Similarities and differences of face and body perception in the dog (*Canis familiaris*) and human brain

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Abstract

Accurately recognizing other individuals is fundamental for successful social interactions. While the neural underpinnings of this skill have been studied extensively in humans, less is known about the evolutionary origins of the brain areas specialized for recognising faces or bodies. Studying dogs (*Canis familiaris*), a non-primate species with the ability to perceive faces and bodies similarly to humans, promises insights into how visuo-social perception has evolved in mammals. We investigated the neural correlates of face and body perception in dogs (N = 15) and humans (N = 40) using functional MRI. Combining uni- and multivariate analysis approaches, we identified activation levels and patterns that suggested potentially homologous occipito-temporal brain regions in both species responding to faces and bodies compared to inanimate objects. Crucially, only human brain regions showed activation differences between faces and bodies and partly responded more strongly to humans compared to dogs. Moreover, only dogs represented both faces and dog bodies in olfactory regions. Overall, these findings advance our understanding of the similarities and differences in brain function between two phylogenetically distant mammal species. This likely reflects differences in the perceptual systems these species rely on to recognize others, and provides important insights into the foundations of social cognition and behaviour.

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.

Therefore, the neural underpinnings of face and body perception have been studied extensively in humans. Decades of research revealed a predominant role of the occipito-temporal cortex for the perception of others with distinct, but adjacent regions specialized for face and body perception as part of the so-called ventral visual pathway [8–17]. While the ventrolateral visual cortex responds to animate compared to inanimate stimuli more generally [18–20], the sensitivity in the occipital face and extrastriate body area (lateral occipital cortex), as well as the fusiform face and fusiform body area (inferior temporal cortex) appear increased for faces or bodies [10–13,15–17,21–28]. Regarding the recognition of another individual's species-identity, previous research suggests a preference for human faces compared to faces of other species (such as dogs or horses) [29,30], potentially reflecting increased salience of conspecifics over heterospecifics.

The evolutionary history of the neural underpinnings of face and body perception has been mainly investigated by comparative research in non-human primates [21–24,28,31], and this has revealed a homologous visual pathway [e.g. 8,32 for reviews]. However, apart from primate species, the neural bases of this socio-cognitive ability and its potential origin in the mammalian brain remain largely unstudied. Dogs' (*Canis familiaris*) ability to perceive and understand humans and conspecifics has already been well-investigated using behavioural and eye-tracking measures and yielded

numerous comparable skills between dogs and humans. For example, dogs can not only differentiate between faces [33,34], but even discriminate facial emotional cues of humans and conspecifics [7,35,36]; and they demonstrate complex behaviours such as visual perspective taking [37,38]. Thus, dogs constitute an excellent model to study the evolution of visuo-social perception in mammals [39].

While first non-invasive canine neuroimaging studies [29,40–43] suggested an involvement of the temporal cortex in face perception, they triggered a debate on whether the occipito-temporal specialization for face perception in dogs matches that of humans [29,40–43]. Previous work reported increased activation for faces compared to objects [41,43], scenes [41], or a mono-coloured surface [40], but not compared to other low-level visual controls (i.e., scrambled images [40,41] or the back of the head [29]). Some studies lacked non-facial controls entirely [42]. Studies additionally investigating responses to con- and heterospecifics were inconclusive ranging from reports of increased responsiveness to dog stimuli in general (i.e., face and back of the head) but no specialization for faces [29], over separate brain regions specialized for human or dog faces [42], to no species- but general face-preference [41]. Further, no previous work investigated the neural bases of body perception. This is a major limitation, as bodies play an important role for social perception in general, but in particular for dogs - as indicated e.g., by dogs' high responsiveness to emotional or ostensive-referential bodily cues, such as tail-wagging [44] or human gestures [44–46]. It is particularly noteworthy in this respect, that dogs even outperform humans' closest living relatives, chimpanzees, in utilizing human ostensive cues [47].

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

of the neural bases of face, body and inanimate object perception in dogs and humans, in order to gain insights into how social perception has evolved in two phylogenetically distant mammalian species. [39,48].

2 Results

Fifteen awake and unrestrained pet dogs (**Figure 1A**) and forty human participants underwent functional magnetic resonance imaging (MRI) while viewing images of human and dog bodies, faces, inanimate objects (e.g., different toys), and grid-scrambled versions of these images serving as visual controls (**Figure 1B**). Over the course of two 5 min runs, participants saw 180 different images presented in a block design interspersed with an implicit visual baseline. We analysed the dog fMRI data with a newly developed analysis protocol shown to significantly improve neural signal detection power [49]. All statistical tests were corrected for multiple comparisons (see **fMRI data analysis, Figures 1-3**, **Supplementary file 1: Tables S1-S5**).

