Neural bases of face and body perception in dogs and humans

# 1 Similarities and differences of face and body perception in

# 2 the dog (*Canis familiaris*) and human brain

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## 16 Abstract

17 Accurately recognizing other individuals is fundamental for successful social 18 interactions. While the neural underpinnings of this skill have been studied 19 extensively in humans, less is known about the evolutionary origins of the brain areas 20 specialized for recognising faces or bodies. Studying dogs (Canis familiaris), a non-21 primate species with the ability to perceive faces and bodies similarly to humans, 22 promises insights into how visuo-social perception has evolved in mammals. We 23 investigated the neural correlates of face and body perception in dogs (N = 15) and 24 humans (N = 40) using functional MRI. Combining uni- and multivariate analysis 25 approaches, we identified activation levels and patterns that suggested potentially 26 homologous occipito-temporal brain regions in both species responding to faces and 27 bodies compared to inanimate objects. Crucially, only human brain regions showed 28 activation differences between faces and bodies and partly responded more strongly 29 to humans compared to dogs. Moreover, only dogs represented both faces and dog 30 bodies in olfactory regions. Overall, our novel findings revealed a prominent role of 31 the occipito-temporal cortex in the perception of animate entities in dogs and humans 32 but suggest a divergent evolution of face and body perception. This may reflect 33 differences in the perceptual systems these species rely on to recognize others.

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# 34 **1** Introduction

The ability to detect and recognize another individual is a socio-cognitive skill crucial for successful social interactions and survival. The face and body of another human or non-human animal convey a wealth of social information beyond their identity, such as when facilitating the correct categorization of another individual's emotional state [1–7]. Consequently, accurate perception of faces and bodies is an important building block for social perception.

41 Therefore, the neural underpinnings of face and body perception have been 42 studied extensively in humans. Decades of research revealed a predominant role of 43 the occipito-temporal cortex for the perception of others with distinct, but adjacent 44 regions specialized for face and body perception as part of the so-called ventral 45 visual pathway [8–17]. While the ventrolateral visual cortex responds to animate 46 compared to inanimate stimuli more generally [18-20], the sensitivity in the occipital 47 face and extrastriate body area (lateral occipital cortex), as well as the fusiform face 48 and fusiform body area (inferior temporal cortex) appear increased for faces or 49 bodies [10,11,24–28,12,13,15–17,21–23]. Regarding the recognition of another 50 individual's species-identity, previous research suggests a preference for human 51 faces compared to faces of other species (such as dogs or horses) [29,30], 52 potentially reflecting increased salience of conspecifics over heterospecifics. 53 The evolutionary history of the neural underpinnings of face and body 54 perception has been mainly investigated by comparative research in non-human 55 primates [23–27,31], and this has revealed a homologous visual pathway [e.g., 1 for 56 review]. However, apart from primate species, the neural bases of this sociocognitive ability and its potential origin in the mammalian brain remain largely 57 58 unstudied. Dogs' (Canis familiaris) ability to perceive and understand humans and 59 conspecifics has already been well-investigated using behavioural and eye-tracking

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60 measures and yielded numerous comparable skills between dogs and humans. For 61 example, dogs can not only differentiate between faces [32,33], but even discriminate 62 facial emotional cues of humans and conspecifics [7,34,35]; and they demonstrate 63 complex behaviours such as visual perspective taking [36,37]. Thus, dogs constitute 64 an excellent model to study the evolution of visuo-social perception in mammals [38]. 65 While first non-invasive canine neuroimaging studies [29.39–42] suggested an 66 involvement of the temporal cortex in face perception, they triggered a debate on 67 whether the occipito-temporal specialization for face perception in dogs matches that 68 of humans [29,39–42]. Previous work reported increased activation for faces 69 compared to objects [40,42], scenes [40], or a mono-coloured surface [39], but not 70 compared to other low-level visual controls (i.e., scrambled images [39,40] or the 71 back of the head [29]). Some studies lacked non-facial controls entirely [41]. Studies 72 additionally investigating responses to con- and heterospecifics were inconclusive 73 ranging from reports of increased responsiveness to dog stimuli in general (i.e., face 74 and back of the head) but no specialization for faces [29], over separate brain 75 regions specialized for human or dog faces [41], to no species- but general face-76 preference [40]. Further, no previous work investigated the neural bases of body 77 perception. This is a major limitation, as bodies play an important role for social 78 perception in general, but in particular for dogs - as indicated e.g., by dogs' high 79 responsiveness to emotional or ostensive-referential bodily cues, such as tail-80 wagging [43] or human gestures [43-45]. It is particularly noteworthy in this respect, 81 that dogs even outperform humans' closest living relatives, chimpanzees, in utilizing 82 human ostensive cues [46].

Thus, the findings so far do not allow for a distinction between face and body or general animacy perception and are inconclusive regarding the influence of the other individual's species-identity. The present comparative neuroimaging study aimed to

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resolve this debate. We performed the, to our knowledge, first systematic comparison

- 87 of the neural bases of face, body and inanimate object perception in dogs and
- 88 humans, in order to gain insights into how social perception has evolved in two
- 89 phylogenetically distant mammalian species [38,47].

# 90 2 Results

91 Fifteen awake and unrestrained pet dogs (Fig 1A) and forty human participants 92 underwent functional magnetic resonance imaging (MRI) while viewing images of 93 human and dog bodies, faces, inanimate objects (e.g., different toys), and grid-94 scrambled versions of these images serving as visual controls (Fig 1B). Over the 95 course of two 5 min runs, participants saw 180 different images presented in a block 96 design interspersed with an implicit visual baseline. We analysed the dog fMRI data 97 with a newly developed analysis protocol shown to significantly improve neural signal 98 detection power [48]. All statistical tests were corrected for multiple comparisons (see 99 fMRI data analysis, Fig 2, Tables S2-S3).

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Fig 1. Overview of the comparative experimental approach to study the neural bases of face and body perception in dogs and humans. (A) We obtained all imaging data using a 3T Siemens Skyra MR-system, equipped with a 15-channel human knee coil to scan the dog participants, and using a 32-channel human head coil for the human participants (not depicted). Dogs received extensive training [49] to stay motionless without restraints or sedation and could leave the MR scanner at any time via a custom-made ramp positioned at the scanner bed. All (dog and human) participants wore earplugs for noise protection and dog participants had an additional head bandage to secure optimal positioning of the earplugs throughout the scan session. (B) All participants viewed images of human and dog bodies, human and dog faces, inanimate objects (e.g., toys) or gridscrambled versions of these images presented in a block design. (C) We split the data sets and used data from the first task run to compare activation for visual stimulation (all stimuli) to the visual baseline (i.e., the localizer data set). In both participant samples, we observed activation in the occipito-temporal cortices. These task-responsive voxels then served as a search space to determine individual functional regions-of-interest (fROIs), additionally constrained by bilateral anatomical regions (see Fig 2A). Results are displayed at p < 0.05, FWE-corrected at cluster-level using a cluster-defining threshold of p < .001(dogs, Table S1), and p < 0.05 whole-brain FWE-corrected (humans; Table S1) Results for the dogs are overlaid onto a canine render [50], and onto the FreeSurfer breed-averaged surface "FsAverage" surface for humans (https://surfer.nmr.mgh.harvard.edu/fswiki). Anatomical nomenclature for all figures refers to the dog brain atlas from Czeibert and colleagues [51] and to the human brain atlas from the Laboratory for Neuro Imaging (LONI) Brain Atlas [52] (LPBA40; http://www.loni.usc.edu/atlases/). R, right; L, left; A, anterior; P, posterior; STS, superior temporal sulcus; MT, middle temporal visual area (V5); LOC, lateral occipital complex.

t-value

# 100 2.1 Mass-univariate analysis: Face- or body-sensitive areas in the 101 occipito-temporal cortices of dogs and humans

R marginal, splenial, L occipital gyrus

- 102 To start out, we investigated whether dogs and humans have specialized cortical
- 103 regions for face and body perception, and whether these regions responded differently
- 104 to images of con- or heterospecifics. To this end, we used a standard functional region-
- 105 of-interest analysis approach (fROI,[53–55]). We split the data into two orthogonal data
- sets, (1) a localizer data set (first task run) to define potential face- or body-sensitive

t-value

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107 areas in visual-responsive brain regions (**Fig 1C, 2A**) and (2) a test data set (second 108 task run) to extract activation levels from these regions and to test potential category 109 sensitivity. We chose this approach for two reasons. First, we aimed at directly testing 110 the potential category-sensitivity, quantified by increased activation levels. Second, our 111 goal was to account for differences in the location of activation peaks between 112 individuals as reported in previous dog imaging studies [40,42].

# 113 **2.1.1 Functional regions-of-interest (fROIs)**

114 For each participant, we defined bilateral fROIs within constrained search spaces 115 to preserve spatial information (i.e., the rough anatomical location of activation peaks). 116 For the human participants, we used previously reported anatomical regions known to 117 be engaged in face and body perception [56]: the extrastriate body area, fusiform body 118 area, occipital face area and fusiform face area (Fig 2A). For the dog participants, we 119 could not build on previous research due to lack of shared template space and 120 availability of data. Therefore, we first compared activation levels associated with the 121 visual presentation of all stimuli compared to implicit baseline (i.e., white cross 122 presented on grey background) using the localizer data set. This revealed task-123 responsive activation within the occipital-, splenial-, ectomarginal-, caudal-, medial 124 suprasylvian- and marginal gyri, partially overlapping with results from previous studies 125 investigating face perception [29,39-42,57,58] (Fig 1C, Table S1). We then used 126 anatomical masks [51] of these regions as search spaces for the dog participants (Fig 127 **2A**). For comparison, we also report task-responsive voxels for the human participants, 128 confirming involvement of the occipito-temporal cortex including the lateral occipital 129 cortex and fusiform gyrus (Fig 1C, Table S1; see also Fig. S1 for schematic figures of 130 the dog and human brain).

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We then defined individual category-sensitive regions within each search space by selecting the top-10% voxels with the strongest activation for bodies or faces compared to inanimate objects based on the individual data from each participant.

