 in the z direction) and per human and per direction was .212 mm (.068 in the x,  
248 .277 in the y, and .289 in the z direction). The average of the maximum scan-to-scan  
249 movement per dog and per rotation axis was .416° (.475 for pitch, .469 for roll, and .305 for  
250 yaw) and per human and per axis was .151° (.281 for pitch, .077 for roll, and .095 for yaw).

### 251 **fMRI Data and Statistical Analysis**

252 All statistical tests were two-tailed unless otherwise noted.

253 **GLM.** A general linear model was applied to the time series, convolved with the  
254 canonical hemodynamic response function and with a 128 s high-pass filter. Condition  
255 regressors were constructed for each condition, resulting in four regressors: DF, DO, HF, and  
256 HO, the effects of which were estimated for each voxel for each participant, with first level  
257 individual models also including movement correction parameters as nuisance regressors, and  
258 taken to the second level for whole-volume random effects analysis on the group level.

259 Threshold for reporting for contrasts were  $p < .001$  uncorrected and  $p < .05$  cluster-corrected for  
260 FWE for dogs and  $p < .000001$  uncorrected and  $p < .001$  cluster-corrected for FWE for humans.  
261 To establish that findings are not a result of shortcomings of experimental design or stimuli,  
262 the overall level of visual responsiveness within the dog and human brain was examined in  
263 GLM analyses comparing all conditions to baseline (i.e., fixation cross) ( $p < .001$  uncorrected  
264 and  $p < .05$  cluster-corrected for FWE).

265 To create a set of all face-sensitive and conspecific-sensitive regions for further  
266 characterization, first, we selected peaks from the F>O and conspecific (C)>heterospecific  
267 (He) (i.e., H>D for humans, D>H for dogs) main contrasts, starting with the strongest peaks.  
268 Peaks closer than 16 mm to those already selected were skipped. Next, in case of unilateral  
269 response, specific contrasts were examined to determine if a contralateral region can be  
270 identified. Two dog regions and eight human regions were thus identified and included in  
271 further analyses: for dogs, bilateral mSSG based on D>H and for humans, bilateral FuG and  
272 IOG, right pMTG, right aMTG and right AMY, based on F>O, and left pMTG based on  
273 HF>HO. (For data on all specific contrasts, see Table 1-1).

274 To further characterize these regions, 2(F, O)x2(H, D)x2(left, right) ANOVAs (2x2 in  
275 case of unilateral activity) were conducted (interpreting only side main effects and  
276 interactions but not interpreting face and species main effects, to avoid double-dipping).

277 *Control tests for low-level visual property effects.* To assess whether observed  
278 differences in brain response were due to differences in visual properties or motion of the  
279 four stimulus categories, the parametric effects of the four visual properties (brightness,  
280 contrast, hue, and saturation) or motion of the experimental stimuli were tested in random  
281 effects parametric modulation analyses. First, to quantify each video's brightness, contrast,  
282 hue, and saturation, the value of each property on each frame was calculated and then  
283 averaged. The brightness, hue, and saturation of each pixel was calculated by converting it to

284 its' representation in the HSL color representation, in which the appearance of a pixel is  
285 determined by a number value of these three components. The contrast of each image was  
286 defined as the standard deviation of the pixel intensities (root mean square contrast). The  
287 level of motion across consecutive frames was evaluated using the motion estimation  
288 functions of MATLAB's Computer Vision System Toolbox, and then averaged over the  
289 whole clip.

290 To this end, we first checked for differences across conditions in 2(F, O)x2(H, D)  
291 ANOVAs. Then, low-level visual properties that emerged as significantly different in  
292 faceness contrasts were modeled as parametric modulators in face-sensitive regions and low-  
293 level visual properties that emerged as significantly different in conspecificity contrasts were  
294 modeled as parametric modulators in conspecific-preferring regions. Obtained mean beta  
295 values were compared to zero, in a total of 23 Benjamini-Hochberg-corrected one-sample *t*-  
296 tests, considering each of eight GLM-derived regions, the contrast based on which the region  
297 was identified, and whether or not there was a difference in any visual property for the  
298 pertinent comparison. For example, the bilateral IOG was selected based on F>O and,  
299 because faces and occiputs differed only in brightness, left and right IOG response to  
300 brightness was compared to zero. Accordingly, we tested R/L mSSG, R AMY and R/L  
301 pMTG response to contrast, hue, and saturation, and R/L FuG, R/L IOG, R/L pMTG, R  
302 aMTG and R AMY response to brightness.

303 As another test of the degree to which variations in visual properties modulated neural  
304 response, GLM analyses and then ANOVAs were repeated controlling for variations in visual  
305 properties, i.e., following removal of a single, visually most deviant block per condition, per  
306 run. To identify the visually most deviant block, we ranked all blocks within each condition  
307 and each run, giving the highest rank to the block which contributed the most to the visual  
308 difference across conditions. This ranking was done for all four visual properties across runs,

309 and ranks were summed. For each condition and each run, the block with the highest rank  
310 was identified as the visually most deviant one. After removal of these deviant blocks, visual  
311 properties did not differ for the remaining trials,  $ps>.05$ .

312 *Comparing conspecific- and face-preference.* To examine the extent to which  
313 visually-responsive voxels respond stronger to the conspecificity or to the faceness of stimuli,  
314 first, the proportion of voxels with greater sensitivity to conspecificity than to faceness and  
315 the proportion with greater sensitivity to faceness than to conspecificity was assessed, by  
316 calculating: (a) the number of voxels with larger positive beta values in the C>He contrast at  
317 the group level than in the F>O contrast and (b) the number of voxels with larger positive  
318 beta values in the F>O contrast at the group level than in the C>He contrast, respectively.  
319 Second, the proportion of these two sets of voxels was determined ( $a/(a+b)$ ).

320 To assess the likelihood of obtaining the observed proportions by chance, we first  
321 modelled the proportion with greater sensitivity to conspecificity than to faceness and the  
322 proportion with greater sensitivity to faceness than to conspecificity under a “no signal”  
323 condition, by randomly re-labelling each stimulus block. Second, we determined the number  
324 of conspecific-preferring and face-preferring voxels and third, we employed permutation  
325 testing with 10000 resamples.