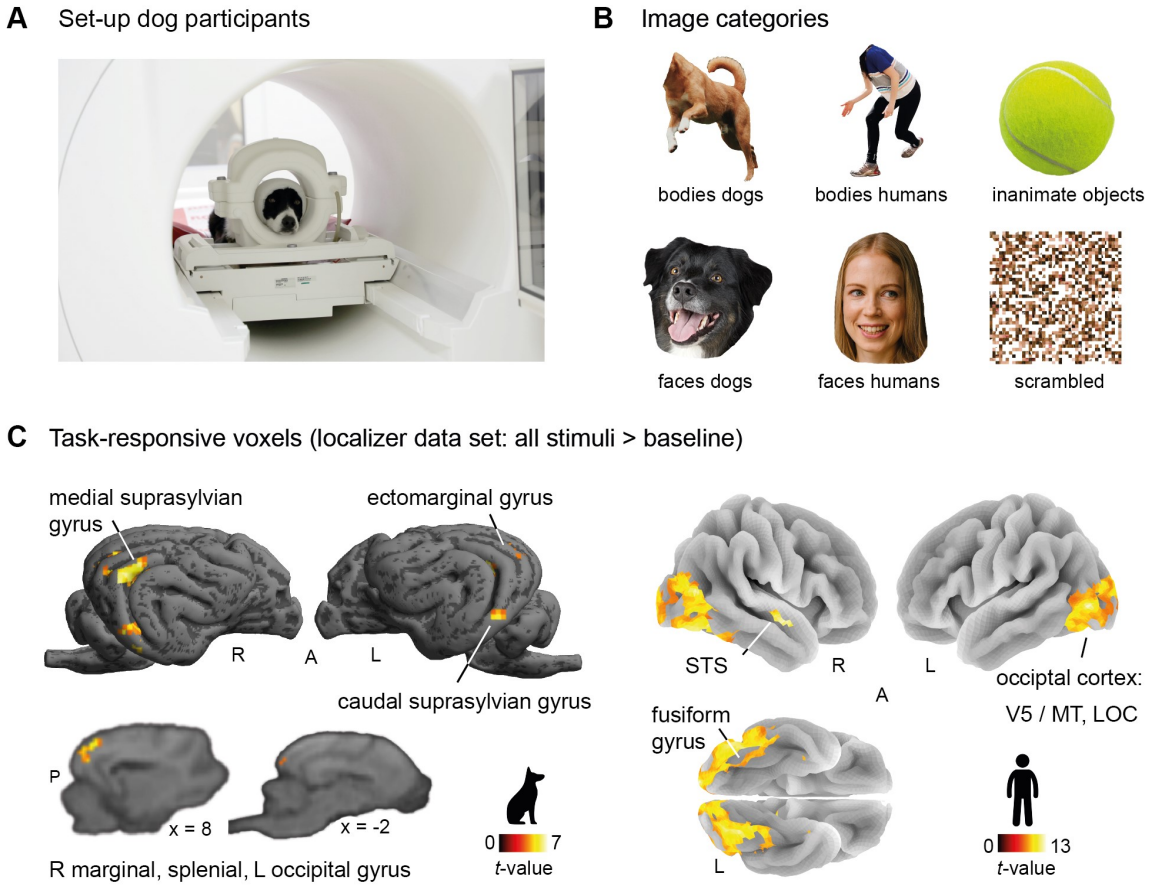

Figure 1. *Overview of the comparative experimental approach to study the neural bases of face and body perception in dogs and humans.* (**A**) We obtained all imaging data using a 3T Siemens Skyra MR-system, equipped with a 15-channel human knee coil to scan the dog participants, and using a 32-channel human head coil for the human participants (not depicted). Dogs received extensive training [50] 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 grid-scrambled 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 **Figure 2A**). Results are displayed at $p < 0.05$, *FWE*-corrected at cluster-level using a cluster-defining threshold of $p < .001$ (dogs, **Supplementary File 1: Table S1**), and $p < 0.05$ whole-brain *FWE*-corrected (humans; **Supplementary File 1: Table S1**) Results for the dogs are overlaid onto a canine breed-averaged surface render [51], and onto the FreeSurfer "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 [52] and to the human brain atlas from the Laboratory for Neuro Imaging (LONI) Brain Atlas [53] (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 cortex.

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

To start out, we investigated whether dogs and humans have specialized cortical regions for face and body perception, and whether these regions responded differently to images of con- or heterospecifics. To this end, we used a standard functional region-

of-interest analysis approach (fROI,[54–56]). We split the data into two orthogonal data sets, (1) a localizer data set (first task run) to define potential face- or body-sensitive areas in visual-responsive brain regions (**Figure 1C**, **2A**) and (2) a test data set (second task run) to extract activation levels from these regions and to test potential category sensitivity. We chose this approach for two reasons. First, we aimed at directly testing the potential category-sensitivity, quantified by increased activation levels. Second, our goal was to account for differences in the location of activation peaks between individuals as reported in previous dog imaging studies [41,43].

2.1.1 Functional regions-of-interest (fROIs)

For each participant, we defined bilateral fROIs within constrained search spaces to preserve spatial information (i.e., the rough anatomical location of activation peaks). For the human participants, we used previously reported anatomical regions known to be engaged in face and body perception [57]: the extrastriate body area, fusiform body area, occipital face area and fusiform face area (**Figure 2A**). For the dog participants, we could not build on previous research due to lack of shared template space and availability of data. Therefore, we first compared activation levels associated with the visual presentation of all stimuli compared to implicit baseline (i.e., white cross presented on grey background) using the localizer data set. This revealed task-responsive activation within the occipital-, splenial-, ectomarginal-, caudal-, medial suprasylvian- and marginal gyri, partially overlapping with results from previous studies investigating face perception [29,40–43,58,59] (**Figure 1C**, **Supplementary File 1: Table S1**). We then used anatomical masks [52] of these regions as search spaces for the dog participants (**Figure 2A**). For comparison, we also report task-responsive voxels for the human participants, confirming involvement of the occipito-temporal cortex including the lateral occipital cortex and fusiform gyrus (**Figure 1C**,

Supplementary File 1: Table S1; see also **Figure 4** for schematic figures of the dog and human brain).

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.

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

Next, we extracted the mean activation signal during viewing of faces, bodies, inanimate objects and scrambled images (all compared to the implicit baseline) from the individual fROIs using the test data set. In dogs, we observed significantly increased activation levels for faces and bodies compared to inanimate objects or scrambled images in both face and body fROIs, located in the medial and caudal suprasylvian- and ectomarginal gyrus. In the caudal suprasylvian face- and ectomarginal body fROI, the increased activation for faces showed the same trend but did not always reach significance. We did not find consistent evidence for a further sub-division into face- and body-selective areas in the occipito-temporal cortex, as there was no significant activation difference between faces and bodies in seven out of eight fROIs. We only observed significantly increased activation for bodies compared to faces in the caudal suprasylvian face but not body fROI. The occipital and splenial face and body fROIs did not result in differential activation changes in response to any of the stimulus categories (**Supplementary File 1: Table S2**). Regarding the parietal cortex, the marginal gyrus appeared solely responsive to bodies compared to all other conditions with no activation differences for faces compared to inanimate objects or scrambled controls (**Figure 2B**).