134 2.1.2 Sensitivity for animate stimuli but sub-division in face- and
 135 body-sensitive regions exclusive to humans

136 Next, we extracted the mean activation signal during viewing of faces, bodies, 137 inanimate objects and scrambled images (all compared to the implicit baseline) from 138 the individual fROIs using the test data set. In dogs, we observed significantly 139 increased activation levels for faces and bodies compared to inanimate objects or 140 scrambled images in both face and body fROIs, located in the medial and caudal 141 suprasylvian- and ectomarginal gyrus. In the caudal suprasylvian face- and 142 ectomarginal body fROI, the increased activation for faces showed the same trend but 143 did not always reach significance. We did not find consistent evidence for a further 144 sub-division into face- and body-selective areas in the occipito-temporal cortex, as 145 there was no significant activation difference between faces and bodies in seven out 146 of eight fROIs. We only observed significantly increased activation for bodies 147 compared to faces in the caudal suprasylvian face but not body fROI. The occipital and 148 splenial face and body fROIs did not result in differential activation changes in 149 response to any of the stimulus categories (Table S2). Regarding the parietal cortex, 150 the marginal gyrus appeared solely responsive to bodies compared to all other 151 conditions with no activation differences for faces compared to inanimate objects or 152 scrambled controls (Fig 2B).

153 Results for the human participants confirmed earlier research [10,11,24– 154 28,12,13,15–17,21–23] with the strongest overall activation levels for bodies in the 155 extrastriate and fusiform body areas and for faces in the occipital and fusiform face 156 areas (**Fig 2B**; **Table S2**). In summary, we found multiple occipito-temporal regions in

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157 the dog and human cortices responsive to animate stimuli, but detected a further sub-

158 division into face- and body-sensitive regions exclusively in the human brain (see also

159 **Fig S1** for a summary of the results).

# 160 2.1.3 Conspecifics preference in human extrastriate body and 161 fusiform face area

162 Next, we investigated whether processing of faces or bodies differed when 163 participants saw images of con- compared to heterospecifics (Table S3). In humans, 164 this revealed increased activation for human (mean: 4.46, SD = 1.83) compared to dog 165 bodies (mean: 3.76, SD = 1.66) in the extrastriate body area (t(39) = 3.14, p = 0.003), 166 as well as a general activation increase for human (mean: 1.89, SD = 0.87) compared 167 to dog (mean: 1.64, SD = 0.81) stimuli in the fusiform face area (t(79) = 3.71, p < 100168 0.0001). For the dogs, we did not find a difference between the perception of dog and 169 human stimuli.

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B fROI analysis: mean activation extracted from independent test data set



a ( i

*Fig 2.* Strongest activation levels for animate stimuli in both species, but differences between faces and bodies exclusive in humans. (**A**) Based on the localizer data set, we defined individual category-specific regions-of-interest (functional region-of-interest approach, fROI) within multiple anatomically constrained search spaces using the contrasts bodies > inanimate objects (body fROIs) and faces > inanimate objects (face fROIs). (**B**) From these individual fROIs, we then extracted activation estimates during the viewing of faces, bodies, inanimate objects and scrambled images (all compared to the implicit baseline) using the data from the independent test data set to test potential face- or body-sensitivity. (**B**) In dogs, we observed increased activation levels for faces and bodies compared to inanimate objects or scrambled images in three occipito-temporal regions (medial and caudal suprasylvian, ectomarginal gyrus) in face and body fROIs. However, no difference between faces and bodies except in the caudal suprasylvian face fROI. The face and body fROIs located in the occipito-parietal marginal gyri resulted in increased activation levels for bodies. In humans, similar to dogs, we observed the strongest activation levels for faces and bodies in all fROIs. In contrast to the dog data, the human data analysis consistently resulted in a significant activation change for bodies compared to faces in body fROIs and vice versa (**Table S2**). Planned comparisons were corrected for multiple comparisons using Tukey method. \*p < .05, \*\*p < .01, \*\*\*p < .001, \*\*\*p < .0001, s.e.m., standard error of the mean; a.u., arbitrary units. Atlas maps and search spaces refer to the dog brain atlas from Czeibert and colleagues [51] and human parcels were retrieved from previous work [56]. A, anterior; P, posterior; S, superior; L, left; R, right

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# 172 **2.2** Multivariate pattern analysis of animacy perception

173 Despite the overall activation (measured using mass-univariate analyses) to 174 stimulus categories may not differ, we reasoned that more fine-grained analyses of 175 multivariate activation patterns could reveal distinctions [59]. Therefore, we 176 investigated the neural representations of faces and bodies in dogs and humans and 177 their potential correspondence using whole-brain representational similarity analyses 178 (RSA). We moved a 4 and 8 mm searchlight across the whole dog and human brain, 179 respectively, in order to determine individual pattern similarity maps between all trials 180 of each stimulus category [60–62] (Fig 3A). On the group-level, we then conducted 181 paired t-tests to compare the pattern similarities maps of (1) animate vs. inanimate 182 stimuli, (2) bodies vs. inanimate objects, (3) faces vs. inanimate objects, (4) faces vs. 183 bodies, and (5,6) within the face and body categories: images of conspecifics vs. 184 heterospecifics (i.e., dog faces vs. human faces; dog bodies vs. human bodies).

Results revealed increased (within-category) pattern similarity for animate compared to inanimate stimuli in the occipito-temporal cortex of dogs (i.e., caudal suprasylvian and splenial gyrus) and humans (i.e., middle occipital gyrus) overlapping with the identified fROIs. In human participants, we additionally observed increased similarity in the cerebellum and fronto-parietal regions (**Tables S4-S5**). In brief, this indicates distinct neural representations of animate compared to inanimate stimuli in higher-order visual regions of both species.

# 192 2.2.1 Similar and divergent neural representations for bodies and 193 faces

Moving on to neural representations for bodies and faces, for bodies we observed increased pattern similarity compared to inanimate objects in higher-order visual areas in the occipito-temporal cortex, partially overlapping with the identified fROIs, and the cerebellum in both species (**Fig 3B**). Within the same regions (and again, in both

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species), we also observed distinct activation patterns for conspecific compared to 198 199 heterospecific bodies. Furthermore, when the dogs viewed dog bodies, results 200 revealed increased similarity in limbic structures and regions associated with olfaction 201 (Fig 3C). In humans, we observed increased similarity for human compared to dog 202 bodies in fronto-parietal regions associated with action perception [63-65] (Fig 3C). 203 Observing faces compared to inanimate objects resulted in significantly 204 increased pattern similarity in occipito-temporal cortices of both species and again in 205 dog olfactory structures (Fig 3D). Comparing similarity patterns for faces vs. bodies, 206 we only found significant differences for the human participants (see Tables S4-5 for 207 detailed results and Fig S1 for a schematic summary of the main results).

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#### A Contrasts representational similarity analysis (RSA): within condition similarities

**Fig 3.** Whole-brain representational similarity analysis (RSA) revealed similar and divergent neural patterns of activation for animate vs. inanimate stimuli but differences between faces and bodies again exclusive in human. (A) We moved a 4/8 mm (dog/human) spherical searchlight across the whole brain to quantify the neural patterns underlying stimuli categories. Pattern similarity matrices were computed across the respective quadrants marked in black. (B,D) In both species, we observed increased pattern similarity for bodies or faces compared to inanimate stimuli in higher-order visual areas in the occipito-temporal cortex and the cerebellum. (C,D) In dogs we additionally detected distinct neural patterns of activation for faces and conspecific (= dog) bodies in olfactory and limbic regions. In humans, we observed an increased pattern similarity for (conspecific) bodies in fronto-parietal regions associated with action perception [63–65]. All results are displayed at p < 0.05 FWE-corrected at cluster-level, and using a cluster-defining threshold of p < .005 for the dog and p < .001 for the human data (**Tables S4-5**). Anatomical locations are shown in panel B for the dog and in D for the human data: superior (S), anterior (A); all sagittal, coronal and axial planes displayed have the same orientation. Coordinates refer to a canine-breed averaged template [50] or to MNI space for the human data. Person's *r*, correlation coefficient; t, *t*-value; g., gyrus; PFC, prefrontal cortex LOC, lateral occipital cortex; MT, middle temporal visual area (V5); pSTS, posterior superior temporal sulcus; R, right; L, left.

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# 209 3 Discussion

210 Our findings revealed that the occipito-temporal cortex has a prominent role in 211 the perception of animate entities in both dogs and humans. This suggests that the 212 neural processing of animate vs. inanimate stimuli across mammalian brains may 213 either have an old evolutionary origin in the common ancestors of canines and primates 214 or is the result of convergent evolution [47]. However, within these regions, only 215 humans displayed an additional sub-division into distinct face- and body-sensitive brain 216 regions. Moreover, only dogs showed distinct responses to human and dog faces as 217 well as dog bodies in olfactory areas (see Fig S1 for summary of the results). These 218 findings suggest a divergent evolution of the neural bases of face and body perception 219 (or processing) in dogs and humans. The differential engagement of visual and 220 olfactory brain functions would fit particularly well with the differential sensitivity and 221 preferential use of these perceptual systems to infer social and contextual information.

222 Detecting biological agents is crucial for survival and social relationships. Hence, 223 the visual differentiation between animate vs. inanimate entities is an evolutionary 224 important category representation. Studies show that dogs target animate agents 225 when, for example, presented with images of wild animals, humans or dogs embedded 226 in natural landscapes [66] or of social interactions between humans and dogs [67]. 227 Further, dividing stimuli into an animate vs. inanimate dimension is one of the first 228 visually salient categorizations formed by human infants [68]. In this way, animacy 229 representation provides the first building block for more complex visual categorizations 230 such as faces vs. bodies. Thus, considering its biological significance and the observed 231 cross-species similarities in our study, animacy might constitute a general organizing 232 principle across mammalian brains.

233 Behavioural [7,33,34,43,69–72] and imaging studies [57,58] have also 234 demonstrated that dogs are able to perceive facial and bodily cues of dogs and humans

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and display high responsiveness to ostensive-referential bodily cues [44,45,73,74], already as puppies [75]. Our results do not contradict these findings, but suggest that visual regions involved in the perception of faces are also involved in the perception of other body parts, and may thus encode animate stimuli. A recent dog neuroimaging study [76] also showed that the visual regions observed in our study play a crucial part in the perception of complex social interactions, which would confirm their important role for social perception.

242 While previous investigations of how dogs perceive bodies have mainly focused 243 on the decoding of human referential cues, we hope that our work will inspire more 244 research on how dogs perceive bodily social as well as emotional cues of con- as well 245 as heterospecifics. The absence of a further sub-specialization for face vs. body 246 perception in the occipito-temporal cortex of dogs might indeed indicate that dogs in 247 comparison to humans focus more on whole body social cues rather than on specific 248 sub-parts. This interpretation is notably well in line with a recent comparative eve-249 tracking study [77].