326 To determine whether, across participants, there are sets of voxels exhibiting  
327 consistently greater conspecific-preference than face-preference (or vice versa), within the  
328 visually-responsive regions of each participant, a “response preference map” was created. A  
329 value of 1 was assigned to each voxel whose beta value of the C>He contrast was positive  
330 and greater than the beta value of the F>O contrast. A value of -1 was assigned to each voxel  
331 whose beta value of the F>O contrast was positive and greater than the beta value of the  
332 C>He contrast and a value of 0 was assigned to all other voxels. Then, the response  
333 preference map was compared to a mean of random permutations in one-sample  $t$ -tests (one-

334 tailed) at the group level, using SnPM. Thresholds for reporting for contrasts were  $p < .005$   
335 uncorrected and  $p < .05$  cluster-corrected for FWE for dogs and  $p < .0001$  uncorrected and  
336  $p < .001$  cluster-corrected for FWE for humans.

337 ***Multivariate pattern analysis.*** To assess which regions can accurately discriminate  
338 faces from occiputs (face-sensitivity, F vs. O) and conspecific from heterospecific stimuli  
339 (species-sensitivity, C vs. He) in each species, we performed multivariate pattern analyses  
340 (MVPA) on stimulus blocks using PyMVPA software package (Hanke, 2009) and the  
341 LibSVM's implementation of the linear support vector machine classifier (LSVM  
342 [www.csie.ntu.edu.tw/~cjlin/libsvm](http://www.csie.ntu.edu.tw/~cjlin/libsvm)). Final processing was done using custom-made  
343 MATLAB scripts. The events in the time series of each acquisition were convolved to the  
344 hemodynamic response function, then each acquisition was linearly detrended and z-scored.  
345 A two-way classification was performed, wherein a LSVM classifier was trained with the  
346 time series values corresponding to the two stimulus categories for each analysis (either F vs.  
347 O or C vs. He). Classifier performance in each participant was evaluated using a leave-one-  
348 out cross-validation scheme, that is, all but one acquisitions were used to train the classifier  
349 (train), and the classifier predicted the stimulus category in the remaining acquisition (test).  
350 This process was repeated so that each acquisition was 'test' once. Classifier performance  
351 was then calculated as the average number of correct classifications across participants and  
352 acquisitions.

353 We searched within the visually-responsive cortex using a searchlight approach  
354 (Kriegeskorte, Goebel, & Bandettini, 2006) and a spherical kernel: In each voxel within the  
355 visually responsive regions of each participant we created a sphere (radius=4 mm for dogs  
356 and 8 mm for humans), all the voxels contained within the sphere were used to train and test  
357 a LSVM classifier using a training and testing scheme identical to the one mentioned above.

358 The resulting classification accuracy was projected back to the center of the sphere. We  
359 repeated this process for every voxel, thus creating an accuracy map for each participant.

360 To determine if classifier performance was better than chance, random permutation  
361 testing (Stelzer, Chen, & Turner, 2013) was used. We calculated classifier performance that  
362 would be expected by chance for each voxel, by randomly re-labelling each stimulus block  
363 and repeating this process 10,000 times (to create a distribution of the possible values each  
364 voxel can have by chance) for dogs, and 1,000,000 times for humans. The probability of a  
365 given group mean classifier performance was then estimated, by comparing such  
366 performance to the performance that would be expected by chance. To test whether a region  
367 encoded information about a stimulus at the group level, we averaged the classification  
368 accuracy of each voxel across all participants. The resulting group map was then thresholded  
369 using permutation testing as described above ( $p < .001$  for dogs and  $p < .000001$  for humans).  
370 To estimate the probability of obtaining a cluster with a certain size, we used random  
371 permutation testing by repeating the same procedure. We then thresholded the obtained maps  
372 and calculated the number and size of clusters under chance conditions, and then used this  
373 distribution of cluster sizes to estimate the cluster size that would be expected by chance.  
374 Only clusters with sizes above threshold were retained ( $p < .05$  for dogs and  $p < .001$  for  
375 humans).

376 ***Representational similarity analysis.*** To assess if stimuli are represented similarly in  
377 GLM-derived human brain regions and the dog brain, across-species representational  
378 similarity analyses (RSA, see Kriegeskorte, Mur, & Bandettini, 2008, for a similar across-  
379 species comparison) were performed, in multiple steps.

380 First, we calculated a representational dissimilarity matrix (RDM) for all stimulus  
381 categories across all runs of each participant. RDMs represent how different the patterns of  
382 activity are, related to a pair of stimuli, in a given set of voxels. For humans, we obtained



383 RDMs for GLM-derived selected human peaks, creating a sphere (radius=8 mm) around each  
384 peak. For dogs, we obtained RDMs using a searchlight approach (Connolly et al., 2012) by  
385 creating a sphere (radius=4 mm) around each voxel in the visually-responsive cortex. (For  
386 completeness, we also report across-species representational similarities between the same  
387 human peaks and the whole dog brain in Figure 4-1) RDMs were calculated as the correlation  
388 distance (1 - Pearson correlation) of each stimulus type-run pair of the activity pattern of the  
389 set of voxels within the sphere. To reduce differences between low- and high-noise voxels  
390 with regard to their impact, a transformation equivalent to univariate noise normalization  
391 suggested by Walther et al. (2016) was implemented. Specifically, prior to calculation of  
392 RDMs, the data of each voxel were rescaled, using the *SD* of changes in its “activation”  
393 during baseline periods.

394         Second, we compared human RDMs to dog RDMs. Two ways of across-species  
395 matching of conditions were tested. (1) Direct matching: human representations of human  
396 stimuli were compared to dog representations of human stimuli, and human representations  
397 of dog stimuli were compared to dog representations of dog stimuli. (2) Functional matching:  
398 human representations of human stimuli were compared to dog representations of dog  
399 stimuli, and human representations of dog stimuli were compared to dog representations of  
400 human stimuli. Direct matching therefore referenced stimulus identity, while functional  
401 matching referenced con/heterospecificity. We calculated Pearson correlation coefficients  
402 between RDMs, repeated this procedure for each voxel, and projected back the result of the  
403 correlation to the center of the sphere, obtaining a similarity map. We repeated this procedure  
404 for all dog-human pairs and averaged the maps of each human. A one-tailed one sample *t*-test  
405 was run on each voxel at the group level ( $p<.001$ ) to test whether the values of the voxel  
406 differed from chance (calculated by taking random coordinates and performing the same  
407 procedure,  $n=1000$ ).