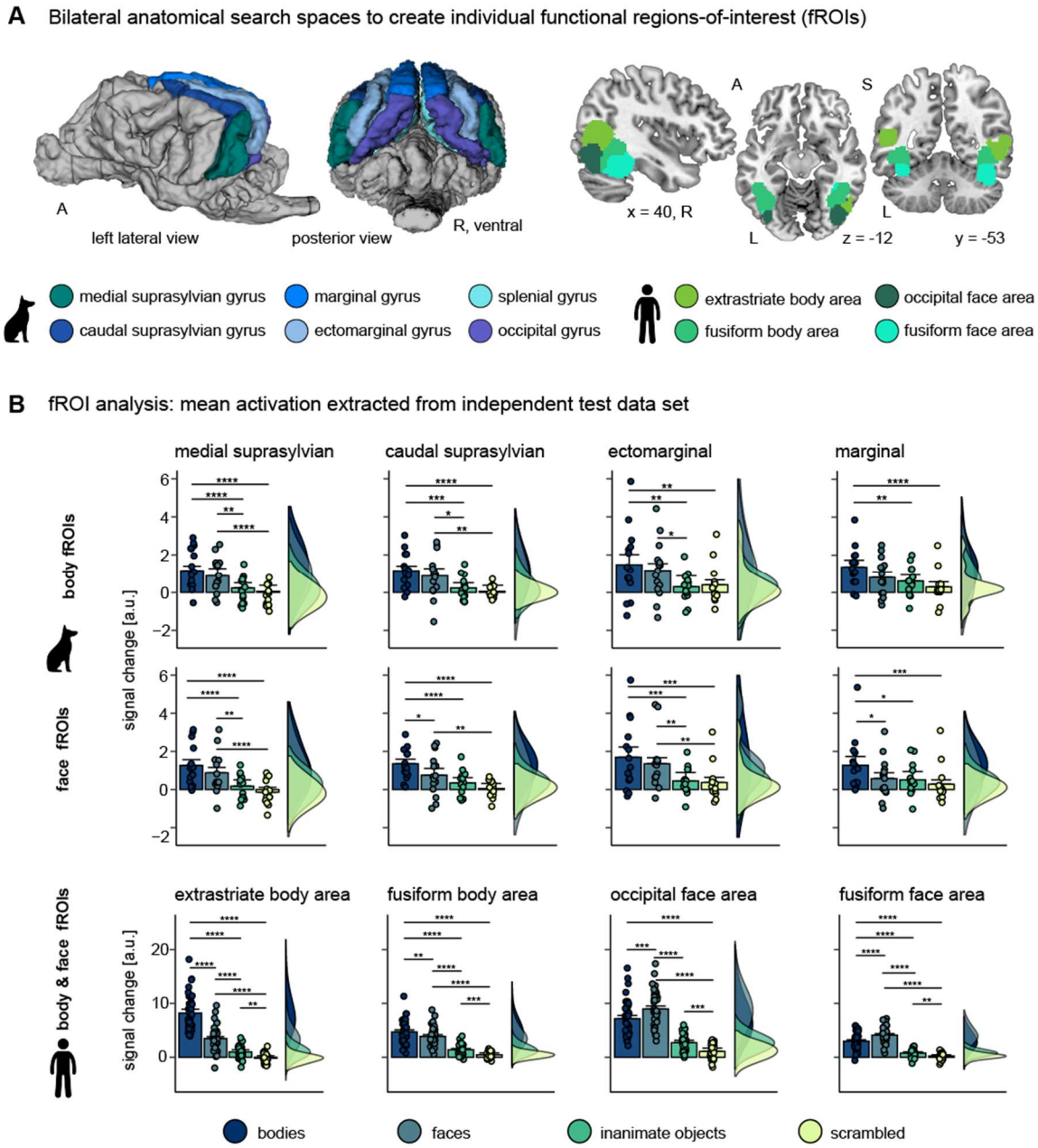

Figure 2. *Strongest activation levels for animate stimuli in both species, but differences between faces and bodies exclusive in humans.* (**A**) Based on the localizer data set, we defined individual category-specific regions-of-interest (functional region-of-interest approach, fROI) within multiple 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 primarily 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 (**Supplementary File 1: Table S2**). Planned comparisons were corrected for multiple comparisons using Tukey method. *$p < .05$, **$p < .01$, ***$p < .001$, ***$p < .0001$, error bars represent the standard error of the mean; a.u., arbitrary units. Atlas maps and search spaces refer to the dog brain atlas from Czeibert and colleagues [52] and human parcels were retrieved from previous work [57]. A, anterior; P, posterior; S, superior; L, left; R, right.

Results for the human participants confirmed earlier research [10–13,15–17,21–28] with the strongest overall activation levels for bodies in the extrastriate and fusiform

body areas and for faces in the occipital and fusiform face areas (**Figure 2B**, **Supplementary File 1: Table S2**). In summary, we found multiple occipito-temporal regions in the dog and human cortices responsive to animate stimuli, but detected a further sub-division into face- and body-sensitive regions exclusively in the human brain (see also **Figure 4** for a summary of the results).

2.1.3 Conspecifics preference in human extrastriate body and fusiform face area

Next, we investigated whether processing of faces or bodies differed when participants saw images of con- compared to heterospecifics (**Supplementary File 1: Table S3**). In humans, this revealed increased activation for human (mean: 4.46, *SD* = 1.83) compared to dog bodies (mean: 3.76, *SD* = 1.66) in the extrastriate body area ($t(39) = 3.14$, $p = 0.003$, $\text{mean}_{\text{Diff}}$: 0.7, 95% CI [0.25, 1.15]), as well as a general activation increase for human (mean: 1.89, *SD* = 0.87) compared to dog (mean: 1.64, *SD* = 0.81) stimuli in the fusiform face area ($t(79) = 3.71$, $p < 0.0001$, $\text{mean}_{\text{Diff}}$: 0.25 , 95% $\text{CI}_{\text{meandiff}}$ [0.16, 0.38]). For the dogs, we did not find a difference between the perception of dog and human stimuli.

2.2 Multivariate pattern analysis of animacy perception

Despite the overall activation (measured using mass-univariate analyses) to stimulus categories may not differ, we reasoned that more fine-grained analyses of multivariate activation patterns could reveal distinctions [60]. Therefore, we investigated the neural representations of faces and bodies in dogs and humans and their potential correspondence using whole-brain representational similarity analyses (RSA). We moved a 4 and 8 mm searchlight across the whole dog and human brain, respectively, in order to determine individual pattern similarity maps between all trials of each stimulus category [61–63] (**Figure 3A**). On the group-level, we then conducted paired *t*-tests to compare the pattern similarities maps of (1) animate vs. inanimate

stimuli, (2) bodies vs. inanimate objects, (3) faces vs. inanimate objects, (4) faces vs. bodies, and (5,6) within the face and body categories: images of conspecifics vs. 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 (**Supplementary File 1: Tables S4-S5**). In brief, this indicates distinct neural representations of animate compared to inanimate stimuli in higher-order visual regions of both species.

2.2.1 Similar and divergent neural representations of bodies and 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 (**Figure 3B**). Within the same regions (and again, in both species), we also observed distinct activation patterns for conspecific compared to heterospecific bodies. Furthermore, when the dogs viewed dog bodies, results revealed increased similarity in limbic structures and regions associated with olfaction (**Figure 3C**). In humans, we observed increased similarity for human compared to dog bodies in fronto-parietal regions associated with action perception [64–66] (**Figure 3C**).

Observing faces compared to inanimate objects resulted in significantly increased pattern similarity in occipito-temporal cortices of both species and again in dog olfactory structures (**Figure 3D**). Comparing similarity patterns for faces vs. bodies, we only found significant differences for the human participants (see **Supplemental file 1: Tables S4-5** for detailed results and **Figure 4** for a schematic summary of the main results).