250 Regarding species perception, our results indicate an increased salience for 251 human compared to dog stimuli in humans, but no evidence for a conspecific-252 preference in the occipito-temporal cortex of dogs. Thus, human and dog stimuli 253 appear to be equally salient for dogs. This is in line with previous behavioural studies 254 suggesting, for example, no significant difference in the perception of human or dog 255 emotional facial [34], whole-body cues [77], or images of social interactions [67]. 256 Further, two recent studies demonstrated that dogs, already as puppies, follow human 257 gestural-communication and show an interest in human faces [75], which has not been 258 observed in wolf puppies [78]. Additionally, half of the variation in these socio-cognitive 259 skills could be accounted for by genetic factors, suggesting that dogs' attention to 260 humans might have been enhanced during domestication [75 for review of both

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studies]. Future studies investigating species-preferences in dogs might thus consideradding further heterospecific stimuli of other familiar species, such as cats.

263 In accordance with a potential divergent evolution of face and body 264 representations in dogs and humans, we also observed distinct neural representations 265 for faces (regardless of species) and conspecific (dog) bodies in dog olfactory regions. 266 Although unexpected, these results might reflect dogs' significantly higher olfactory 267 sensitivity and its use to infer social and contextual information [54 for review]. 268 However, the link between cognition and olfaction remains speculative since 269 behavioural studies using olfactory cues so far mainly explored dogs' odour and 270 disease detection abilities (e.g., [81-85]), while dog imaging studies on olfaction 271 focused on reward-processing [86,87] or general sensory abilities [88–90]. However, 272 a recent behavioural study investigating dog cognition using olfactory cues showed 273 first evidence that dogs form representations of their owners when smelling their tracks 274 [91].

In humans, results revealed distinct activation patterns for bodies in frontoparietal regions that have been consistently associated with the perception of actions [63–65]. In dogs, we did not find activation in (pre-)motor cortices, but the increased neural sensitivity for bodies in the occipito-parietal marginal gyrus might be initial evidence for an analogous visual pathway to encode actions. However, this is beyond our study's scope, and the precise neural underpinnings of action observation in dogs have not yet been investigated.

We have taken several steps to maximize neural signal sensitivity already when designing our study (e.g., by using a block design) and at the analysis stage (e.g., by using dog-tailored hemodynamic models increasing response detection power [48]). Nevertheless, the extensive training required for dogs [49] resulted in different sample sizes for the two species, and the more extensive prior work in humans [56] resulted

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in more constrained search spaces, and likely higher spatial sensitivity for the human
data. Further, the majority (80%) of our pet dogs were pure-bred herding dogs, which
prevented us from testing potential breed-specific differences and may limit
generalizability.

In conclusion, our study reveals novel evidence for similarities and differences of animacy perception between two phylogenetically distant mammal species, advancing our understanding of the foundations of social cognition and behaviour. Finally, we provide insights into the differentially evolved sensory systems of dogs and humans for the perception of faces and bodies.

296 4 Materials and Methods

#### 297 4.1 Participants

Fifteen pet dogs (*Canis familiaris*; 11 females, age range: 4-11 years, mean age: 7.8 years) consisting of 10 Border collies, 2 Australian shepherds, 1 Labrador retriever and 2 mixed-breed dogs and forty human participants (22 females, age range: 19-28 years, mean age: 23 years) participated in the present study.

302 Prior to MRI scanning, all dogs underwent initial medical examination concerning 303 their eyesight and general health and received extensive training to habituate to the 304 MRI environment [49]. They were fully awake, able to exit the MRI scanner at any time 305 and equipped with noise protection (Fig 1A). All caregivers gave informed written 306 consent to their dogs' participation. Human participants were right handed, had normal 307 or corrected-to-normal vision, they reported no history of neurological or psychiatric 308 disease, nor phobia of dogs, fulfilled the standard inclusion criteria for functional MRI, 309 and gave informed written consent to participate. Dog data collection was approved by 310 the institutional ethics and animal welfare commission in accordance with Good 311 Scientific Practice (GSP) guidelines and national legislation at the University of 312 Veterinary Medicine Vienna (ETK-06/06/2017), based on a pilot study conducted at

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the University of Vienna. Human data collection was approved by the ethics committee
of the University of Vienna (reference number: 00565) and performed in line with the
latest revision of the Declaration of Helsinki (2013).

## 316 4.2 Task and procedure

317 We employed a block design (duration: 12 s) split in two 5 min runs where 318 participants saw images of faces and bodies of dogs or humans, objects and 319 scrambled versions of these images (5 images per block; Fig 1B, see below) on an 320 MR-compatible screen (32 inch) positioned at the end of the scanner bore. Crucially, 321 we used the same task for dogs and humans. Human participants were instructed to 322 watch the images presented on the MR screen and dogs were trained to attend to the 323 MR screen (passive viewing paradigm). Each run contained three blocks per condition, 324 block order was randomized but the same condition was never presented twice in a 325 row. Between blocks, participants saw a visual baseline jittered between 3-7 s with a 326 white cross presented on a grey background. Image composition for each block and 327 order within each block was randomized across participants to ensure effects are not 328 driven by specific blocks; each image was presented once. The task was implemented 329 using PsychoPy [92]. Overall motion and wakefulness were live monitored via the 330 camera of an eye-tracker (Eyelink 1000 Plus, SR Research, Ontario, Canada) 331 positioned below the MR-compatible screen. For the dogs, the trainer stayed within the 332 scanner room but out-of-sight throughout the scan session to monitor and handle the 333 dogs. Human participants saw both runs within a single scanner session with a short 334 break in-between. For the dogs, the number of attempted sessions varied depending 335 on how many repetitions they needed to complete one run without substantive motion 336 and with sufficient attentiveness (i.e., eyes open and gazing towards the centre of the 337 screen); in-between task runs the dogs always were given a short break outside the 338 MR scanner. Realignment parameters were evaluated after each scan session. If

# Neural bases of face and body perception in dogs and humans overall motion exceeded 4 mm in any of the three translation directions, the dog was re-invited to repeat the run in a subsequent session and sessions were scheduled at least one week apart. On average, dogs needed three sessions to complete both runs. No data of the non-successful sessions were used for analysis.

343 4.2.1 Stimulus material

344 The stimulus set comprised 180 coloured images of faces and bodies of dogs 345 and humans, everyday inanimate objects (e.g., a toy, a chair), and phase-grid 346 scrambled versions of each category (30 images per condition) derived from Wagner and colleagues [93], the Hemera Photo-Object data base (Hemera Technologies) and 347 348 the internet (see Fig 1B for examples). The images were resized to 600 × 600 pixels 349 and presented in the centre of the MR screen on grey background. We cut out the 350 heads off from the body images, as well as objects from body images (e.g., a coffee 351 cup, a soccer ball). The images showed a variety of postures (e.g., jumping, looking 352 up), neutral and positive emotional displays (e.g., sleeping, smiling) and viewing perspectives (e.g., from above, from a side angle). Luminance was set homogeneously 353 354 across stimuli and we controlled for spatial extent (see supporting information for 355 details).

### 356 4.3 MRI data acquisition

We acquired all MRI data with a 3T Siemens Skyra MR-system (Siemens Medical, Erlangen, Germany) and a 15-channel coil (initially designed for measurements of the human knee) for data acquisition in dogs and a 32-channel human head coil for data acquisition in humans. Functional scans of dogs used a 2fold multiband (MB) accelerated echo planar imaging (EPI) sequence including the following parameters: voxel size =  $1.5 \times 1.5 \times 2 \text{ mm}^3$ , repetition time (TR) / echo time (TE) = 1000/38 ms, field of view (FoV) =  $144 \times 144 \times 58 \text{ mm}^3$ , flip angle =  $61^\circ$ , 20%

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364	gap and 24 axial slices covering the whole brain (interleaved acquisition, descending
365	order). Structural scans had a voxel size of 0.7 mm isotropic (TR/TE = 2100/3.13 ms,
366	FoV = $230 \times 230 \times 165 \text{ mm}^3$ ) and were acquired in a separate scan session prior to
367	functional data collection. Human functional scans were acquired using a 4-fold MB
368	accelerated EPI sequence including the following parameters: voxel size = 2 mm
369	isotropic, TR/TE = 1200/34 ms, FoV = 192 × 192 × 124.8 mm <sup>3</sup> , flip angle = 66°, 20%
370	gap and 52 axial slices coplanar to the connecting line between anterior and posterior
371	commissure (interleaved acquisition, ascending order). Additionally, we obtained field
372	map scans to correct functional scans for magnetic field inhomogeneities using a
373	double echo gradient echo sequence with the following parameters: voxel size = 1.72
374	x 1.72 x 3.85 mm <sup>3</sup> , TR/TE1/TE2 = 400/4.92/7.38 ms, FoV = 220 × 220 × 138 mm <sup>3</sup> , flip
375	angle = 60° and 36 axial slices (same orientation as functional scans). Structural scans
376	had a voxel size of 0.8 mm isotropic (TR/TE = 2300/2.43 ms,
377	FoV = 256 × 256 × 166 mm <sup>3</sup> ) and were acquired after functional data acquisition.

## 378 **4.4 Data processing and statistical analysis**

Imaging data was preprocessed and analyzed using SPM12
(<u>https://www.fil.ion.ucl.ac.uk/spm/software/spm12/</u>), Matlab 2018b (MathWorks) and R
3.6.3 [94].

382 4.4.1 MRI data preprocessing

In both samples, we slice-time corrected (reference: middle slice) and realigned functional images to the mean image. Human imaging data was also unwarped using the acquired field map. Dog imaging data was manually reoriented with the rostral commissure set as a visual reference (SPM module: *"Reorient images / Set origin"*) to match the template orientation [50] and structural images were skull-stripped using individual binary brain masks created using itk-SNAP [95]. Next, we co-registered the

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389 structural and functional images to the mean functional image, segmented the 390 structural images in both samples and normalized the human data to the Montreal 391 Neurological Institute (MNI) template space and the dog data to a breed-averaged 392 stereotaxic template space [50]. Normalized images were resliced to 1.5 mm isotropic 393 and smoothed with a 3-dimensional Gaussian kernel (full-width-at-half-maximum, 394 FWHM: with twice the raw voxel resolution: dogs/humans = 3/4 mm: see [48] for an in-395 depth description of our dog data preprocessing pipeline). We then calculated 396 individual scan-to-scan motion (frame wise displacement, FD) and added motion 397 regressors to first-level GLMs for each scan exceeding the a priori set FD threshold of 398 0.5 mm (motion scrubbing [96,97]) to account for both translational and rotational 399 displacements. For the dog participants, we removed on average 8% of the scans from 400 each run (run 1: mean FD = 0.23 mm, 90<sup>th</sup> percentile = 0.36 mm; run 2: mean FD = 401 0.24 mm, 90<sup>th</sup> percentile = 0.38 mm) and 1% of the scans from each run of the human participants (run 1: mean FD = 0.17 mm, 90<sup>th</sup> percentile = 0.22 mm; run 2: mean FD = 402 403  $0.18 \text{ mm}, 90^{\text{th}} \text{ percentile} = 0.21 \text{ mm}$ ).