408 Third, in cases where suprathreshold representational similarity across species was  
409 observed (this happened only for Functional matching), to determine what is driving that  
410 similarity, follow-up pairwise comparisons were calculated in one sample *t*-tests, comparing  
411 observed mean  $\rho$  values to expected (by chance) mean  $\rho$  values. (To obtain mean  $\rho$  values,  
412 correlation coefficients were calculated for every stimulus pair for each human\*dog pair and  
413 then the means of these correlation coefficients for every stimulus pair were calculated for  
414 each participant. To obtain expected mean  $\rho$  values, the same procedure as for observed mean  
415  $\rho$ s was followed, except we randomly swapped condition labels, thereby obtained a chance  
416 mean  $\rho$ , repeated this 10,000 times and calculated their mean). Comparisons of stimulus pairs  
417 CF vs. CO (indicative of face-sensitivity for conspecifics), HeF vs. HeO (face-sensitivity for  
418 heterospecifics), HeF vs. CF (species-sensitivity for faces), HeO vs. CO (species-sensitivity  
419 for occiputs) were performed. To determine the magnitude of the obtained differences,  
420 Cohen's *D* values as indices of effect size were calculated for each pair compared.

#### 421 **Data Availability**

422 The datasets generated and/or analyzed during the current study are available from the  
423 corresponding author on reasonable request.

#### 424 **Results**

425 **GLM.** For GLM results for each main contrast (F>O, O>F, H>D, D>H) and  
426 interactions in dogs and humans, see Table 1 and Figure 1. For visual responsiveness results  
427 in dogs and humans, see Figure 2–1 and Figure 2–2.

428 In dogs, we found significant main effects only for the D>H contrast. Specifically, the  
429 bilateral mSSG responded more strongly to dog relative to human stimuli. Even with a more  
430 liberal,  $p<.005$  uncorrected voxel threshold, we obtained no face-preferring >3-voxel clusters,  
431  $ps(\text{cluster-corrected for FWE})>.991$  for 1-3-voxel clusters. In dogs, we found no interaction  
432 effects.

433 In humans, we found significant main effects for all four contrasts, with H>D regions  
434 essentially being a subset of F>O regions. Specifically, the bilateral fusiform gyrus (FuG) and  
435 inferior occipital gyrus (IOG), right posterior middle temporal gyrus (pMTG), right anterior  
436 middle temporal gyrus (aMTG) and right amygdala/hippocampus (AMY) responded more  
437 strongly to faces relative to occiputs. Both the right pMTG and the right AMY responded  
438 more strongly to human than to dog stimuli. In the left hemisphere, the middle occipital gyrus  
439 (MOG), precuneus (PCUN), and inferior parietal lobule (IPL) and in the right hemisphere a  
440 medial FuG region (mFuG) and the superior frontal gyrus (SFG) responded more strongly to  
441 occiputs than to faces; and the left superior occipital region spanning to the cuneus (SOG)  
442 and bilateral lateral occipitotemporal cortex (LOTC) showed stronger response to dog than to  
443 human stimuli. In humans, we also found interaction effects: in the right pMTG and aMTG,  
444 there was stronger face-preference for conspecifics than heterospecifics. Follow-up  
445 comparisons indicated that response was greatest to human faces relative to all other stimuli  
446 (pMTG  $ps < .007$ , aMTG  $ps < .001$ ), with no response difference among the other three  
447 conditions (pMTG  $ps > .877$ , aMTG  $ps > .993$ ). This reveals conspecific face-sensitivity in the  
448 right pMTG and aMTG. In the bilateral FuG/MOG, response was weaker to human faces  
449 than to either dog faces (L  $p = .012$ , R  $p = .071$ ) or human occiputs (L  $p = .033$ , R  $p = .094$ ), with  
450 no difference among other conditions (L  $ps > .129$ , R  $ps > .500$ ).

451 Activity response profiles for selected GLM-derived regions in dogs and humans are  
452 shown in Figures 1A-B.

453 Further characterizing these regions, in dogs, for mSSG, neither the side main effect,  
454 nor any of the two- or three-way interactions were significant (all  $ps > .164$ ). In humans, for  
455 IOG, the main effect of side was significant,  $F(1, 239) = 20.286$ ,  $p < .001$  (left > right), and so  
456 was the interaction effect between face and species on IOG response,  $F(1, 239) = 8.530$ ,  
457  $p = .004$ , with greatest IOG response to dog faces. For FuG, neither the main effect of side, nor

458 any of the two- or three-way interactions were significant (all  $p$ s>.092). For pMTG, the main  
459 effect of side was significant,  $F(1, 239)=66.947$ ,  $p<.001$  (right>left). Interactions between  
460 face and species,  $F(1, 239)=6.396$ ,  $p=.012$  and face and side,  $F(1, 239)=4.073$ ,  $p=.045$  were  
461 also significant. In case of the face by species interaction, greatest pMTG response was to  
462 human faces. In case of the face by side interaction, greatest pMTG response was to faces in  
463 the right hemisphere. For right AMY and right aMTG, the face by species interactions were  
464 not significant ( $p=.079$  and  $.053$ , respectively).

465 *Control tests for low-level visual property effects.* 2(F, O)x2(H, D) ANOVAs  
466 indicated a visual difference for four properties: for F>O, there was a difference in brightness  
467  $F(1, 144)=6.187$ ,  $p=.014$ ; but not hue, contrast, or saturation (all  $p$ s>.404). For H>D, there  
468 was a difference in contrast,  $F(1, 144)=8.334$ ,  $p=.004$ ; hue,  $F(1, 144)=4.007$ ,  $p=.047$ ; and  
469 saturation,  $F(1, 144)=7.252$ ,  $p=.008$ . There was no difference in motion (both  $p$ s>.353).

470 One-sample  $t$ -tests indicated three cases with visual effects, all for humans: brightness  
471 contributed with a negative parametric modulatory effect to the right IOG response,  $t(29)=-$   
472  $3.588$ ,  $p=.001$  (faces had greater brightness than occiputs), contrast contributed with a  
473 positive parametric modulatory effect to the right pMTG response,  $t(29)=3.453$ ,  $p=.001$   
474 (human stimuli had greater contrast than dog stimuli), and brightness contributed with a  
475 positive parametric modulatory effect to the right pMTG response,  $t(29)=3.301$ ,  $p=.002$  (face  
476 stimuli had greater brightness than occiput stimuli) (see Table 1–2).

477 When GLM analyses and then ANOVAs were repeated following removal of a single,  
478 visually most deviant block per condition, there were no changes in face or species main  
479 effects in any of the selected regions: all previously significant effects remained significant  
480 and no nonsignificant face or species main effect emerged as significant (see Table 1–3).