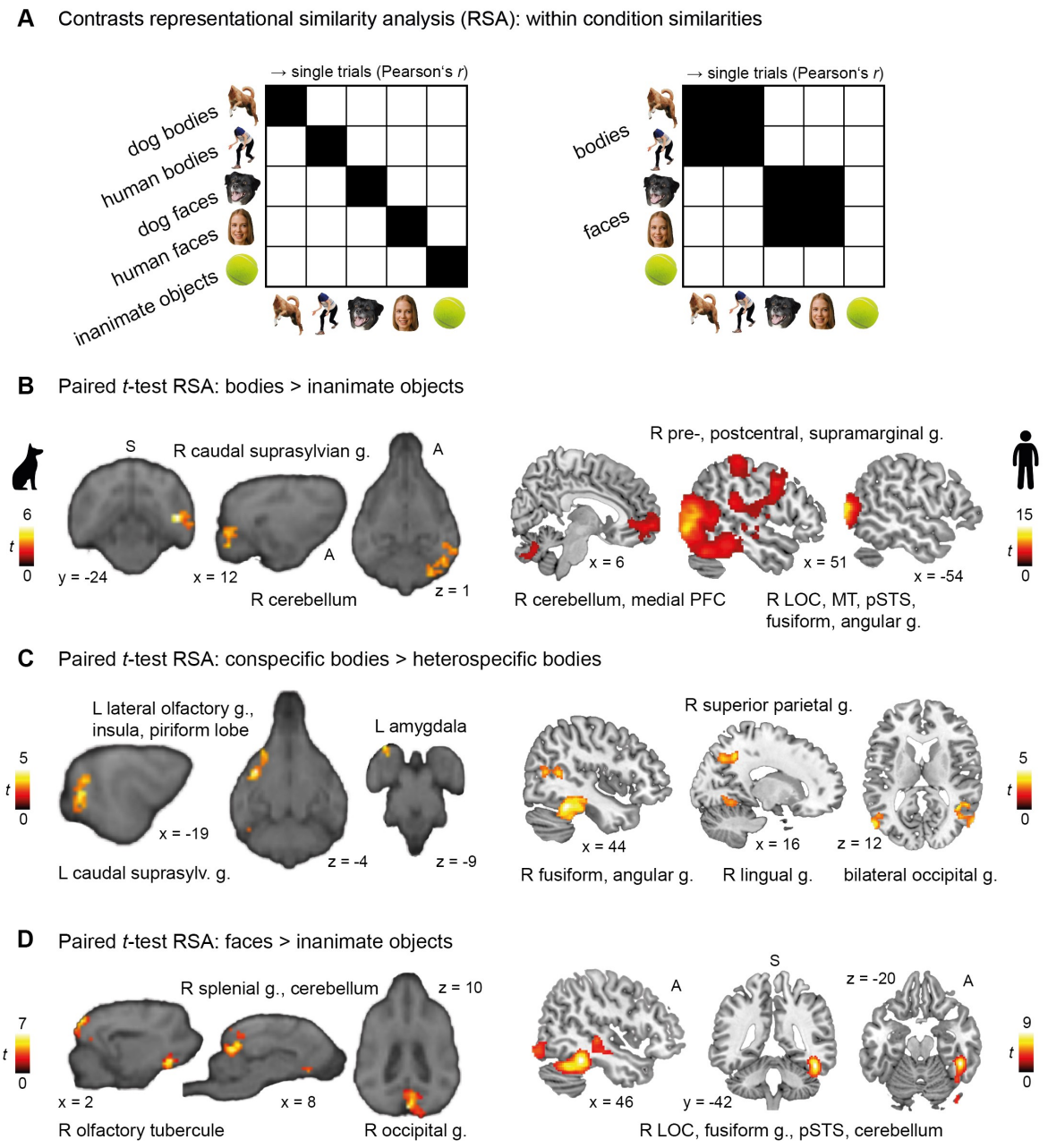

Figure 3. *Whole-brain representational similarity analysis (RSA) revealed similar and divergent neural patterns of activation for animate vs. inanimate stimuli but differences between faces and bodies again exclusive in human.* (**A**) We moved a 4/8 mm (dog/human) spherical searchlight across the whole 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 [64–66]. 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 (**Supplementary file 1: 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 [51] 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.

3 Discussion

Our findings revealed that the occipito-temporal cortex has a prominent role in the perception of animate entities in both dogs and humans. This suggests that the neural processing of animate vs. inanimate stimuli across mammalian brains may either have an old evolutionary origin in the common ancestors of canines and primates or is the result of convergent evolution [48]. However, within these regions, only humans displayed an additional sub-division into distinct face- and body-sensitive brain regions. Moreover, only dogs showed distinct responses to human and dog faces as well as dog bodies in olfactory areas (see **Figure 4** for schematic summary of the results). These findings suggest a divergent evolution of the neural bases of face and body perception (or processing) in dogs and humans. The differential engagement of visual and olfactory brain functions would fit particularly well with the differential sensitivity and preferential use of these perceptual systems to infer social and contextual information.

Detecting biological agents is crucial for survival and social relationships. Hence, the visual differentiation between animate vs. inanimate entities is an evolutionary important category representation. Studies show that dogs target animate agents when, for example, presented with images of wild animals, humans or dogs embedded in natural landscapes [67] or of social interactions between humans and dogs [68]. Further, dividing stimuli into an animate vs. inanimate dimension is one of the first visually salient categorizations formed by human infants [69]. In this way, animacy representation provides the first building block for more complex visual categorizations such as faces vs. bodies. Thus, considering its biological significance and the observed cross-species similarities in our study, animacy might constitute a general organizing principle across mammalian brains.

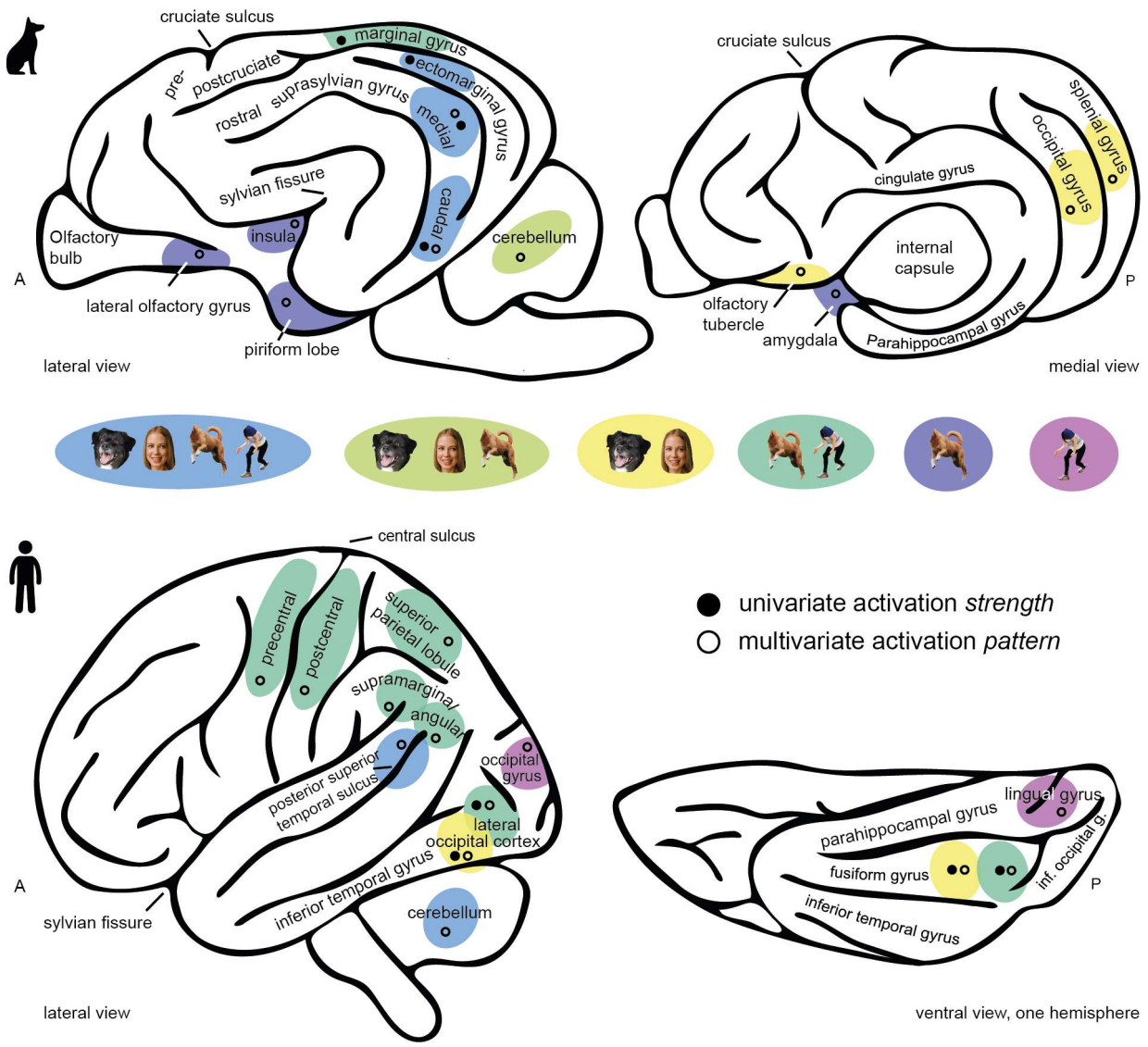

Figure 4. *Summary of the main study findings.* Results from the functional regions of interest (univariate activation strength) and representational similarity analysis (multivariate activation pattern) illustrating the results on schematic brain figures. For simplification, observed results are always summarized on one hemisphere; they do not mark the exact but the approximate anatomical location.