#### 404 **4.4.2 fMRI data analysis**

405 Mass-univariate activation analysis. We analysed the functional data using a 406 general linear model (GLM) approach implemented in SPM12. Individual GLM 407 matrices included six regressors of interest for task (dog faces, dog bodies, human 408 faces, human bodies, inanimate objects, scrambled) and the six regressors from the 409 realignment procedure (see above) were added as nuisance regressors. All blocks 410 were estimated using a boxcar function time-locked to the onset of each block with a 411 duration of 12 s. For the dog data, the signal was convolved with a tailored dog 412 haemodynamic response function [48] (HRF), while the standard human canonical 413 HRF (i.e., the default HRF parameters provided by SPM12) was used for the human 414 data. The dog HRF reflects a previously observed 2-3 s earlier peak of the BOLD signal

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415 than expected by the human HRF model [48]. Normalized, individual binary masks 416 served as explicit masks and we applied a high-pass filter with a cut-off at 128 s. We 417 then split the data in two sets (task run 1, task run 2). Based on the data from the first 418 task run, we estimated three subject-level contrast maps for the difference between 419 our conditions of interest (i.e., faces, bodies with equal weights for human and dog 420 images) and objects, and a visual stimulation contrast (all conditions > implicit visual 421 baseline). For the second task run, we computed eight subject-level contrasts, one for 422 each task regressor (i.e., dog bodies, human bodies, dog faces, human faces, everyday inanimate objects, scrambled), averaged for faces (i.e., dog and human 423 424 faces) and averaged for bodies (i.e., dog and human bodies) compared to implicit 425 visual baseline.

Functional region of interest (fROI) approach. We implemented a standard functional region-of-interest (fROI, [53–55]) approach to investigate potential categoryspecificity of cortical regions. This approach allows us to directly test the potential category-sensitivity quantified by increased activation level while accounting for slight differences in the location of activation peaks between individuals as which have been reported in previous dog imaging studies [40,42].

432 The participant-level contrast images from the first run served as localizer data to 433 define individual category-sensitive regions. Within anatomically constrained search 434 spaces (Fig 2A) we selected the top-10% voxel from each hemisphere with the 435 strongest signal for the condition-of-interest (i.e., face areas: faces > objects, body 436 areas: bodies > objects) to form bilateral individual fROIs. Selecting the top-10% voxel 437 was an *a priori* decision we made because the resulting fROI sizes (on average: 30 voxels) were similar to the average cluster size observed in a previous dog imaging 438 439 study that used two visual paradigms and the same smoothing kernel [48]. Further, 440 percentages instead of absolute numbers took also the varying search space sizes

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into account (see **supporting material** and **Fig S2-3** for more information). The data from the left out second task run allowed then to directly test potential category specificity in an independent data set. Thus, we extracted the activation levels from the conditions-of-interest contrasted against implicit visual baseline from both body and faces areas (= individual fROIs).

446 Group functional ROI analyses were performed running repeated measures 447 analyses of variance (ANOVAs). First, we tested our main research question, whether 448 the body areas resulted in increased sensitivity for bodies regardless of species and 449 vice versa for faces, and added everyday objects and scrambled images as further 450 conditions. Thus, we ran a one-way ANOVA with stimuli category (faces, bodies, 451 everyday objects, scrambled) as dependent variable. Next, to investigate if there is a 452 difference in activation between conspecific and heterospecific stimuli, we used 2 x 2 453 within-subjects ANOVAs (species: conspecific, heterospecific; image category: face, 454 body). P-values for group comparisons investigating the same research questions 455 were Bonferroni-adjusted, e.g., if the 6 potential body fROIs result in increased 456 sensitivity for bodies compared to all other categories results in an adjusted p-value of 457 0.008 (= 0.05/6). Adjusted p-values are reported along with the results (**Tables S2-3**). 458 For whole-brain group analyses, we tested significance applying a whole-brain 459 familywise error (FWE) correction for the human data and a cluster-level inference with 460 a cluster defining threshold of p < 0.001 and a cluster probability of p < 0.05 FWE 461 corrected for multiple comparisons for the dog data. Cluster extent (i.e., minimum 462 spatial extend to be labelled significant) was calculated using the SPM extension 463 "CorrClusTh.m" (by Thomas Nichols, University of Warwick, United Kingdom, and 464 Marko Wilke, University of Tübingen, Germany; 465 https://warwick.ac.uk/fac/sci/statistics/staff/academic-research/nichols/scripts/spm/).

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Representational similarity analysis. Next, we investigated the neural 466 467 representations for faces, bodies and objects and their potential convergence in dogs 468 and humans. To this end, we performed a whole-brain representational similarity 469 analysis (RSA; [60-62]) to determine neural pattern similarities within image 470 categories. GLMs were modelled identical to univariate GLMs (see above) but for each 471 block, we ran a separate GLM with the block as task regressor and remaining blocks 472 were combined in one regressor of no interest [98]; runs were modelled independently. 473 Thus, the analysis resulted in 36 beta images for each participant (6 conditions × 6 474 trials). RSA was performed using the smoothed functional data. For all RSA analyses, 475 we moved a spherical searchlight [99] (dogs: r = 4 mm, 81 voxel; humans: r = 8 mm, 476 251 voxel) throughout individual whole-brain grey matter masks computed based on 477 the normalised segmentation output considering only searchlights with a minimum of

478 15 grey matter voxel for the dog and 30 for the human data.

479 Within a given searchlight, we extracted single-trial beta estimates from all voxels 480 and sorted them according to their stimuli category (Fig 3A; dog / human bodies, dog 481 / human faces, inanimate objects) and reshaped the data to a trial × voxel matrix. Next, 482 we z-scored the data across trials and runs and computed a trial x trial similarity matrix 483 by correlating each beta estimate of each trial to all other trial estimates. Finally, in 484 order to retrieve overall similarity scores, we then Fisher's z-transformed the data and 485 calculated overall similarity matrices by averaging scores across the respective 486 quadrants. We were specifically interested in pattern similarities across animate vs. 487 inanimate (faces × bodies vs. inanimate objects), faces or bodies vs. inanimate objects, 488 faces vs. bodies and conspecific vs. heterospecific species dimensions within face and 489 body categories. We then assigned the overall similarity values to the centre voxel of 490 each searchlight resulting in individual whole-brain pattern similarity maps.

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491 On the group-level, we then used paired *t*-tests to compare the pattern similarities 492 between trials of (1) faces vs. inanimate objects (i.e., [dog faces × human faces] vs. 493 inanimate objects), (2) bodies vs. inanimate objects (i.e., [dog bodies × human bodies] 494 vs. inanimate objects), (3) animate vs. inanimate images (i.e., [dog faces × human 495 faces x dog bodies × human bodies] vs. inanimate objects), (4) faces vs. bodies (i.e., 496 [dog faces × human faces] vs. [dog bodies × human bodies]), and (5,6) within the face 497 and body categories: images of conspecifics vs. heterospecifics (i.e., dog faces vs. 498 human faces; dog bodies vs. human bodies). We computed permutation tests [100] to 499 determine group-level significance using the Statistical nonParametric Mapping 500 (SnPm13) toolbox running 5000 permutations for each paired *t*-test and applied 501 cluster-level inference with a cluster defining threshold of p < .005/.001 (dogs/humans) 502 and a cluster probability of p < 0.05 familywise error corrected (*FWE*) for multiple 503 comparisons.

504 **Data visualization**. Data was visualized using SPM12 505 (<u>https://www.fil.ion.ucl.ac.uk/spm/software/spm12/</u>), Matlab 2018b (MathWorks), itk-506 SNAP [95], R 3.6.3 [94] with mainly the packages ggplot2 [101] and RainCloudPlots 507 [102] and the python project nilearn (<u>http://nilearn.github.io</u>).

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# 519 6 CRediT authorship statement

520 Magdalena Boch: Conceptualization, Methodology, Software, Validation, 521 Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & 522 editing, Visualization, Project administration. Isabella C. Wagner: Conceptualization, 523 Methodology, Resources, Writing - original draft, Writing - review & editing, 524 Supervision. Sabrina Karl: Investigation, Writing - review & editing. Ludwig Huber: 525 Conceptualization, Resources, Writing - review & editing, Supervision, Funding 526 acquisition. Claus Lamm: Conceptualization, Methodology, Resources, Writing -527 original draft, Writing - review & editing, Supervision, Funding acquisition.

# 528 7 Declaration of Competing Interests

529 The authors declare no competing financial interests.

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# 530 8 References

# 531

- Rajhans P, Jessen S, Missana M, Grossmann T. Putting the face in context: Body expressions
   impact facial emotion processing in human infants. Dev Cogn Neurosci. 2016;19: 115–121.
   doi:10.1016/J.DCN.2016.01.004
- 5352.Aviezer H, Trope Y, Todorov A. Body cues, not facial expressions, discriminate between536intense positive and negative emotions. Science. 2012;338: 1225–1229.
- 537 doi:10.1126/science.1224313
- 538 3. Barrett LF, Mesquita B, Gendron M. Context in emotion perception. Curr Dir Psychol Sci.
  539 2011;20: 286–290. doi:10.1177/0963721411422522
- 5404.Lecker M, Dotsch R, Bijlstra G, Aviezer H. Bidirectional contextual influence between faces and541bodies in emotion perception. Emotion. 2020;20: 1154–1164. doi:10.1037/EMO0000619
- 542 5. Poyo Solanas M, Zhan M, Vaessen M, Hortensius R, Engelen T, de Gelder B. Looking at the
  543 face and seeing the whole body. Neural basis of combined face and body expressions. Soc
  544 Cogn Affect Neurosci. 2018;13: 135–144. doi:10.1093/scan/nsx130
- 5456.de Gelder B, de Borst AW, Watson R. The perception of emotion in body expressions. Wiley546Interdiscip Rev Cogn Sci. 2015;6: 149–158. doi:10.1002/wcs.1335
- 5477.Müller CA, Schmitt K, Barber ALA, Huber L. Dogs can discriminate emotional expressions of548human faces. Curr Biol. 2015;25: 601–605. doi:10.1016/j.cub.2014.12.055
- 549 8. Kravitz DJ, Saleem KS, Baker CI, Ungerleider LG, Mishkin M. The ventral visual pathway: An
  550 expanded neural framework for the processing of object quality. Trends Cogn Sci. 2013;17:
  551 26–49. doi:10.1016/j.tics.2012.10.011
- 552 9. Ungerleider LG, Haxby J V. "What" and "where" in the human brain. Curr Opin Neurobiol.
  553 1994;4: 157–165. doi:10.1016/0959-4388(94)90066-3
- 55410.Schwarzlose RF, Baker CI, Kanwisher N. Separate face and body selectivity on the fusiform555gyrus. J Neurosci. 2005;25: 11055–11059. doi:10.1523/JNEUROSCI.2621-05.2005
- 556 11. Peelen M V., Downing PE. Selectivity for the human body in the fusiform gyrus. J