481 *Comparing conspecific- and face-preference.* Analyses of the extent to which  
482 visually-responsive voxels respond stronger to the conspecificity or to the faceness of stimuli

483 indicated that in dogs, 94.6% of the visually-responsive cortex showed greater preference for  
484 conspecificity than for faces (likelihood of obtaining the observed proportions by chance,  
485 using permutation testing:  $p < .01$ ). In humans, 10.8% of the visually-responsive cortex  
486 showed this pattern ( $p < .05$ ). Consequently, 5.4% of dog and 89.2% of human visually-  
487 responsive cortex showed greater preference for faces than for conspecificity (see Figure 2).

488 Non-parametric group analyses of the subject-level binary response preference maps  
489 (see Figure 2–2) showed that, in dogs, the bilateral mSSG and a splenial gyrus (SpG) cluster  
490 exhibited greater conspecific- than face-preference, and these clusters were overlapping with  
491 those responding stronger to dog relative to human stimuli. In humans, the opposite pattern  
492 emerged: a bilateral IOG cluster and a right inferior temporal gyrus (ITG) cluster exhibited  
493 greater face- than conspecific-preference, and these clusters were overlapping with those  
494 responding stronger to face than to occiput stimuli.

495 **Multivariate pattern analysis.** We found two clusters in dogs for the C vs. He  
496 comparison, one in the left mSSG, with group mean classifier accuracy  $M = .642$ ,  $SD = .124$   
497 and one in the right caudal suprasylvian gyrus (cSSG),  $M = .629$ ,  $SD = .136$ . No clusters were  
498 revealed in dogs for the F vs. O comparison. In humans, a cluster was revealed for the C vs.  
499 He comparison, in the right pMTG,  $M = .675$ ,  $SD = .163$ . Four clusters were revealed for the F  
500 vs. O comparison: a large cluster including parts of the right FuG, IOG, MOG and MTG,  
501  $M = .761$ ,  $SD = .180$ , a large cluster including parts of the left FuG, IOG, MOG and MTG,  
502  $M = .797$ ,  $SD = .148$ , the right inferior frontal gyrus (IFG),  $M = .672$ ,  $SD = .152$ , and a left MOG  
503 cluster,  $M = .667$ ,  $SD = .112$ . All results were cluster corrected for FWE  $p < .05$  for dogs and  
504  $p < .001$  for humans (Figure 3; for the full list of peaks and subpeaks see Figure 3–1).

505 **Representational similarity analysis.** Across-species RSA using the direct matching  
506 model indicated no visually-responsive dog regions that represented stimuli similarly to the  
507 GLM-derived human regions. Across-species RSA using the functional matching model

508 showed that the canine left mid ectosylvian gyrus (mESG),  $t(29)=4.994$ , right ectomarginal  
509 gyrus (EMG),  $t(29)=4.882$ , left cSSG,  $t(29)=4.732$  and right and left mSSG,  $t(29)=[6.378$  and  
510  $4.997]$  represented stimuli similarly to the human right AMY ( $p<.001$ ), and the canine left  
511 rESG,  $t(29)=4.383$ , right MG,  $t(29)=4.741$  and right mSSG,  $t(29)=4.632$  represented stimuli  
512 similarly to the human right FuG ( $p<.001$ ) (see Figure 4). Follow-up pairwise comparisons  
513 indicated that a medium species effect for faces (i.e., HeF-CF) drove the representational  
514 similarity effect between the dog left ( $D=.657$ ) and right mSSG ( $D=.581$ ), left mESG  
515 ( $D=.640$ ), and right EMG ( $D=.641$ ) and the human right AMY; a medium species effect for  
516 faces in case of the representational similarity between the dog right MG ( $D=.656$ ) and the  
517 human right FuG; and a medium faceness effect for heterospecifics (i.e., HeF-HeO) in case of  
518 the representational similarity between the dog right mSSG ( $D=.580$ ) and the human right  
519 FuG. All across-species RSA results are summarized in Figure 4–1, Figure 4–2, and Figure  
520 4–3.

521 *Individual difference-focused analyses.* To determine if lack of support for face-  
522 sensitivity in dogs generalizes across the 20 dogs tested, we assessed for face-preference in  
523 each dog, by testing whether there is suprathreshold F>O or DF>DO sensitivity in any  
524 individual. Using a  $p<.001$  uncorrected voxel threshold on individual contrast maps, we  
525 found that no dogs had a meaningful number of suprathreshold face-preferring voxels (3 dogs  
526 had such F>O voxels,  $M_{nr\ of\ voxels}=1.33$ , range 1-2; 2 dogs had such DF>DO voxels,  $M_{nr\ of\ voxels}=2.5$ , range 2-3). In comparison, similarly thresholded individual D>H contrast maps  
527 yielded sizeable clusters in many dogs (10 dogs had such voxels,  $M_{nr\ of\ voxels}=61$ , range 1-  
528 227).

530 To assess for any effects that relevant dog individual difference variables may have  
531 had on our results, experience and breeding variables (see Table 1–4 for details) were entered  
532 into GLM analyses as covariates to assess their effects on HF-preference (quantified in the

533 HF>HO and HF>DF contrasts) in the visually-responsive cortex of dogs. To index  
534 “experience”, the type of training each dog received was considered, quantifying the degree  
535 to which such training was face-oriented (involved/ necessitated attending to human faces) on  
536 a four-point scale. To index “breeding”, a brain-based cephalic index was calculated for each  
537 dog. Not only is a brain-based cephalic index appropriate to quantify the effects of breeding  
538 on the architecture of the dog brain (Hecht et al., 2019), it is also relevant with regard to  
539 attraction to human faces in dogs (Bognár, Iotchev, & Kubinyi, 2018). Findings indicated  
540 neither individual difference variable covaried with HF-preference, neither at a more standard  
541 ( $p<.001$ ), nor at a more liberal voxel threshold ( $p<.01$ ),  $p<.05$  cluster-corrected for FWE.