Behavioural [7,34,35,44,70–73] and imaging studies [58,59] have also demonstrated that dogs are able to perceive facial and bodily cues of dogs and humans and display high responsiveness to ostensive-referential bodily cues [45,46,74,75], already as puppies [76]. 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 [77] 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.

While previous investigations of how dogs perceive bodies have mainly focused on the decoding of human referential cues, we hope that our work will inspire more research on how dogs perceive bodily social as well as emotional cues of con- as well as heterospecifics. The absence of a further sub-specialization for face vs. body perception in the occipito-temporal cortex of dogs might indeed indicate that dogs in comparison to humans focus more on whole body social cues rather than on specific sub-parts. This interpretation is notably well in line with a recent comparative eye-tracking study [78].

Regarding species perception, our results indicate an increased salience for human compared to dog stimuli in humans, but no evidence for a conspecific-preference in the occipito-temporal cortex of dogs. Thus, human and dog stimuli appear to be equally salient for dogs. This is in line with previous behavioural studies suggesting, for example, no significant difference in the perception of human or dog emotional facial [35], whole-body cues [78], or images of social interactions [68]. Further, two studies demonstrated that dogs, already as puppies, follow human gestural-communication and show an interest in human faces [76], which has not been observed in wolf puppies [79]. Additionally, half of the variation in these socio-cognitive skills could be accounted for by genetic factors, suggesting that dogs' attention to humans might have been enhanced during domestication [75 for review of both studies]. Future studies investigating species-preferences in dogs might thus consider adding further heterospecific stimuli of other familiar species, such as cats.

In accordance with a potential divergent evolution of face and body representations in dogs and humans, we also observed distinct neural representations for faces (regardless of species) and conspecific (dog) bodies in dog olfactory regions.

271 Although unexpected, these results might reflect dogs' significantly higher olfactory
272 sensitivity and it's use to infer social and contextual information [54 for review].
273 However, the link between cognition and olfaction remains speculative since
274 behavioural studies using olfactory cues so far mainly explored dogs' odour and
275 disease detection abilities (e.g., [82–86] while dog imaging studies on olfaction focused
276 on reward-processing [87,88] or general sensory abilities [89–91]. However, a recent
277 behavioural study investigating dog cognition using olfactory cues showed first
278 evidence that dogs form representations of their owners when smelling their tracks
279 [92].

280 In humans, results revealed distinct activation patterns for bodies in fronto-
281 parietal regions that have been consistently associated with the perception of actions
282 [64–66]. In dogs, we did not find activation in (pre-)motor cortices, but the increased
283 neural sensitivity for bodies in the occipito-parietal marginal gyrus might be initial
284 evidence for an analogous visual pathway to encode actions. However, this is beyond
285 our study's scope, and the precise neural underpinnings of action observation in dogs
286 have not yet been investigated.

287 We have taken several steps to maximize neural signal sensitivity already when
288 designing our study (e.g., by using a block design) and at the analysis stage (e.g., by
289 using dog-tailored hemodynamic models increasing response detection power [49]).
290 Nevertheless, the extensive training required for dogs [50] resulted in different sample
291 sizes for the two species, and the more extensive prior work in humans [57] resulted
292 in more constrained search spaces, and likely higher spatial sensitivity for the human
293 data. Further, the majority (80%) of our pet dogs were pure-bred herding dogs, which
294 prevented us from testing potential breed-specific differences [as in e.g. 90] and may
295 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.

4 Materials and Methods

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.

For the dog sample size we aimed to collect data from a minimum of N = 12 dogs during the data collection period from April 2019 to July 2020 which was the median sample size of task-based dog fMRI studies at the time of planning the study (the median sample size in 2021 is also N = 12). For the human participants, we aimed for a sample size of N = 40 participants, based on previous studies in our lab with similar task designs, and also being in line with a previous study [57] investigating the neural bases of face and body perception using a functional region-of-interest approach with a sample size of N = 35 participants (reporting F-values above 40 for all repeated measures analyses).

Prior to MRI scanning, all dogs underwent initial medical examination concerning their eyesight and general health and received extensive training to habituate to the MRI environment [50]. They were fully awake, able to exit the MRI scanner at any time and equipped with noise protection (**Figure 1A**). All caregivers gave informed written consent to their dogs' participation. Human participants were right handed, had normal

or corrected-to-normal vision, they reported no history of neurological or psychiatric disease, nor phobia of dogs, fulfilled the standard inclusion criteria for functional MRI, and gave informed written consent to participate. The study complies with the ARRIVE guidelines [94]. Dog data collection was approved by the institutional ethics and animal welfare commission in accordance with Good Scientific Practice (GSP) guidelines and national legislation at the University of Veterinary Medicine Vienna (ETK-06/06/2017), based on a pilot study conducted at 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).

4.2 Task and procedure

We employed a block design (duration: 12 s) split in two 5 min runs where participants saw images of faces and bodies of dogs or humans, objects and scrambled versions of these images (5 images per block; **Figure 1B**, see below) on an MR-compatible screen (32 inch) positioned at the end of the scanner bore. Crucially, we used the same task for dogs and humans. Human participants were instructed to watch the images presented on the MR screen and dogs were trained to attend to the MR screen (passive viewing paradigm). Each run contained three blocks per condition, block order was randomized but the same condition was never presented twice in a row. Between blocks, participants saw a visual baseline jittered between 3-7 s with a white cross presented on grey background. Image composition for each block and order within each block was randomized across participants to ensure effects are not driven by specific blocks; each image was presented once. The task was implemented using PsychoPy [95]. Overall motion and wakefulness were live monitored via the camera of an eye-tracker (Eyelink 1000 Plus, SR Research, Ontario, Canada) positioned below the MR-compatible screen. For the dogs, the trainer stayed within the

347 scanner room but out-of-sight throughout the scan session to monitor and handle the
348 dogs. Human participants saw both runs within a single scanner session with a short
349 break in-between. For the dogs, the number of attempted sessions varied depending
350 on how many repetitions they needed to complete one run without substantive motion
351 and with sufficient attentiveness (i.e., eyes open and gazing towards the centre of the
352 screen); in-between task runs the dogs always were given a short break outside the
353 MR scanner. Realignment parameters were evaluated after each scan session. If
354 overall motion exceeded 4 mm in any of the three translation directions, the dog was
355 re-invited to repeat the run in a subsequent session and sessions were scheduled at
356 least one week apart. On average, dogs needed three sessions to complete both runs.
357 No data of the non-successful sessions were used for analysis.