557 Neurophysiol. 2005;93: 603–608. doi:10.1152/jn.00513.2004

- 558 12. Peelen M V., Downing PE. The neural basis of visual body perception. Nat Rev Neurosci.
  559 2007;8: 636–648. doi:10.1038/nrn2195
- 56013.Downing PE, Jiang Y, Shuman M, Kanwisher N. A cortical area selective for visual processing561of the human body. Science. 2001;293: 2470–2473. doi:10.1126/science.1063414
- 562 14. Spiridon M, Fischl B, Kanwisher N. Location and spatial profile of category-specific regions in
  563 human extrastriate cortex. Hum Brain Mapp. 2006;27: 77–89. doi:10.1002/hbm.20169
- 564 15. Kanwisher N. Domain specificity in face perception. Nat Neurosci. 2000;3: 759–763.
- 565 doi:10.1038/77664
- 566 16. Yovel G, Kanwisher N. Face perception: domain specific, not process specific. Neuron.
  567 2004;44: 889–898. doi:10.1016/j.neuron.2004.11.018
- 568 17. Wegrzyn M, Riehle M, Labudda K, Woermann F, Baumgartner F, Pollmann S, et al.
- 569 Investigating the brain basis of facial expression perception using multi-voxel pattern analysis.
- 570 Cortex. 2015;69: 131–140. doi:10.1016/J.CORTEX.2015.05.003

571	18.	Wiggett AJ, Pritchard IC, Downing PE. Animate and inanimate objects in human visual cortex:
572		Evidence for task-independent category effects. Neuropsychologia. 2009;47: 3111–3117.
573		doi:10.1016/J.NEUROPSYCHOLOGIA.2009.07.008
574	19.	Chao LL, Haxby J V., Martin A. Attribute-based neural substrates in temporal cortex for
575		perceiving and knowing about objects. Nat Neurosci. 1999;2: 913–919. doi:10.1038/13217
576	20.	Downing PE, Chan AW-Y, Peelen M V., Dodds CM, Kanwisher N. Domain specificity in visual
577		cortex. Cereb Cortex. 2006;16: 1453–1461. doi:10.1093/CERCOR/BHJ086
578	21.	Kanwisher N, Yovel G. The fusiform face area: a cortical region specialized for the perception
579		of faces. Philos Trans R Soc B Biol Sci. 2006;361: 2109–2128. doi:10.1098/rstb.2006.1934
580	22.	Tsao DY, Freiwald WA, Tootell RBH, Livingstone MS. A cortical region consisting entirely of
581		face-selective cells. Science. 2006;311: 670–674. doi:10.1126/science.1119983
582	23.	Tsao DY, Moeller S, Freiwald WA. Comparing face patch systems in macaques and humans.
583		Proc Natl Acad Sci U S A. 2008;105: 19514–19519. doi:10.1073/pnas.0809662105
584	24.	Tsao DY, Freiwald WA, Knutsen TA, Mandeville JB, Tootell RBH. Faces and objects in
585		macaque cerebral cortex. Nat Neurosci. 2003;6: 989–995. doi:10.1038/nn1111
586	25.	Desimone R, Albright TD, Gross CG, Bruce C. Stimulus-selective properties of inferior
587		temporal neurons in the macaque. J Neurosci. 1984;4: 2051–2062. doi:10.1523/jneurosci.04-
588		08-02051.1984
589	26.	Wachsmuth E, Oram MW, Perrett DI. Recognition of objects and their component parts:
590		Responses of single units in the temporal cortex of the macaque. Cereb Cortex. 1994;4: 509–
591		522. doi:10.1093/cercor/4.5.509
592	27.	Gross CG, Bender DB, Rocha-Miranda CE. Visual receptive fields of neurons in inferotemporal
593		cortex of the monkey. Science. 1969;166: 1303–1306. doi:10.1126/science.166.3910.1303
594	28.	Haxby J V., Horwitz B, Ungerleider LG, Maisog JM, Pietrini P, Grady CL. The functional
595		organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and
596		locations. J Neurosci. 1994;14: 6336–6353. doi:10.1523/JNEUROSCI.14-11-06336.1994
597	29.	Bunford N, Hernández-Pérez R, Farkas EB, Cuaya L V., Szabó D, Szabó ÁG, et al.
598		Comparative Brain Imaging Reveals Analogous and Divergent Patterns of Species and Face
599		Sensitivity in Humans and Dogs. J Neurosci. 2020;40: 8396–8408.
600		doi:10.1523/JNEUROSCI.2800-19.2020
601	30.	Kanwisher N, Stanley D, Harris A. The fusiform face area is selective for faces not animals.
602		Neuroreport. 1999;10: 183–187. doi:10.1097/00001756-199901180-00035
603	31.	Pinsk MA, Arcaro M, Weiner KS, Kalkus JF, Inati SJ, Gross CG, et al. Neural representations
604		of faces and body parts in macaque and human cortex: a comparative fMRI study. J
605		Neurophysiol. 2009;101: 2581–2600. doi:10.1152/jn.91198.2008
606	32.	Racca A, Amadei E, Ligout S, Guo K, Meints K, Mills D. Discrimination of human and dog faces
607		and inversion responses in domestic dogs (Canis familiaris). Anim Cogn. 2010;13: 525–533.
608		doi:10.1007/s10071-009-0303-3
609	33.	Huber L, Racca A, Scaf B, Virányi Z, Range F. Discrimination of familiar human faces in dogs
610		(Canis familiaris). Learn Motiv. 2013;44: 258–269. doi:10.1016/J.LMOT.2013.04.005
611	34.	Albuquerque N, Guo K, Wilkinson A, Savalli C, Otta E, Mills D. Dogs recognize dog and human
612		emotions. Biol Lett. 2016;12: 20150883. doi:10.1098/rsbl.2015.0883

613	35.	Huber L. How Dogs Perceive and Understand Us. Curr Dir Psychol Sci. 2016;25: 339–344.
614		doi:10.1177/0963721416656329
615	36.	Maginnity ME, Grace RC. Visual perspective taking by dogs (Canis familiaris) in a Guesser-
616		Knower task: evidence for a canine theory of mind? Anim Cogn. 2014;17: 1375–1392.
617		doi:10.1007/s10071-014-0773-9
618	37.	Catala A, Mang B, Wallis L, Huber L. Dogs demonstrate perspective taking based on
619		geometrical gaze following in a Guesser–Knower task. Anim Cogn. 2017;20: 581–589.
620		doi:10.1007/s10071-017-1082-x
621	38.	Bunford N, Andics A, Kis A, Miklósi Á, Gácsi M. Canis familiaris As a Model for Non-Invasive
622		Comparative Neuroscience. Trends Neurosci. 2017;40: 438–452.
623		doi:10.1016/J.TINS.2017.05.003
624	39.	Szabó D, Gábor A, Gácsi M, Faragó T, Kubinyi E, Miklósi Á, et al. On the Face of It: No
625		Differential Sensitivity to Internal Facial Features in the Dog Brain. Front Behav Neurosci.
626		2020;14. doi:10.3389/fnbeh.2020.00025
627	40.	Dilks DD, Cook PF, Weiller SK, Berns HP, Spivak M, Berns GS. Awake fMRI reveals a
628		specialized region in dog temporal cortex for face processing. PeerJ. 2015; 3:e1115.
629		doi:10.7717/peerj.1115
630	41.	Thompkins AM, Ramaiahgari B, Zhao S, Gotoor SSR, Waggoner P, Denney TS, et al.
631		Separate brain areas for processing human and dog faces as revealed by awake fMRI in dogs
632		(Canis familiaris). Learn Behav. 2018;46: 561–573. doi:10.3758/s13420-018-0352-z
633	42.	Cuaya L V., Hernández-Pérez R, Concha L. Our faces in the dog's brain: Functional imaging
634		reveals temporal cortex activation during perception of human faces. PLoS One. 2016;11:
635		e0149431. doi:10.1371/journal.pone.0149431
636	43.	Siniscalchi M, Lusito R, Vallortigara G, Quaranta A. Seeing Left- or Right-Asymmetric Tail
637		Wagging Produces Different Emotional Responses in Dogs. Curr Biol. 2013;23: 2279–2282.
638		doi:10.1016/J.CUB.2013.09.027
639	44.	Duranton C, Range F, Virányi Z. Do pet dogs (Canis familiaris) follow ostensive and non-
640		ostensive human gaze to distant space and to objects? R Soc Open Sci. 2017;4: 170349.
641		doi:10.1098/rsos.170349
642	45.	Topál J, Kis A, Oláh K. Dogs' Sensitivity to Human Ostensive Cues: A Unique Adaptation? The
643		Social Dog: Behavior and Cognition. Elsevier Inc.; 2014. pp. 319–346. doi:10.1016/B978-0-12-
644		407818-5.00011-5
645	46.	Bräuer J, Kaminski J, Riedel J, Call J, Tomasello M. Making inferences about the location of
646		hidden food: Social dog, causal ape. J Comp Psychol. 2006;120: 38–47. doi:10.1037/0735-
647		7036.120.1.38
648	47.	Fitch WT, Huber L, Bugnyar T. Social Cognition and the Evolution of Language: Constructing
649		Cognitive Phylogenies. Neuron. 2010;65: 795–814. doi:10.1016/J.NEURON.2010.03.011
650	48.	Boch M, Karl S, Sladky R, Huber L, Lamm C, Wagner IC. Tailored haemodynamic response
651		function increases detection power of fMRI in awake dogs (Canis familiaris). Neuroimage.
652		2021;224: 117414. doi:10.1016/j.neuroimage.2020.117414
653	49.	Karl S, Boch M, Virányi Z, Lamm C, Huber L. Training pet dogs for eye-tracking and awake
654		fMRI. Behav Res Methods. 2020;52. doi:10.3758/s13428-019-01281-7