542 To assess for any effects that relevant human individual difference variables may have  
543 had on our results, self-reported dog ownership (as a proxy for expertise), was entered into  
544 GLM analyses as a covariate. We assessed the covariate effect on D>H, DF>HF and DF>DO  
545 responses – interest was in whether individuals who owned a dog would show greater  
546 responses to dog stimuli overall, or to dog face stimuli specifically, compared to those who  
547 did not own a dog – in the visually responsive cortex of humans. Results indicated that  
548 expertise covaried with D>H response in the right lingual gyrus (LiG) (an 11-voxel-large  
549 cluster, peak at 8,-80,-8) (thresholded at  $p<.000001$  uncorrected and  $p<.001$  cluster-corrected  
550 for FWE). This pattern was driven by a difference in dog owners ( $n=11$ ), who showed greater  
551 right LiG response to dog ( $M=3.212$ ,  $SD=1.628$ ) than human stimuli ( $M=3.212$ ,  $SD=1.628$ ),  
552  $t(10)=6.934$ ,  $p<.001$ . In non-owners ( $n=19$ ), R LiG response was not affected by species,  
553  $t(18)=1.459$ ,  $p=.162$ . Expertise did not covary with DF>HF or DF>DO response.

554

### Discussion

555 Univariate and multivariate pattern analyses identified species-sensitive visual regions in both  
556 human and dog brains, but face-sensitive regions in humans only. Our findings also  
557 demonstrate that the relative roles of conspecific- and face-preference in visuo-social

558 perception differ between humans and dogs. In humans, all conspecific-preferring regions  
559 were face-preferring whereas in dogs none of the conspecific-preferring regions exhibited  
560 face-preference. Direct comparisons of conspecific- and face-preference in the visually-  
561 responsive cortex confirmed this difference in the relative roles of processing preferences  
562 across species. In humans, only regions exhibiting greater face- than conspecific-preference  
563 were identified. In contrast, in dogs, only regions exhibiting greater conspecific- than face-  
564 preference were identified. These results imply that, unlike in humans, face-preference is not  
565 primary to conspecific-preference in the dog visually-responsive cortex.

#### 566 **Face-preference**

567 Regarding face-preference, in humans, the cortical regions that showed stronger response to  
568 faces relative to occiputs corresponded to key structures of the face network (Duchaine &  
569 Yovel, 2015). In contrast, in dogs, no cortical regions preferred faces to occiputs.  
570 Accordingly, although neural face-sensitivity appears general across primates, it may not be a  
571 general organizing principle of visuo-social perception across mammals. Neural face-  
572 sensitivity does not appear to be such an organizing principle in dogs, who, e.g., for  
573 assessment of attentional or motivational state, rely less on information in faces and more on  
574 information in larger bodily units (Emery, 2000). Related, in dogs, there is no evidence that  
575 for kin recognition or mate selection facial cues would be more important than non-facial  
576 bodily cues, acoustic or chemical signals (Leopold & Rhodes, 2010). However, behaviorally,  
577 dogs are attracted to faces (Adachi, Kuwahata, & Fujita, 2007; Gácsi, Miklósi, Varga, Topál,  
578 & Csányi, 2004) and can differentiate dog from human faces (Racca et al., 2010), though this  
579 ability is limited: even after training, only a minority (20%) can discriminate their owner's  
580 and a stranger's face in the absence of head-contour (but with eyes, mouth, and nose clearly  
581 visible) (Huber et al., 2013). All current and prior data considered, we propose that our  
582 results are reconcilable with earlier neuroimaging findings that indicated face-preferring dog



583 brain regions based on faces vs. objects (Cuaya et al., 2016; Dilks et al., 2015) and human  
584 faces vs. dog faces (Dilks et al., 2015; Thompkins et al., 2018) comparisons. As further  
585 support for reconcilability of current and these past findings, none of the earlier studies  
586 involved examination of face-preference, controlling for animate-inanimate and conspecific-  
587 heterospecific confounds. Of note, consistent with the current results, no face-preference was  
588 observed in earlier studies to faces vs. scrambled faces comparisons (Dilks et al., 2015; Szabó  
589 et al., 2020). In these prior studies, however, pertinent comparisons were not of *dog* faces vs.  
590 *scrambled dog* faces (Dilks et al., 2015 report data for dog and human faces pooled together;  
591 and Szabó et al., 2020 for human faces only). Accordingly, although the corresponding  
592 findings may be indicative of lack of face-preference in dogs, those may also reflect  
593 limitations of chosen experimental stimuli. Contrasts involving conspecific stimuli, rather  
594 than human stimuli, may be more sensitive to probe face-sensitivity in dogs. Nevertheless, in  
595 further support of our conclusion, we observe neither any clusters with greater response to  
596 DF>DO (see Table 1–1), nor a meaningful number of suprathreshold face-preferring (F>O or  
597 DF>DO) voxels in any individual dog.

598         It is important to note that our negative findings are not conclusive evidence against  
599 dog face areas. It is possible that our measurement settings may have not been sufficiently  
600 sensitive. However, the (1) relatively high number of dogs tested (compared to prior  
601 neuroimaging studies), (2) consistency between the herein and earlier identified (Dilks et al.,  
602 2015) dog visually-responsive areas, (3) clear positive effects for the D vs. H contrast in  
603 dogs, (4) clear F vs. O effects for the same stimuli in humans, and (5) consistency of our  
604 univariate (macromap-level) and MVPA (micromap-level) (Dehaene & Cohen, 2007)  
605 findings – in combination – make the measurement insensitivity explanation unlikely.  
606 Instead, across-study differences in findings of face-preference may reflect differences in  
607 control conditions, underscoring the importance of re-assessing earlier claims of dog face

608 areas using stricter controls. It is further possible that the lack of observed face-preferring  
609 regions in dogs can be partly explained by power issues, i.e., it may have been a result of our  
610 “strict” threshold that we did not detect a weak face-preference effect in our (lower-than-  
611 human quality) dog data. However, that we found strong conspecific effects in dogs suggests  
612 otherwise. Also, that at the group level, even a lower threshold did not indicate a face-  
613 preference effect, and at the individual level, no dogs had a meaningful number of face-  
614 preferring voxels make this improbable.

### 615 **Conspecific-preference**

616 Findings of conspecific-preferring regions in the visually-responsive cortex of humans and  
617 dogs support the hypothesis that, similarly to the auditory modality (Andics et al., 2014;  
618 Petkov et al., 2008), neural conspecific-preference is present in phylogenetically distant  
619 mammal species in the visual modality. In dogs, we identified a robust conspecific-preferring  
620 cluster in the bilateral mSSG; a visual association area at the parieto-temporo-occipital  
621 junction (Kowalska, 2000). The involvement of the mSSG in visuo-social perception is  
622 consistent with corresponding regions having been broadly implicated in visual processing in  
623 cats (e.g., Dow & Dubner, 1971; Yin & Greenwood, 1992) and marmosets (Hupfeld, Distler,  
624 & Hoffmann, 2007), with homologies across the cat suprasylvian sulcus and the macaque V5  
625 (involved in early visual processing) (Payne, 1993) and the cat mSSG and monkey inferior  
626 parietal lobe (IPL; involved in directing visual attention) (Krüger, Kiefer, Groh, Dinse, & von  
627 Seelen, 1993). In humans, only face-preferring regions (specifically, the pMTG, the aMTG  
628 (for faces) and the AMY) showed conspecific-preference. This corroborates previous  
629 findings of the AMY being conspecific-preferring (Blonder et al., 2004). Within the face  
630 network, both AMY and pMTG are thought to be involved in emotional cue processing  
631 (Duchaine & Yovel, 2015) – our findings may thus reflect a greater relevance of  
632 conspecificity in emotional than in structural information processing for faces in humans.