358 ### 4.2.1 Stimulus material

359 The stimulus set comprised 180 coloured images of faces and bodies of dogs
360 and humans, everyday inanimate objects (e.g., a toy, a chair), and phase-grid
361 scrambled versions of each category (30 images per condition) derived from Wagner
362 and colleagues [96], the Hemera Photo-Object data base (Hemera Technologies) and
363 the internet (see **Figure 1B** for examples). The images were resized to 600 × 600
364 pixels and presented in the centre of the MR screen on grey background. We cut out
365 the heads off from the body images, as well as objects from body images (e.g., a coffee
366 cup, a soccer ball). The images showed a variety of postures (e.g., jumping, looking
367 up), neutral and positive emotional displays (e.g., sleeping, smiling) and viewing
368 perspectives (e.g., from above, from a side angle). Luminance was set homogeneously
369 across stimuli and we controlled for spatial extent (see **Supplementary file 2A** for
370 details).

371 ## 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 2-fold multiband (MB) accelerated echo planar imaging (EPI) sequence including the following parameters: voxel size = 1.5 x 1.5 x 2 mm^3, repetition time (TR) / echo time (TE) = 1000/38 ms, field of view (FoV) = 144 × 144 × 58 mm^3, flip angle = 61°, 20% gap and 24 axial slices covering the whole brain (interleaved acquisition, descending order). Structural scans had a voxel size of 0.7 mm isotropic (TR/TE = 2100/3.13 ms, FoV = 230 × 230 × 165 mm^3) and were acquired in a separate scan session prior to functional data collection. Human functional scans were acquired using a 4-fold MB accelerated EPI sequence including the following parameters: voxel size = 2 mm isotropic, TR/TE = 1200/34 ms, FoV = 192 × 192 × 124.8 mm^3, flip angle = 66°, 20% gap and 52 axial slices coplanar to the connecting line between anterior and posterior commissure (interleaved acquisition, ascending order). Additionally, we obtained field map scans to correct functional scans for magnetic field inhomogeneities using a double echo gradient echo sequence with the following parameters: voxel size = 1.72 x 1.72 x 3.85 mm^3, TR/TE1/TE2 = 400/4.92/7.38 ms, FoV = 220 × 220 × 138 mm^3, flip angle = 60° and 36 axial slices (same orientation as functional scans). Structural scans had a voxel size of 0.8 mm isotropic (TR/TE = 2300/2.43 ms, FoV = 256 × 256 × 166 mm^3) and were acquired after functional data acquisition.

4.4 Data processing and statistical analysis

Imaging data was preprocessed and analyzed using SPM12 (https://www.fil.ion.ucl.ac.uk/spm/software/spm12/), Matlab 2018b (MathWorks) and R 3.6.3 [97].

397 **4.4.1 MRI data preprocessing**

398 In both samples, we slice-time corrected (reference: middle slice) and realigned
399 functional images to the mean image. Human imaging data was also unwarped using
400 the acquired field map. Dog imaging data was manually reoriented with the rostral
401 commissure set as a visual reference (SPM module: "*Reorient images / Set origin*") to
402 match the template orientation [51] and structural images were skull-stripped using
403 individual binary brain masks created using itk-SNAP [98]. Next, we co-registered the
404 structural and functional images to the mean functional image, segmented the
405 structural images in both samples and normalized the human data to the Montreal
406 Neurological Institute (MNI) template space and the dog data to a breed-averaged
407 stereotaxic template space [51]. Normalized images were resliced to 1.5 mm isotropic
408 and smoothed with a 3-dimensional Gaussian kernel (full-width-at-half-maximum,
409 FWHM; with twice the raw voxel resolution: dogs/humans = 3/4 mm; see [49] for an in-
410 depth description of our dog data preprocessing pipeline). We then calculated
411 individual scan-to-scan motion (frame wise displacement, FD) and added motion
412 regressors to first-level GLMs for each scan exceeding the a priori set FD threshold of
413 0.5 mm (motion scrubbing [99,100]) to account for both translational and rotational
414 displacements. For the dog participants, we removed on average 8% of the scans from
415 each run (run 1: mean FD = 0.23 mm, 90th percentile = 0.36 mm; run 2: mean FD =
416 0.24 mm, 90th percentile = 0.38 mm) and 1% of the scans from each run of the human
417 participants (run 1: mean FD = 0.17 mm, 90th percentile = 0.22 mm; run 2: mean FD =
418 0.18 mm, 90th percentile = 0.21 mm).

419 **4.4.2 fMRI data analysis**

420 **Mass-univariate activation analysis**. We analysed the functional data using a
421 general linear model (GLM) approach implemented in SPM12. Individual GLM
422 matrices included six regressors of interest for task (dog faces, dog bodies, human

423 faces, human bodies, inanimate objects, scrambled) and the six regressors from the
424 realignment procedure (see above) were added as nuisance regressors. All blocks
425 were estimated using a boxcar function time-locked to the onset of each block with a
426 duration of 12 s. For the dog data, the signal was convolved with a tailored dog
427 haemodynamic response function [49] (HRF), while the standard human canonical
428 HRF (i.e., the default HRF parameters provided by SPM12) was used for the human
429 data. The dog HRF reflects a previously observed 2-3 s earlier peak of the BOLD signal
430 than expected by the human HRF model [49]. Normalized, individual binary masks
431 served as explicit masks and we applied a high-pass filter with a cut-off at 128 s. We
432 then split the data in two sets (task run 1, task run 2). Based on the data from the first
433 task run, we estimated three subject-level contrast maps for the difference between
434 our conditions of interest (i.e., faces, bodies with equal weights for human and dog
435 images) and objects, and a visual stimulation contrast (all conditions > implicit visual
436 baseline). For the second task run, we computed eight subject-level contrasts, one for
437 each task regressor (i.e., dog bodies, human bodies, dog faces, human faces,
438 everyday inanimate objects, scrambled), averaged for faces (i.e., dog and human
439 faces) and averaged for bodies (i.e., dog and human bodies) compared to implicit
440 visual baseline.

441 **Functional region of interest (fROI) approach.** We implemented a standard
442 functional region-of-interest (fROI, [54–56]) approach to investigate potential category-
443 specificity of cortical regions. This approach allows us to directly test the potential
444 category-sensitivity quantified by increased activation level while accounting for slight
445 differences in the location of activation peaks between individuals as which have been
446 reported in previous dog imaging studies [41,43].

447 The participant-level contrast images from the first run served as localizer data to
448 define individual category-sensitive regions. Within anatomically constrained search

449 spaces (**Figure 2A**) we selected the top-10% voxel from each hemisphere with the
450 strongest signal for the condition-of-interest (i.e., face areas: faces > objects, body
451 areas: bodies > objects) to form bilateral individual fROIs. Selecting the top-10% voxel
452 was an *a priori* decision we made because the resulting fROI sizes (on average: 30
453 voxels) were similar to the average cluster size observed in a previous dog imaging
454 study that used two visual paradigms and the same smoothing kernel [49]. Further,
455 percentages instead of absolute numbers took also the varying search space sizes
456 into account (see **Supplementary file 2B** and **Figure 2 – figure supplements 1-2** for
457 more information). The data from the left out second run allowed then to directly test
458 potential category specificity in an independent data set. Thus, we extracted parameter
459 estimates from the conditions-of-interest contrasted against implicit visual baseline
460 from both body and faces areas (= individual fROIs) using the REX toolbox [101].