655	50.	Nitzsche B, Boltze J, Ludewig E, Flegel T, Schmidt MJ, Seeger J, et al. A stereotaxic breed-
656		averaged, symmetric T2w canine brain atlas including detailed morphological and volumetrical
657		data sets. Neuroimage. 2019;187: 93–103. doi:10.1016/j.neuroimage.2018.01.066
658	51.	Czeibert K, Andics A, Petneházy Ö, Kubinyi E. A detailed canine brain label map for
659		neuroimaging analysis. Biol Futur. 2019;70: 112–120. doi:10.1556/019.70.2019.14
660	52.	Shattuck DW, Mirza M, Adisetiyo V, Hojatkashani C, Salamon G, Narr KL, et al. Construction of
661		a 3D probabilistic atlas of human cortical structures. Neuroimage. 2008;39: 1064–1080.
662		doi:10.1016/j.neuroimage.2007.09.031
663	53.	Fedorenko E, Hsieh P-J, Nieto-Castañón A, Whitfield-Gabrieli S, Kanwisher N. New method for
664		fMRI investigations of language: Defining ROIs functionally in individual subjects. J
665		Neurophysiol. 2010;104: 1177–1194. doi:10.1152/jn.00032.2010
666	54.	Poldrack RA. Region of interest analysis for fMRI. Soc Cogn Affect Neurosci. 2007;2: 67–70.
667		doi:10.1093/scan/nsm006
668	55.	Saxe R, Brett M, Kanwisher N. Divide and conquer: A defense of functional localizers.
669		Neuroimage. 2006;30: 1088–1096. doi:10.1016/J.NEUROIMAGE.2005.12.062
670	56.	Julian JB, Fedorenko E, Webster J, Kanwisher N. An algorithmic method for functionally
671		defining regions of interest in the ventral visual pathway. Neuroimage. 2012;60: 2357–2364.
672		doi:10.1016/j.neuroimage.2012.02.055
673	57.	Karl S, Boch M, Zamansky A, van der Linden D, Wagner IC, Völter CJ, et al. Exploring the
674		dog–human relationship by combining fMRI, eye-tracking and behavioural measures. Sci Rep.
675		2020;10: 22273. doi:10.1038/s41598-020-79247-5
676	58.	Thompkins AM, Lazarowski L, Ramaiahgari B, Gotoor SSR, Waggoner P, Denney TS, et al.
677		Dog-human social relationship: representation of human face familiarity and emotions in the
678		dog brain. Anim Cogn. 2021;24: 251–266. doi:10.1007/s10071-021-01475-7
679	59.	Cohen MA, Dilks DD, Koldewyn K, Weigelt S, Feather J, Kell AJE, et al. Representational
680		similarity precedes category selectivity in the developing ventral visual pathway. Neuroimage.
681		2019;197: 565–574. doi:10.1016/j.neuroimage.2019.05.010
682	60.	Kriegeskorte N, Kievit RA. Representational geometry: integrating cognition, computation, and
683		the brain. Trends Cogn Sci. 2013;17: 401–412. doi:10.1016/J.TICS.2013.06.007
684	61.	Kriegeskorte N, Mur M, Bandettini P. Representational similarity analysis - connecting the
685		branches of systems neuroscience. Front Syst Neurosci. 2008;2.
686		doi:10.3389/neuro.06.004.2008
687	62.	Kriegeskorte N, Mur M, Ruff DA, Kiani R, Bodurka J, Esteky H, et al. Matching Categorical
688		Object Representations in Inferior Temporal Cortex of Man and Monkey. Neuron. 2008;60:
689		1126–1141. doi:10.1016/J.NEURON.2008.10.043
690	63.	Rizzolatti G, Fogassi L, Gallese V. Neurophysiological mechanisms underlying the
691		understanding and imitation of action. Nat Rev Neurosci. 2001;2: 661–670.
692		doi:10.1038/35090060
693	64.	Hamilton AF de C, Grafton ST. Goal Representation in Human Anterior Intraparietal Sulcus. J
694		Neurosci. 2006;26: 1133–1137. doi:10.1523/JNEUROSCI.4551-05.2006
695	65.	Kilner JM, Neal A, Weiskopf N, Friston KJ, Frith CD. Evidence of Mirror Neurons in Human
696		Inferior Frontal Gyrus. J Neurosci. 2009;29: 10153–10159. doi:10.1523/JNEUROSCI.2668-

697		09.2009
698	66.	Törnqvist H, Somppi S, Kujala M V., Vainio O. Observing animals and humans: Dogs target
699		their gaze to the biological information in natural scenes. PeerJ. 2020;8: e10341.
700		doi:10.7717/peerj.10341
701	67.	Törnqvist H, Somppi S, Koskela A, Krause CM, Vainio O, Kujala M V. Comparison of dogs and
702		humans in visual scanning of social interaction. R Soc Open Sci. 2015;2: 150341.
703		doi:10.1098/rsos.150341
704	68.	Spriet C, Abassi E, Hochmann J-R, Papeo L. Visual object categorization in infancy. bioRxiv.
705		2021; 2021.02.25.432436. doi:10.1101/2021.02.25.432436
706	69.	Buttelmann D, Tomasello M. Can domestic dogs (Canis familiaris) use referential emotional
707		expressions to locate hidden food? Anim Cogn. 2013. doi:10.1007/s10071-012-0560-4
708	70.	Nagasawa M, Murai K, Mogi K, Kikusui T. Dogs can discriminate human smiling faces from
709		blank expressions. Anim Cogn. 2011;14: 525–533. doi:10.1007/s10071-011-0386-5
710	71.	Barber ALA, Randi D, Müller CA, Huber L. The Processing of Human Emotional Faces by Pet
711		and Lab Dogs: Evidence for Lateralization and Experience Effects. Guo K, editor. PLoS One.
712		2016;11: e0152393. doi:10.1371/journal.pone.0152393
713	72.	Racca A, Guo K, Meints K, Mills DS. Reading Faces: Differential Lateral Gaze Bias in
714		Processing Canine and Human Facial Expressions in Dogs and 4-Year-Old Children. PLoS
715		One. 2012;7: e36076. doi:10.1371/journal.pone.0036076
716	73.	Range F, Viranyi Z, Huber L. Selective Imitation in Domestic Dogs. Curr Biol. 2007;17: 868–
717		872. doi:10.1016/J.CUB.2007.04.026
718	74.	Soproni K, Miklósi Á, Topál J, Csányi V. Dogs' (Canis familiaris) Responsiveness to Human
719		Pointing Gestures. J Comp Psychol. 2002;116: 27–34. doi:10.1037//0735-7036.116.1.27
720	75.	Bray EE, Gnanadesikan GE, Horschler DJ, Levy KM, Kennedy BS, Famula TR, et al. Early-
721		emerging and highly heritable sensitivity to human communication in dogs. Curr Biol. 2021;31:
722		1–5. doi:10.1016/j.cub.2021.04.055
723	76.	Karl S, Sladky R, Lamm C, Huber L. Neural Responses of Pet Dogs Witnessing their
724		caregiver's Positive Interactions with a Conspecific: An fMRI Study. Cereb Cortex Commun.
725		2021;tgab047. doi:10.1093/TEXCOM/TGAB047
726	77.	Correia-Caeiro C, Guo K, Mills D. Bodily emotional expressions are a primary source of
727		information for dogs, but not for humans. Anim Cogn. 2021;1: 3. doi:10.1007/s10071-021-
728		01471-x
729	78.	Salomons H, Smith KCM, Callahan-Beckel M, Callahan M, Levy K, Kennedy BS, et al.
730		Cooperative Communication with Humans Evolved to Emerge Early in Domestic Dogs. Curr
731		Biol. 2021;31: 3137-3144.e11. doi:10.1016/J.CUB.2021.06.051
732	79.	Kaminski J. Domestic dogs: Born human whisperers. Curr Biol. 2021;31: R891–R893.
733		doi:10.1016/J.CUB.2021.05.063
734	80.	Siniscalchi M, D'Ingeo S, Minunno M, Quaranta A. Communication in Dogs. Animals. MDPI
735		AG; 2018. p. 131. doi:10.3390/ani8080131
736	81.	Long RA, Donovan TM, Mackay P, Zielinski WJ, Buzas JS. Effectiveness of Scat Detection
737		Dogs for Detecting Forest Carnivores. J Wildl Manage. 2007;71: 2007–2017.
738		doi:10.2193/2006-230

739	82.	Jamieson LTJ, Baxter GS, Murray PJ. Identifying suitable detection dogs. Applied Animal
740		Behaviour Science. Elsevier B.V.; 2017. pp. 1–7. doi:10.1016/j.applanim.2017.06.010
741	83.	Grimm-Seyfarth A, Harms W, Berger A. Detection dogs in nature conservation: A database on
742		their world-wide deployment with a review on breeds used and their performance compared to
743		other methods. Methods in Ecology and Evolution. British Ecological Society; 2021. pp. 568–
744		579. doi:10.1111/2041-210X.13560
745	84.	Dunn M, Degenhardt L. The use of drug detection dogs in Sydney, Australia. Drug Alcohol
746		Rev. 2009;28: 658–662. doi:10.1111/j.1465-3362.2009.00065.x
747	85.	Guest C, Otto CM. Editorial: Canine Olfactory Detection. Frontiers in Veterinary Science.
748		Frontiers Media S.A.; 2020. p. 100. doi:10.3389/fvets.2020.00100
749	86.	Berns GS, Brooks AM, Spivak M. Scent of the familiar: An fMRI study of canine brain
750		responses to familiar and unfamiliar human and dog odors. Behav Processes. 2015;110: 37–
751		46. doi:10.1016/J.BEPROC.2014.02.011
752	87.	Prichard A, Chhibber R, Athanassiades K, Spivak M, Berns GS. Fast neural learning in dogs: A
753		multimodal sensory fMRI study. Sci Rep. 2018;8: 14614. doi:10.1038/s41598-018-32990-2
754	88.	Jia H, Pustovyy OM, Wang Y, Waggoner P, Beyers RJ, Schumacher J, et al. Enhancement of
755		Odor-Induced Activity in the Canine Brain by Zinc Nanoparticles: A Functional MRI Study in
756		Fully Unrestrained Conscious Dogs. Chem Senses. 2016;41: 53–67.
757		doi:10.1093/chemse/bjv054
758	89.	Jia H, Pustovyy OM, Waggoner P, Beyers RJ, Schumacher J, Wildey C, et al. Functional MRI
759		of the Olfactory System in Conscious Dogs. Dhenain M, editor. PLoS One. 2014;9: e86362.
760		doi:10.1371/journal.pone.0086362
761	90.	Ramaihgari B, Pustovyy OM, Waggoner P, Beyers RJ, Wildey C, Morrison E, et al. Zinc
762		nanoparticles enhance brain connectivity in the canine olfactory network: Evidence from an
763		fMRI study in unrestrained awake dogs. Front Vet Sci. 2018;5: 127.
764		doi:10.3389/fvets.2018.00127
765	91.	Bräuer J, Blasi D. Dogs display owner-specific expectations based on olfaction. Sci Reports
766		2021 111. 2021;11: 1–10. doi:10.1038/s41598-021-82952-4
767	92.	Peirce JW. PsychoPy-Psychophysics software in Python. J Neurosci Methods. 2007;162: 8–
768		13. doi:10.1016/j.jneumeth.2006.11.017
769	93.	Wagner IC, van Buuren M, Bovy L, Fernández G. Parallel engagement of regions associated
770		with encoding and later retrieval forms durable memories. J Neurosci. 2016;36: 7985–7995.
771		doi:10.1523/JNEUROSCI.0830-16.2016
772	94.	R Core Team. R: A Language and Environment for Statistical Computing. Vienna, Austria: R
773		Foundation for Statistical Computing; 2020. Available: https://www.r-project.org/
774	95.	Yushkevich PA, Piven J, Hazlett HC, Smith RG, Ho S, Gee JC, et al. User-guided 3D active
775		contour segmentation of anatomical structures: Significantly improved efficiency and reliability.
776		Neuroimage. 2006;31: 1116–1128. doi:10.1016/J.NEUROIMAGE.2006.01.015
777	96.	Power JD, Barnes KA, Snyder AZ, Schlaggar BL, Petersen SE. Spurious but systematic
778		correlations in functional connectivity MRI networks arise from subject motion. Neuroimage.
779		2012;59: 2142–2154. doi:10.1016/J.NEUROIMAGE.2011.10.018
780	97.	Power JD, Mitra A, Laumann TO, Snyder AZ, Schlaggar BL, Petersen SE. Methods to detect,