633 Regarding the right aMTG, our findings are consistent with earlier results indicating this  
634 region is involved in dynamic human face processing (Duchaine & Yovel, 2015) and suggest  
635 that, similarly to ventral subregions of the face-sensitive anterior temporal lobe (Collins &  
636 Olson, 2014), this dorsal face area prefers conspecific face stimuli.

637         Conspecific-preference, as observed here in the dog parieto-temporo-occipital  
638 junction, a region purportedly involved in structural processing, may be of a different nature  
639 than face-preference, as observed in the human occipito-temporal cortex. The hypothesized  
640 underlying neural mechanism behind face-preference in the human visual cortex is category  
641 selectivity (Kanwisher, 2017; Op de Beeck, Pillot, & Ritchie, 2019). Conspecific-preference,  
642 however, may also be explainable by sensitivity to motivational relevance, a mechanism that  
643 in humans modulates visual cognition through attention (Summerfield & Egner, 2009), and  
644 not category-selectivity. In support, in humans, we observed conspecific-preference only in  
645 (face-preferring) regions involved in emotional cue processing (Duchaine & Yovel, 2015) but  
646 not in (face-preferring) regions involved in structural processing. Additionally, fine-grained,  
647 feature-based category-selectivity in visual processing may be better developed in species  
648 with greater visual acuity, such as primates (Leopold & Rhodes, 2010), but less so in species  
649 with poorer visual acuity, such as dogs (Odom, Bromberg, & Dawson, 1983; Pongrácz,  
650 Ujvári, Faragó, Miklósi, & Péter, 2017). In the absence of empirical data, it remains an open  
651 question whether conspecific-preference is driven by category-selectivity or motivational  
652 relevance in the dog visual cortex.

### 653 **Neural mechanisms controlling processing preferences**

654 Processing preferences for natural stimulus classes may not necessarily reflect functional  
655 distinctions. Rather, such differences may be explained by sensitivity to visual similarity  
656 (Kriegeskorte, Mur, & Bandettini, 2008). In our findings, differences in processing  
657 preferences being driven by functional distinctions are supported by results of two analyses.

658 First, all species and face main effects were unchanged when controlling for differences in  
659 low-level visual properties across conditions. Second, it was only in the functional matching  
660 RSA model (i.e., when representation of dog stimuli in dogs was matched with representation  
661 of human stimuli in humans and vice versa), but not in the direct matching RSA model (i.e.,  
662 when representation of dog stimuli in dogs was matched with representation of dog stimuli in  
663 humans and vice versa) that we identified dog regions with a response pattern comparable to  
664 any human face- or conspecific-preferring region's response pattern. Specifically, visually-  
665 responsive dog regions, involving the mSSG, showed representational similarity to the  
666 human FuG and AMY in the functional matching model. Arguably, this functional matching  
667 model advantage indicates that response pattern similarities reference a relative,  
668 motivationally relevant distinction between conspecific and heterospecific stimuli to the  
669 perceiver, rather than absolute visual differences between dog and human stimuli. Of note,  
670 representational similarities across species were primarily driven by species distinctions for  
671 faces. Accordingly, visual conspecific-preference for faces may involve functionally  
672 analogue neural response patterns in dogs and humans.

### 673 **Effects of individual differences in dogs and humans**

674 In dogs, we found no evidence to indicate that individual differences in experience  
675 with human faces or breeding-related structural properties systematically affect brain  
676 response to human faces. Of note, our sample was relatively homogeneous in these aspects;  
677 all 20 dogs were highly trained (similar to in [Dilks et al., 2015]) family dogs, regularly  
678 exposed to human faces (as such, any experience-related bias in this sample would have been  
679 in the direction of increased likelihood of human face-sensitivity). Further, most dogs  
680 represented modern, cooperative breed types. Thus, although generalizing our findings across  
681 all domestic dogs in absence of a more heterogeneous sample may be inappropriate, there is  
682 no reason to assume that dogs with less experience or dogs representing basal or non-

683 cooperative breed types would show greater neural human face-sensitivity. Finally, even  
684 though brain shape varied across the sample, all dogs were mesocephalic (medium-headed).  
685 Given a potential association between differences in cephalic index (Hecht et al., 2019) and  
686 readiness to attend to faces (Bognár et al., 2018), additional research with brachycephalic  
687 (short-headed) dogs may be informative.

688 In humans, regarding individual differences in experience findings are both consistent  
689 with and extend prior findings, in indicating that participants who owned a dog, unlike those  
690 who did not, exhibited greater right LiG response to dog than to human stimuli. It has been  
691 argued that real-world expertise shapes human behavior and neural processing (Harel,  
692 Kravitz, & Baker, 2013). Neural evidence suggests that experts exhibit greater brain response  
693 to objects of expertise than to other objects throughout (and outside of) the visual cortex  
694 (Harel et al., 2013), including the FFA (Gauthier, Skudlarski, Gore, & Anderson, 2000; Xu,  
695 2005), collateral sulcus/LiG, precuneus, and STS (Harel, Gilaie-Dotan, Malach, & Bentin,  
696 2010; McGugin, Gatenby, Gore, & Gauthier, 2012). Dog ownership can be conceptualized as  
697 real-world expertise. Relevant behavioral evidence indicates that dog experts (i.e., dog show  
698 judges) have enhanced recognition of individual dogs (only) of the specific breeds with  
699 which they are familiar (Diamond & Carey, 1986; Robbins & McKone, 2007). We suggest  
700 that the activity pattern we found in the right LiG is thus consistent with an account of  
701 expertise-based individual differences in human visual processing. Notably, we found no  
702 such expertise effects in any other brain regions.