461 Group functional ROI analyses were performed running repeated measures
462 analyses of variance (ANOVAs). First, we tested our main research question, whether
463 the body areas resulted in increased sensitivity for bodies regardless of species and
464 vice versa for faces, and added everyday objects and scrambled images as further
465 conditions. Thus, we ran a one-way ANOVA with *stimuli category* (faces, bodies,
466 everyday objects, scrambled*)* as dependent variable. Next, to investigate if there is a
467 difference in activation between conspecific and heterospecific stimuli, we used 2 x 2
468 within-subjects ANOVAs (*species*: conspecific, heterospecific; *image category*: face,
469 body). *P*-values for group comparisons investigating the same research questions
470 were Bonferroni-adjusted, e.g., if the 6 potential body fROIs result in increased
471 sensitivity for bodies compared to all other categories results in an adjusted *p*-value of
472 0.008 (= 0.05/6). Adjusted *p*-values are reported along with the results
473 (**Supplementary File 1: Tables S2-3**). For whole-brain group analyses, we tested
474 significance applying a whole-brain familywise error (*FWE*) correction for the human

475 data and a cluster-level inference with a cluster defining threshold of $p < 0.001$ and a
476 cluster probability of $p < 0.05$ *FWE* corrected for multiple comparisons for the dog data.
477 Cluster extent (i.e., minimum spatial extend to be labelled significant) was calculated
478 using the SPM extension "CorrClusTh.m" (by Thomas Nichols, University of Warwick,
479 United Kingdom, and Marko Wilke, University of Tübingen, Germany;
480 https://warwick.ac.uk/fac/sci/statistics/staff/academic-research/nichols/scripts/spm/).

481 **Representational similarity analysis**. Next, we investigated the neural
482 representations for faces, bodies and objects and their potential convergence in dogs
483 and humans. To this end, we performed a whole-brain representational similarity
484 analysis (RSA; [61–63]) to determine neural pattern similarities within image
485 categories. GLMs were modelled identical to univariate GLMs (see above) but for each
486 block, we ran a separate GLM with the block as task regressor and remaining blocks
487 were combined in one regressor of no interest [102]; runs were modelled
488 independently. Thus, the analysis resulted in 36 beta images for each participant (6
489 conditions × 6 trials). RSA was performed using the smoothed functional data. For all
490 RSA analyses, we moved a spherical searchlight [103] (dogs: r = 4 mm, 81 voxel;
491 humans: r = 8 mm, 251 voxel) throughout individual whole-brain grey matter masks
492 computed based on the normalised segmentation output considering only searchlights
493 with a minimum of 15 grey matter voxel for the dog and 30 for the human data.

494 Within a given searchlight, we extracted single-trial beta estimates from all voxels
495 and sorted them according to their stimuli category (**Figure 3A**; dog / human bodies,
496 dog / human faces, inanimate objects) and reshaped the data to a trial × voxel matrix.
497 Next, we *z*-scored the data across trials and runs and computed a trial × trial similarity
498 matrix by correlating each beta estimate of each trial to all other trial estimates. Finally,
499 in order to retrieve overall similarity scores, we then Fisher's *z*-transformed the data
500 and calculated overall similarity matrices by averaging scores across the respective

quadrants. We were specifically interested in pattern similarities across animate vs. inanimate (faces × bodies vs. inanimate objects), faces or bodies vs. inanimate objects, faces vs. bodies and conspecific vs. heterospecific species dimensions within face and body categories. We then assigned the overall similarity values to the centre voxel of each searchlight resulting in individual whole-brain pattern similarity maps.

On the group-level, we then used paired *t*-tests to compare the pattern similarities between trials of (1) faces vs. inanimate objects (i.e., [dog faces × human faces] vs. inanimate objects), (2) bodies vs. inanimate objects (i.e., [dog bodies × human bodies] vs. inanimate objects), (3) animate vs. inanimate images (i.e., [dog faces × human faces x dog bodies × human bodies] vs. inanimate objects), (4) faces vs. bodies (i.e., [dog faces × human faces] vs. [dog bodies × human bodies]), and (5,6) within the face and body categories: images of conspecifics vs. heterospecifics (i.e., dog faces vs. human faces; dog bodies vs. human bodies). We computed permutation tests [104] to determine group-level significance using the Statistical nonParametric Mapping (SnPm13, http://www.nisox.org/Software/SnPM13/) toolbox running 5000 permutations for each paired *t*-test and applied cluster-level inference with a cluster defining threshold of $p < .005/.001$ (dogs/humans) and a cluster probability of $p < 0.05$ familywise error corrected (*FWE*) for multiple comparisons.

Data visualization. Data was visualized using SPM12 (https://www.fil.ion.ucl.ac.uk/spm/software/spm12/), Matlab 2018b (MathWorks), itk-SNAP [98], R 3.6.3 [97] mainly using the packages ggplot2 [105] and RainCloudPlots [106] and the python project nilearn (http://nilearn.github.io).

5 Data availability statement

The code to create functional regions-of-interest (fROIs) within anatomical search spaces and to extract activations levels, as well as the representational

similarity analysis (RSA) code are openly available on Github (https://github.com/magdalenaboch/fROI-analysis, https://github.com/isabellawagner/searchlight-rsa). The extracted fROI activation levels along with the R code to visualize and analyse the data, the overlap maps of individual fROIs, thresholded and unthresholded statistical maps of univariate (all > implicit baseline) and RSA analysis and averaged structural images to serve as background images to overlay the data on have been uploaded to the Open Science Framework and are openly available at https://osf.io/kzcs2/.

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7 CRediT authorship statement

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

8 Declaration of Competing Interests

The authors declare no competing financial interests.

9 Supplementary Files

Supplementary file 1. Supplementary tables: **Table S1.** Task-related activation: localizer data set (task run 1), **Table S2.** Results from one-way[a] repeated measures analyses of variance (ANOVAs), **Table S3.** Results from 2 × 2[a] repeated measures analyses of variance (ANOVAs), **Table S4.** Dog data: Pattern similarity during face, body and object perception and **Table S5.** Human data: Pattern similarity during face, body and object perception.

Supplementary file 2. 2A: Stimulus material: luminance and spatial extent, **2B:** Anatomical search spaces and size individual fROIs