781		characterize, and remove motion artifact in resting state fMRI. Neuroimage. 2014;84: 320–341.
782		doi:10.1016/j.neuroimage.2013.08.048
783	98.	Mumford JA, Turner BO, Ashby FG, Poldrack RA. Deconvolving BOLD activation in event-
784		related designs for multivoxel pattern classification analyses. Neuroimage. 2012;59: 2636-
785		2643. doi:10.1016/j.neuroimage.2011.08.076
786	99.	Kriegeskorte N, Goebel R, Bandettini P. Information-based functional brain mapping. Proc Natl
787		Acad Sci U S A. 2006;103: 3863–3868. doi:10.1073/pnas.0600244103
788	100.	Nichols TE, Holmes AP. Non-parametric procedures. Statistical Parametric Mapping: The
789		analysis of Functional Brain Images. Amsterdam: Elsevier; 2007. pp. 253–272.
790	101.	Wickham H. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York; 2016.
791		Available: https://ggplot2.tidyverse.org
792	102.	Allen M, Poggiali D, Whitaker K, Marshall TR, Kievit RA. Raincloud plots: A multi-platform tool
793		for robust data visualization [version 1; peer review: 2 approved]. Wellcome Open Res. 2019;4.
794		doi:10.12688/wellcomeopenres.15191.1
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# 797 9 Supporting information

# 798 9.1 Stimulus material: luminance and spatial extent

799 Luminance was set to 100 for all images and background, grid-scrambled images 800 were created based on images equally drawn from each category to control for 801 potential low-level visual differences. Face and body images vary in spatial extent (= 802 ratio image / background) due to their shape (mean values: faces = 58.53; bodies = 803 29.42; t(118) = 21.17, p < 0.0001), matching them in spatial extent would have required 804 resizing the face images to half their size resulting in less ecologically valid images, 805 but we matched dog and human images within the body and face categories (mean 806 values faces: dogs = 58.55; humans = 58.50; t(58) = 0.03, p = 0.98; means bodies: 807 dogs = 30.97; humans = 27.87; t(58) = 1.33, p = 0.19). Further, half of the object images 808 were matched in spatial extent to either body (mean values: bodies = 29.42, matched 809 objects = 29.86, t(73) = -0.17, p = 0.86) or face (mean values: faces = 58.53, matched 810 objects = 57.23, t(73) = 0.78, p = 0.44) images and scrambled images were created 811 based on images equally drawn from each category.

# 812 9.2 Anatomical search spaces

813 We localized face and body areas in restrained search spaces to also retrieve 814 anatomically more precise information. For the dog participants, we could not build on 815 previous research due to different template spaces or data unavailability and therefore 816 selected all task-responsive gyri as search spaces. We determined them performing a group-level activation comparison entering the visual stimulation contrast (all 817 818 conditions > implicit visual baseline) from the first task run in a second-level one 819 sample *t*-test. Since the majority of significant clusters expanded across more than one 820 anatomical region, we decided to not only select regions with a significant local maxima 821 (Table S1, section "dog participants", Fig 1C) but all gyri with visual responsive voxels. 822 This resulted in six search spaces for potential face or body regions: medial

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823 suprasylvian, caudal suprasylvian, ectomarginal, occipital, marginal and splenial gyrus 824 (Fig 2A). For the human participants, we used bilateral fusiform and occipital face area 825 parcels as face area search spaces and bilateral fusiform and extrastriate body area 826 parcels as body area search spaces derived from previous research [56]. Selecting the 827 top-10% voxels resulted in the following functional region of interest (fROI) sizes for 828 each hemisphere: medial suprasylvian gyrus (32 voxels), caudal suprasylvian gyrus 829 (27 voxels), marginal gyrus (35 voxels; for one dog 23 voxels in the left hemisphere 830 due to lower number of active voxels in contrast bodies > inanimate objects). 831 ectomarginal gyrus (31 voxels), splenial gyrus (34 voxels) and occipital gyrus (23 832 voxels). For the human participants, selecting the top-10% voxels from each of the four 833 parcels [56] resulted in the following fROI sizes: extrastriate body area (each 834 hemisphere: 137 voxels), fusiform body area (left: 53 voxels; right: 102 voxels), 835 occipital face area (left: 21 voxels, except one participant only had 15 active voxels, 836 and another had no active voxels; right: 79 voxels), fusiform face area (left: 216 voxels, 837 right: 241 voxels).

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# 838 9.3 Supplemental figures

# 839



**Fig S1.** Summary of the main study findings. Results from the functional regions of interest (univariate activation strength) and representational similarity analysis (multivariate activation pattern) illustrating the results on schematic brain figures. For simplification, observed results are always summarized on one hemisphere; they do not mark the exact but the approximate anatomical location.

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*Fig* S2. Overlap of individual functional regions-of-interest (fROIs) from dog participants. Individual fROIs were defined for faces (> inanimate objects) and bodies (> inanimate objects) within multiple anatomical search spaces (A-D) based on the data from localizer data set (i.e., first task run). The colour of the heat map indicates the amount of overlap between the fROIs of all dog participants. We observed slight individual differences in anatomical location between participants as indicated by a maximum overlap of N = 7 from overall 15 participants. The axial plane in panel A (top row) shows the anatomical locations posterior (P) and right hemisphere (R); all axial planes displayed have the same orientation. The sagittal plane displays the cut coordinates (z) and the anatomical locations superior (S) and anterior (A); z-coordinates refer to a canine-breed averaged template [50].

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*Fig S3.* Overlap of individual functional regions-of-interest (fROIs) from human participants. Individual fROIs were defined for faces (> inanimate objects) and bodies (> inanimate objects) within multiple anatomical search spaces (A-D) based on the data from the localizer data set (i.e. first task run). The colour of the heat map indicates the amount of overlap between the fROIs of all humans. We observed slight individual differences in anatomical location between participants as indicated by a maximum overlap of N = 30 from overall 40 participants. The axial plane in panel A shows the anatomical locations posterior (P) and right hemisphere (R); all axial planes displayed have the same orientation. The sagittal planes display the cut coordinates (z) and the anatomical locations superior (S) and anterior.

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# 843 9.4 Supplemental tables

		•			
	С	oordinate	es	_	
Contrast & brain region	х	у	z	z-value	cluster size
All conditions > implicit visual base	line				
Dog participants					
L medial suprasylvian gyrus	-16	-23	15	4.56	16
L caudal suprasylvian gyrus	-22	-26	-1	4.39	17
L medial suprasylvian gyrus	17	-26	16	4.32	74
L ectomarginal gyrus	-9	-27	21	4.29	52
R ectomarginal gyrus	10	-29	21	4.12	37
R caudal suprasylvian gyrus	22	-24	-1	4.04	24
Human participants					
R middle occipital gyrus	48	-70	-8	Inf	13423
R middle frontal gyrus	20	30	0	Inf	248
L hippocampus	-20	-30	-4	Inf	252
L inferior temporal gyrus	-28	-4	-36	6.89	65
R cerebellum	22	-42	-44	6.80	45

Table S1. Task-related activation: localizer data set (task run 1)

Effects were tested for significance with a cluster defining threshold of p < .001 and a cluster probability threshold of p < 0.05 FWE corrected for multiple comparisons for the dog data and a whole-brain FWE correction for the human data. We report the first local maximum within each cluster for both one sample *t*-tests and for the human data we limit the list to the first five cluster with the highest peak *z*-values. Coordinates for the dog data represent the location of the peak voxels referring to the canine breed-averaged template space[50]; the template along with another dog atlas[51] served to determine anatomical nomenclature for the dog data. Human data coordinates refer to the stereotactic Montreal Neurological Institute (MNI) space we obtained anatomical nomenclature from the Laboratory for Neuro Imaging (LONI) Brain Atlas[52] (LBPA40, <u>http://www.loni.usc.edu/atlases/</u>). Data of both samples is also presented in **Fig 1C**. L, left; R, right.

#### Neural bases of face and body perception in dogs and humans

Table S2. Results from one-way <sup>a</sup> repeated measures analyses of variance (ANOVAs)						
Search space (predictor: image category)	<i>df</i> <sub>Num</sub>	<i>df</i> <sub>Den</sub>	F	p	$\eta^2_g$	
Dog participants						
Individual body fROIs defined based on bodies > inanimate objects contrast from run 1						
Medial suprasylvian gyrus	2.26	31.68	26.01	< .0001	.37	
Caudal suprasylvian gyrus	2.26	31.66	12.53	< .0001	.25	
Ectomarginal gyrus	1.87	26.23	7.48	.003	.13	
Marginal gyrus	2.36	33.08	8.69	.001	.17	
Splenial gyrus	2.66	37.19	1.69	.191	.07	
Occipital gyrus	2.26	31.58	0.74	.499	.02	
Individual face fROIs defined based on face	s > inani	mate obje	ects contra	ast from run	1	
Medial suprasylvian gyrus	2.05	28.77	22.13	< .0001	.30	
Caudal suprasylvian gyrus	2.49	34.90	17.34	< .0001	.30	
Ectomarginal gyrus	1.75	24.55	12.11	< .0001	.18	
Marginal gyrus	1.95	27.30	6.38	.006	.12	
Splenial gyrus	2.34	32.72	1.61	.214	.06	
Occipital gyrus	2.26	31.58	0.74	.499	.02	
Human participants						
Individual body fROIs defined based on bod	lies > ina	nimate o	bjects con	trast from r	un 1	
Extrastriate body area	1.73	67.49	227.01	< .0001	.71	
Fusiform body area	2.00	77.98	152.22	< .0001	.59	
Individual face fROIs defined based on face	s > inani	mate obje	ects contra	ast from run	1	
Occipital face area	1.98	77.04	175.25	< .0001	.64	
Fusiform face area	2.12	82.86	187.29	< .0001	.63	
Note <sup>a</sup> Dependent variable: <i>image</i> category (level	s: hodies	faces inc	nimate ob	iects scram	aled) P	

*Note.* <sup>a</sup>Dependent variable: *image category* (levels: bodies, faces, inanimate objects, scrambled). *P*-values for group comparison investigating the same research question (i.e., species sensitivity for bodies) are Bonferroni-adjusted, resulting in an adjusted *p*-value of 0.008 (= 0.05/6) for the dog body functional regions of interest (fROIs) and face fROIs respectively and an adjusted *p*-value of 0.025 (= 0.05/2) for the human face and body fROIs. *P*-values surviving the adjusted threshold are in bold. Post-hoc comparison results are presented in **Fig 2B**. *df*<sub>Num</sub>, degrees of freedom numerator; *df*<sub>Den</sub> degrees of freedom denominator;  $\eta^2_g$ , generalized eta-squared.