703 **Potential mechanisms for greater response to heterospecific and occiput stimuli in**  
704 **humans**

705 In humans, greater response to heterospecific than conspecific stimuli was observed in the  
706 (also face-preferring) IOG/LOC; a left superior occipital region (SOG); and in bilateral lateral  
707 occipitotemporal cortex (LOTC). Finally, in a large bilateral cluster including parts of FuG,

708 IOG, MOG and SOG, response was weaker to human than to dog faces (or human occiputs).  
709 Greater response to occiput than face stimuli was also observed mainly in regions associated  
710 with visual functions, i.e., the left MOG, the PCUN, the left IPL and the right mFuG; and  
711 also in the right SFG. There are a handful of accounts – albeit related, presuming different  
712 mechanisms – that may explain observed greater response to heterospecific and occiput  
713 stimuli. Which, if any of these accounts best explains these results, cannot be determined in  
714 the absence of further control conditions and the current study was not designed to do so.

715 *First*, increased processing demands (e.g., due to addition of phase noise to face  
716 stimuli) are associated with greater bilateral LOC (Bankó, Gál, Körtvélyes, Kovács, &  
717 Vidnyánszky, 2011) and bilateral MOG (Hermann, Bankó, Gál, & Vidnyánszky, 2015)  
718 response and processing heterospecific and occiput stimuli may be more effortful. *Second*,  
719 norm-based processing involves evaluation of degree to which a stimulus differs from a  
720 prototype (Rhodes et al., 2005). Face stimuli further from the prototype generate stronger  
721 neural responses in face-sensitive brain regions in humans (Loffler, Yourganov, Wilkinson,  
722 & Wilson, 2005; Tsao & Livingstone, 2008) and monkeys (Leopold, Bondar, Giese, &  
723 Logothetis, 2006). Conspecific (face) stimuli may better match a potentially referenced  
724 (face) prototype. *Third*, findings may be explainable by a novelty effect; others found  
725 greater response to novel relative to familiar stimuli in the IOG (Geiger et al., 2018; Kiehl,  
726 Laurens, Duty, Forster, & Liddle, 2001; Manahova, Mostert, Kok, Schoffelen, & de Lange,  
727 2018; Ousdal, Andreassen, Server, & Jensen, 2014) and heterospecific and occiput stimuli  
728 are arguably less familiar than conspecific and face stimuli. *Fourth*, others observed greater  
729 response in the SOG to dog barking/ monkey lipsmacking than human lipreading (Buccino  
730 et al., 2004) and the LOTC to human bodies/ body parts than human faces (Lingnau &  
731 Downing, 2015). Representations of the human body may extend to animals (Konkle &  
732 Caramazza, 2013), although such animal/body category-sensitive regions are small.

**733 Lateralization**

734 Regarding lateralization, human temporal and limbic structures implicated here showed  
735 greater involvement of the right hemisphere. In both the pMTG and the AMY, both  
736 conspecific-preference and face-preference were observed only on the right side. In the  
737 pMTG, direct hemispheric comparisons confirmed a right bias in face-preference. In the  
738 aMTG, face-preference was observed only in the right hemisphere. These findings of right  
739 hemispheric dominance are consistent with prior behavioral and neural studies on face  
740 perception (Duchaine & Yovel, 2015). Of note, the human ventral face-selective areas  
741 exhibited no clear right-hemisphere dominance of face-preference in the present study. This  
742 may be explained by our use of occiputs as comparison stimuli. Although traditionally  
743 reported core- and extended face network regions were identified by our face vs. occiput  
744 contrast, a different response pattern from that for e.g., faces vs. objects (as was done in  
745 studies indicating lateralization in the human FFA) (Kanwisher, McDermott, & Chun, 1997;  
746 Kanwisher & Yovel, 2006) may have been elicited by it. This finding may also be explained  
747 by our relatively more coarse and macro-level design, experimental manipulations, and peak  
748 selection (Rossion, 2014). Finally, visual association areas revealed by our contrasts in dogs  
749 exhibited no lateralization in conspecific-preference. This is consistent with earlier findings  
750 on human and dog auditory conspecificity processing in auditory association areas (Andics et  
751 al., 2014).

**752 Summary**

753 The research presented here constitutes the first directly comparative, noninvasive visual  
754 neuroimaging study of a non-primate and a primate species. We presented neuroimaging  
755 evidence for visual species-sensitivity in both dogs and humans and showed that in  
756 dogs, conspecific-preference is primary over face-preference whereas in humans, face-  
757 preference is primary over conspecific-preference. Further, we identified dog and human

758 brain regions with a similar representational pattern for processing visuo-social stimuli, and  
759 this similarity effect was mainly driven by species distinctions based on faces. Together,  
760 these results indicate functional analogies in dog and human visuo-social processing of  
761 conspecificity, but suggest that cortical specialization for face perception may not be  
762 ubiquitous across mammals.



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Table 1

*Main GLM results for dogs and humans.*

	Brain region	cluster size (voxels)	peak T	coordinates (x, y, z)
Dogs				
<u>D&gt;H</u>	<b>R mSSG<sup>a</sup></b>	347	6.600	<b>14, -32, 22</b>
	<b>L mSSG<sup>a</sup></b>		4.964	<b>-16, -22, 20</b>
Humans – Main Effects				
<u>F&gt;O</u>	<b>R aMTG</b>	180	10.318	<b>48, -12, -14</b>
	<b>R IOG</b>	398	10.262	<b>28, -92, -2</b>
	<b>L IOG</b>	410	9.932	<b>-38, -82, -10</b>
	<b>R pMTG</b>	307	9.407	<b>52, -50, 10</b>
	<b>L FuG</b>	230	8.984	<b>-42, -54, -22</b>
	<b>R FuG</b>	235	8.952	<b>42, -46, -20</b>
	<b>R AMY</b>	56	8.260	<b>22, -6, -12</b>
	<b>L pMTG<sup>b</sup></b>	51	7.520	<b>-50, -46, 12</b>
<u>O&gt;F</u>	L IPL	122	8.279	-54, -30, 42
	L MOG	65	7.942	-28, -78, 42
	R SFG	44	7.595	22, 10, 58
	R mFuG	83	6.914	30, -52, -2
	L PCUN	81	6.824	-10, -68, 56
<u>H&gt;D</u>	R pMTG	197	8.110	50, -40, 6
	R AMY	77	7.745	18, -12, -16
<u>D&gt;H</u>	L LOTC	251	8.537	-52, -68, -4
	R LOTC	204	7.817	44, -62, 2
	L SOG	47	7.755	-8, -92, 24
Humans – Interaction Effects				
HF-DF>HO-DO	R pMTG	210	8.508	52, -44, 16
	R aMTG	33	7.691	56, -8, -14
DF-HF>DO-HO	L FuG/MOG	2562	12.093	-32, -86, 14
	R FuG/MOG	2045	9.741	24, -70, -16

*Note.* Threshold for reporting for all higher-level contrasts was  $p < .000001$  and cluster  $p < .001$  for FWE for humans and  $p < .001$  and cluster  $p < .05$  for FWE for dogs. All peaks  $\geq 16$  mm apart are reported.