10 Figure supplements

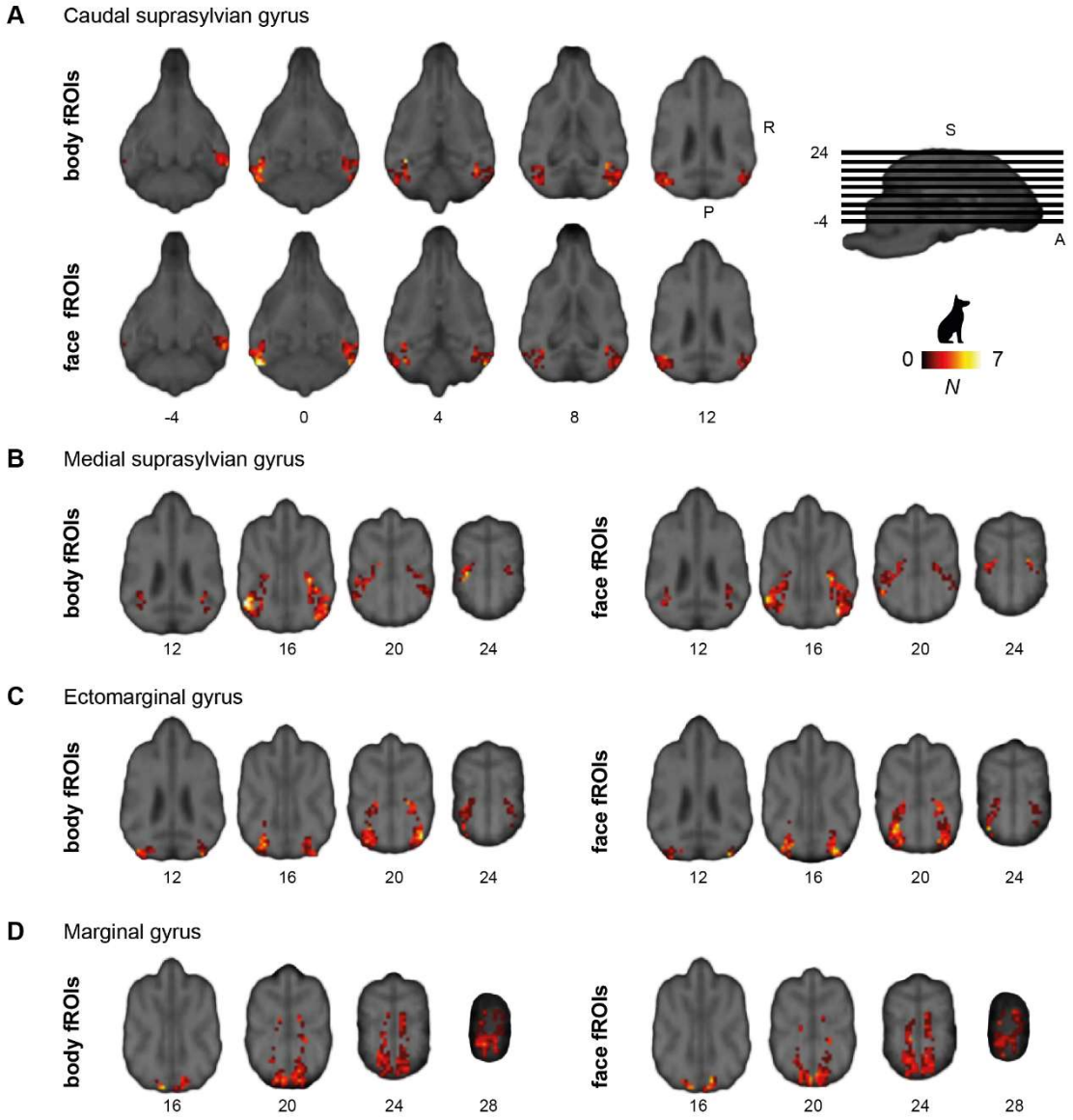

Figure 2 – figure supplement 1. *Overlap of individual functional regions-of-interest (fROIs) from dog participants.* Individual fROIs were defined for faces (> inanimate objects) and bodies (> inanimate objects) within multiple anatomical search spaces (A-D) based on the data from localizer data set (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 [51].

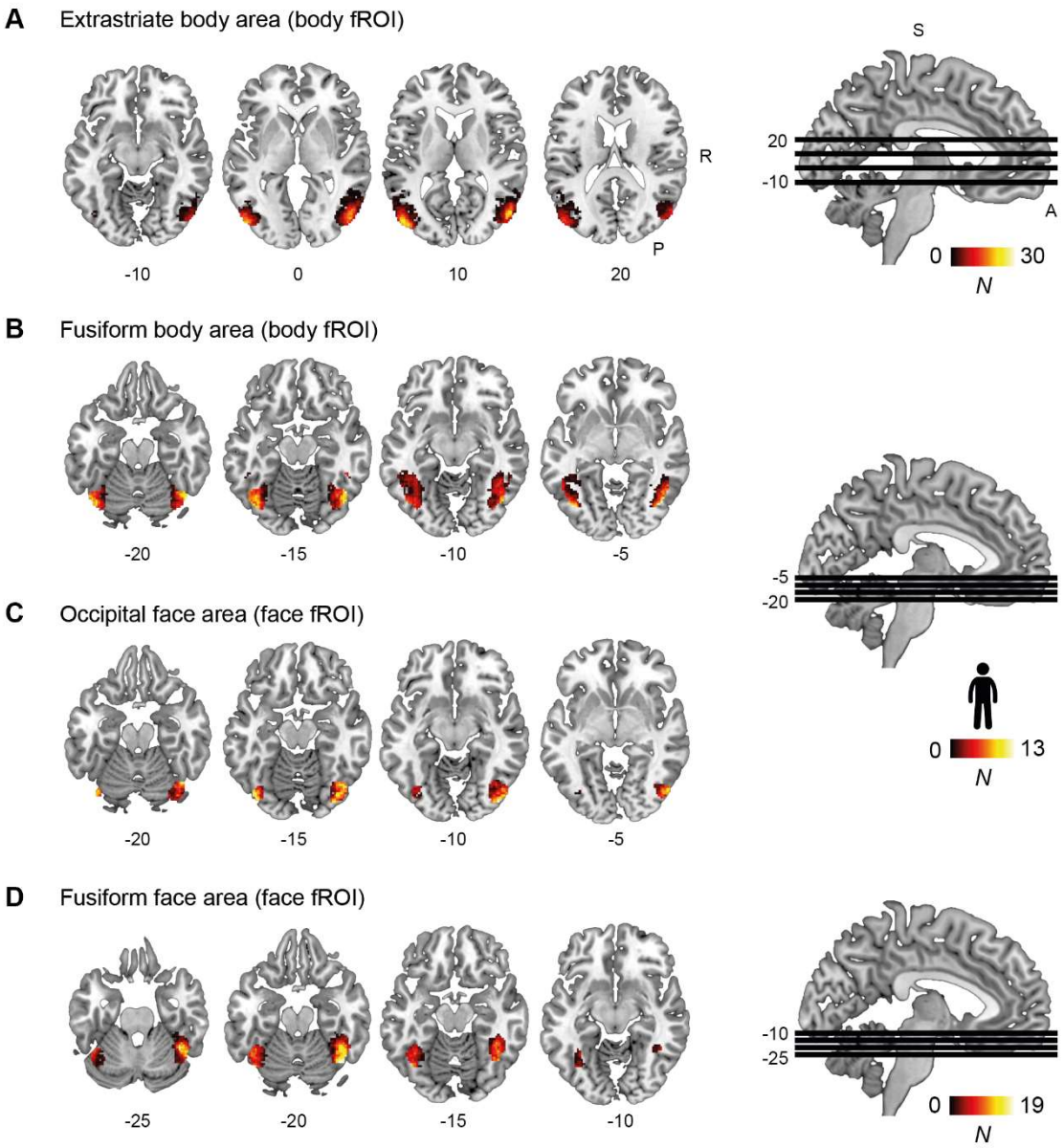

Figure 2 – figure supplement 2. *Overlap of individual functional regions-of-interest (fROIs) from human participants*. Individual fROIs were defined for faces (> inanimate objects) and bodies (> inanimate objects) within multiple anatomical search spaces (A-D) based on the data from the localizer data 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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