Table S3. Results from 2 >	<sup>c</sup> 2 <sup>a</sup> repeated measures analy	vses of variance (ANOVAs)
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Search space, predictor	<i>df</i> <sub>Num</sub>	<i>df</i> <sub>Den</sub>	F	, р	n²a
Dog participants		2311		<u> </u>	13
Individual body fROIs defined based on bod	ies > ina	nimate ol	biects cont	rast from	run 1
Medial suprasylvian gyrus					
Species	1	14	3.54	.081	.02
Image category	1	14	7.26	.017	.03
Species × image category	1	14	2.18	.167	.02
Caudal suprasylvian gyrus					
Species	1	14	3.75	.073	.02
Image category	1	14	0.206	.174	.01
Species × image category	1	14	.01	.926	.00
Ectomarginal gyrus					
Species	1	14	2.57	.131	.01
Image category	1	14	1.42	.253	.01
Species × image category	1	14	4.57	.051	.02
Marginal gyrus					
Species	1	14	0.50	.493	.00
Image category	1	14	7.90	.014	.05
Species × image category	1	14	2.25	.156	.03
Splenial gyrus					
Species	1	14	0.03	.859	.00
Image category	1	14	3.71	.074	.03
Species × image category	1	14	1.26	.281	.02
Occipital gyrus					
Species	1	14	1.10	.312	.01
Image category	1	14	0.01	.921	.00
Species × image category	1	14	0.26	.620	.00
Individual face fROIs defined based on faces	s > inanir	nate obje	ects contra	st from rui	n 1
Medial suprasylvian gyrus					
Species	1	14	2.51	.135	.01
Image category	1	14	7.11	.018	.03
Species × image category	1	14	1.95	.185	.02
Caudal suprasylvian gyrus					
Species	1	14	1.61	.225	.02
Image category	1	14	10.20	.007	.06
Species × image category	1	14	0.03	.857	.00
Ectomarginal gyrus					
Species	1	14	2.75	.120	.02
Image category	1	14	1.86	.194	.01
Species × image category	1	14	4.22	.059	.03
Marginal gyrus					

Neural bases of face and body perception in dogs and humans					
Species	1	14	0.08	.786	.00
Image category	1	14	10.03	.007	.07
Species × image category	1	14	1.23	.286	.01
Splenial gyrus					
Species	1	14	0.26	.617	.00
Image category	1	14	1.73	.209	.02
Species × image category	1	14	.70	.416	.01
Occipital gyrus					
Species	1	14	1.21	.289	.02
Image category	1	14	0.03	.855	.00
Species × image category	1	14	3.90	.068	.02
Human participants					
Individual body fROIs defined bas	sed on bodies > i	nanimate	objects con	trast from i	run 1
Extrastriate body area					
Species	1	39	3.15	.084	.01
Image category	1	39	187.26	< .0001	.39
Species × image category	1	39	14.15	.001	.02
Fusiform body area					
Species	1	39	0.54	.469	.00
Image category	1	39	15.24	< .0001	.04
Species × image category	1	39	1.43	.239	.00
Individual face fROIs defined bas	ed on faces > ina	inimate ol	ojects contra	ast from rur	า 1
Occipital face area					
Species	1	39	0.02	.889	.00
Image category	1	39	36.99	< .0001	.07
Species × image category	1	39	1.14	.292	.00
Fusiform face area					
Species	1	39	12.24	.001	.02

*Note.* <sup>a</sup>Dependent variables are *species* (levels: dog, human) and *image category* (levels: bodies, faces). *P*-values for group comparison investigating the same research question (i.e., category selectivity for bodies, category selectivity for faces) are Bonferroni-adjusted, resulting in an adjusted *p*-value of 0.008 (= 0.05/6) for the dog body functional regions of interest (fROIs) and face fROIs respectively and an adjusted *p*-value of 0.025 (= 0.05/2) for the human face and body fROIs. *P*-values surviving the adjusted threshold are in bold, for the dog data none of the *p*-values survived the adjusted threshold. *df<sub>Num</sub>*, degrees of freedom numerator; *df<sub>Den</sub>* degrees of freedom denominator;  $\eta^2_g$ , generalized eta-squared.

1

1

39

39

45.23

0.28

< .0001

.600

.11

.00

846

Image category

Species × image category

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	Coordinates (breed-averaged template)					
Contrast & brain region	х	У	Z	<i>t</i> -value	cluster size	
Bodies [dog bodies × human bodies] > inanimate objects						
R caudal suprasylvian gyrus	19	-24	4	5.77	116	
Faces [dog faces × human faces] > inanimate objects						
R marginal gyrus	5	-35	21	7.01	245	
R olfactory tuberculum	8	8	-2	6.16	80	
Conspecific (dog) bodies > heterospecific (human) bodies						
L caudal suprasylvian gyrus	-16	-27	4	5.21	99	
L piriform lobe	-15	-3	-4	5.18	95	
Animate [dog bodies × human bodies × dog faces × human faces] > inanimate stimuli						
R splenial gyrus	5	-32	7	5.38	70	
R caudal suprasylvian gyrus	19	-24	3	5.25	72	

Table S4. Dog data: Pattern similarity during face, body and object perception

Effects were tested for significance with a cluster defining threshold of p < .005 and a cluster probability threshold of p < 0.05 FWE corrected for multiple comparisons. We report the first local maximum within each cluster for all paired sample *t*-tests. The results from the paired sample *t*-tests comparing faces [dog faces × human faces] vs. bodies [dog bodies × human bodies] and conspecific (dog) faces vs. heterospecific (human) faces along with the reversed contrasts [dog bodies × human bodies] < inanimate objects, [dog faces × human faces] < inanimate objects, conspecific (dog) bodies < heterospecific (human) bodies and [dog bodies × human bodies] < inanimate objects, [dog bodies < human bodies] < inanimate objects, [dog bodies < human bodies] < inanimate objects, [dog bodies] < inanimate objects, [dog bodies] < inanimate objects, [dog bodies] <

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	Coordinates (MNI space)						
Contrast & brain region	х	У	z	<i>t</i> -value	cluster size		
Bodies [dog bodies × human bodies] > inanimate objects							
R middle occipital gyrus	56	-72	6	14.98	14018		
L middle occipital gyrus	-54	-78	10	12.32	1622		
L cerebellum	-4	-70	-40	7.33	585		
L superior parietal gyrus	-26	-62	68	6.65	1383		
R superior frontal gyrus	6	62	-4	6.17	881		
L precentral gyrus	-26	-10	50	5.26	570		
Bodies [dog bodies × human bodies] < inanimate objects							
L inferior temporal gyrus	-22	-48	-12	11.26	6678		
Faces [dog faces × human faces] > inar	nimate object	s					
R fusiform gyrus	46	-42	-20	9.35	1088		
Faces [dog faces × human faces] < inanimate objects							
L cerebellum	-20	-54	-18	14.20	7002		
R lingual gyrus	24	-56	-8	11.84	5198		
L precentral gyrus	-46	6	32	4.77	353		
Faces [dog faces × human faces] > bodies [dog bodies × human bodies]							
R lingual gyrus	6	-88	0	11.35	3461		
Faces [dog faces × human faces] < bod	ies [dog bodi	ies × hu	man bodies	5]			
R middle occipital gyrus	34	-72	10	14.21	39057		
R middle orbitofrontal gyrus	24	42	-14	5.53	1087		
R cerebellum	8	-72	-38	5.19	572		
R cingulate gyrus	2	6	26	4.76	267		
Conspecific (human) bodies > heterosp	ecific (dog) b	odies					
R fusiform gyrus	44	-44	-22	5.76	1053		
L middle occipital gyrus	-54	-72	12	4.87	267		
R middle temporal gyrus	40	-54	12	4.81	468		
R superior parietal gyrus	16	-54	42	4.60	466		
Heterospecific (dog) faces > conspecific (human) faces							
L middle occipital gyrus	-16	-94	6	7.20	8147		
Brainstem	6	-40	-26	4.64	618		
R middle occipital gyrus	56	-72	0	5.71	349		

Table S5. Human data: Pattern similarity during face, body and object perception

Animate [dog bodies × human bodies × dog faces × human faces] > inanimate objects

	Neural bases of face and body perception in dogs and humans				
R middle occipital gyrus	56	-72	0	9.09	2035
L cerebellum	-4	-70	-42	7.30	277
R postcentral gyrus	36	-26	48	5.09	403
R superior parietal gyrus	38	-44	68	4.82	338
R superior frontal gyrus	8	52	-8	4.77	564

Animate [dog bodies × human bodies × dog faces × human faces] < inanimate objects

L cerebellum	-22	-50 -18	12.63	11878

Effects were tested for significance with a cluster defining threshold of p < .001 and a cluster probability threshold of p < 0.05 FWE corrected for multiple comparisons. We report the first local maximum within each cluster for all paired sample *t*-tests. Results from the reversed contrasts conspecific (human) bodies < heterospecific (dog) bodies and heterospecific (dog) faces < conspecific (human) did not survive the statistical threshold. Coordinates refer to the stereotactic Montreal Neurological Institute (MNI) space and represent the location of the peak voxels. We obtained anatomical nomenclature from the Laboratory for Neuro Imaging (LONI) Brain Atlas [52] (LBPA40, <u>http://www.loni.usc.edu/atlases/</u>). Data is also presented in **Fig 3B-D**.