<sup>a</sup> At  $p < .001$  these two peaks result from D>H as a single cluster's two main peaks. When checked with a stricter  $p < .0005$  threshold, a left and a right, cluster-corrected significant cluster are obtained, with the same peaks. Thus, in dogs, the main and the subpeak are reported but in humans, in the absence of *single* bilateral clusters, subpeaks are not reported. <sup>b</sup> Region identified based on HF>HO.

L=left; R=right; mSSG=mid suprasylvian gyrus; aMTG=anterior middle temporal gyrus; IOG=inferior occipital gyrus; pMTG=posterior middle temporal gyrus; FuG=fusiform gyrus; AMY=amygdala/hippocampus; IPL=inferior parietal lobule; MOG=middle occipital gyrus; SFG=superior frontal gyrus; medial fusiform gyrus=mFuG; PCUN=precuneus; LOTC=lateral occipitotemporal cortex; SOG=superior occipital gyrus/cuneus; FuG/MOG=a cluster including parts of FuG, IOG, MOG and SOG. Selected conspecific-preferring and face-sensitive regions are in **bold**.

See also Table 1–1, Table 1–2, Table 1–3, and Table 1–4.

### Figure legends

**Figure 1. GLM results in dogs ( $n=20$ ) and humans ( $n=30$ ).** **A.** Dog contrast maps superimposed on a template brain (Czeibert et al., 2019). Threshold was  $p<.001$  uncorrected and  $p<.05$  cluster-corrected for FWE. None of the other main or interaction contrasts yielded significant effects. The bar graph represents parameter estimates (beta weights) in select GLM-derived peaks (sphere radius=4 mm) to each condition; error bars represent SE. **B-C.** Human contrast maps (main and interaction effects) superimposed on a template brain. Threshold was  $p<.000001$  uncorrected and  $p<.001$  cluster-corrected for FWE. **B.** Conspecific>heterospecific, face>occiput, and their interaction. The bar graphs represent parameter estimates (beta weights) in select GLM-derived peaks (sphere radius=8 mm) to each condition; error bars represent SE. **C.** Heterospecific>conspecific, occiput>face, and their interaction. D=dog; H=human; F=face; O=occiput; L=left; R=right; mSSG=mid suprasylvian gyrus; AMY=amygdala/hippocampus; aMTG=anterior middle temporal gyrus; FuG=fusiform gyrus; FuG/MOG=a cluster including parts of FuG, IOG, MOG and SOG; IOG=inferior occipital gyrus; IPL=inferior parietal lobule; LOTC=lateral occipitotemporal cortex; mFuG=medial fusiform gyrus; MOG=middle occipital gyrus; PCUN=precuneus; pMTG=posterior middle temporal gyrus; SFG=superior frontal gyrus; SOG=superior occipital gyrus, extending to cuneus.

**Figure 2. Visually-responsive regions and processing preference differences in dogs and humans.** **A.** Visually-responsive regions (color coded with warm) as determined by the contrast of experimental conditions versus fixation baseline in the dog brain (left), thresholded at  $p<.001$  uncorrected and  $p<.05$  cluster-corrected for FWE and in the human brain (right), thresholded at  $p<.000001$  uncorrected and  $p<.001$  cluster-corrected for FWE. **B.** Group-level binary map of stronger conspecific- than face-preference (red) and stronger face- than conspecific-preference (blue) in visually-responsive regions. See Results for corresponding permutation statistics comparing the proportions of voxels with either preference and on random effects analyses of individual binary preference maps. See also Figure 2–1 and Figure 2–2.

**Figure 3. Multivariate pattern analysis using searchlight.** **A.** Brain regions within the visually-responsive cortex of dogs and humans that discriminate conspecific from heterospecific (red) and face from occiput (blue) stimuli. The mean classifier accuracy significance level ( $p$ ) on each voxel was calculated using permutation testing (see Methods)  $p<.001$  uncorrected and  $p<.05$  cluster-corrected for FWE for dogs and  $p<.000001$  uncorrected and  $p<.001$  cluster corrected for FWE for humans, the searchlight used a spherical kernel with a radius of 4 mm for dogs and 8 mm for humans. **B.** Histograms depicting classification accuracy across participants for each cluster peak. L=left; R=right; cSSG=caudal ectosylvian gyrus; mSSG=mid suprasylvian gyrus; FuG=fusiform gyrus; IFG=inferior frontal gyrus; IOG=inferior occipital gyrus; ITG=inferior temporal gyrus; MOG=middle occipital gyrus; pMTG=posterior middle temporal gyrus. See also Figure 3–1.

**Figure 4. Across-species representational similarity analyses.** **A.** Representational dissimilarity matrices (RDM) between select GLM-derived human peaks (first column, sphere radius=8 mm) and matching dog brain peaks (second column, sphere radius=4 mm) using a searchlight approach (one sample  $t$ -test,  $p<.001$  uncorrected and  $p<.05$  cluster corrected for FWE), in visually-responsive regions. All RDMs are represented as percentile of Pearson distance ( $1 - \text{Pearson correlation}$ ). **B.** Observed effect sizes (Cohen's  $D$ ) for the

across-species matching of RDMs for each peak-pair (first column), and modelled effect size patterns reflecting potential driving forces underlying across-species matching (second column), see also Figure 4–3. C=conspecific; He=heterospecific; F=face; O=occiput; L=left; R=right; AMY=amygdala/hippocampus; FuG=fusiform gyrus; cSSG=caudal suprasylvian gyrus; EMG=ectomarginal gyrus; mESG=mid ectosylvian gyrus; MG=marginal gyrus; mSSG=mid suprasylvian gyrus; rESG=rostral ectosylvian gyrus.

See also Figure 4–1, Figure 4–2, Figure 4–3.

#### **Video legends**

**Movie 1. fMRI stimuli.** Video shows sample dynamic images, presented in color and dynamically for 2 s, representing each of four conditions human face, human occiput, dog face, and dog occiput. *Note.* Stimulus design was identical for dogs and humans.











