

2D or Not 2D? An fMRI Study of How Dogs Visually Process Objects

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Competing Interests

G.B. & M.S. own equity in Dog Star Technologies and developed technology used in some of the research described in this paper. The terms of this arrangement have been reviewed and approved by Emory University in accordance with its conflict of interest policies.

Ethics Statement

This study was performed in accordance with the recommendations in the Guide for the Care and Use of Laboratory Animals of the National Institutes of Health. The study was approved by the Emory University IACUC (Protocols DAR-2002879-091817BA and DAR-4000079-ENTPR-A), and all owners gave written consent for their dog's participation in the study.

Data Availability

The datasets generated during the current study are available from the corresponding author on reasonable request.

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Author Contributions

A.P. and G.B. designed the research; A.P., R.C., K.A., V.C. and G.B. collected the data; A.P, M.S. and G.B trained the dogs, A.P. and G.B. analyzed data; and A.P. and G.B. wrote the paper.

Keywords

Dogs, fMRI, 2D, 3D, objects, brain

ABSTRACT

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Given humans' habitual use of screens, they rarely consider potential differences when viewing two dimensional (2D) stimuli and real-world versions of dimensional stimuli. Dogs also have access to many forms of screens and touch pads, with owners even subscribing to dog-directed content. Humans understand that 2D stimuli are representations of real-world objects, but do dogs? In canine cognition studies, 2D stimuli are almost always used to study what is normally 3D, like faces, and may assume that both 2D and 3D stimuli are represented in the brain the same way. Here, we used awake fMRI of 15 dogs to examine the neural mechanisms underlying dogs' perception of two- and three-dimensional objects after the dogs were trained on either a two- or three-dimensional version of the objects. Activation within reward processing regions and parietal cortex of the dog brain to 2D and 3D versions of objects was determined by their training experience, as dogs trained on one dimensionality showed greater activation to the dimension on which they were trained. These results show that dogs do not automatically generalize between two- and three-dimensional stimuli and caution against implicit assumptions when using pictures or videos with dogs.

INTRODUCTION

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62 Studies of canine cognition frequently rely on two-dimensional (2D) pictures to test
63 dogs' ability to discriminate between objects, species, or faces (Albuquerque et al. 2016; Autier-
64 Derian et al. 2013; Barber et al. 2016; Huber et al. 2013; Muller et al. 2015; Pitteri et al. 2014;
65 Wallis et al. 2017). Visual stimuli for these studies are utilized because they are easy to obtain
66 from studies on humans and nonhuman primates and are easy to implement in laboratory
67 settings. But the ecological validity of this line of research hinges on the extent to which the
68 findings transfer to real-world stimuli and contexts (Romero and Snow 2019). As dogs may not
69 perceive 2D visual stimuli as humans do, are images appropriate stimuli for the study of dog
70 cognition?

71 Visual stimuli are often selected without considering the nature of dogs' visual
72 perception (Miller and Murphy 1995). For example, dogs have a higher flicker fusion rate than
73 humans. This means that they may perceive the flickering of a video display if the refresh rate is
74 too low. With movies, dogs may notice a gap or flicker between frames. Dogs also have a visual
75 streak as opposed to a fovea (as in primates), causing increased sensitivity to stimuli in the
76 periphery of the visual field. This means that displaying a picture or playing a video to a dog
77 may not accurately reflect what a dog sees in the real world because they may focus on
78 different aspects of the video than we do (Byosiere et al. 2018; Byosiere et al. 2019). Although
79 there is ample evidence that dogs can perceptually discriminate features of images, this does
80 not mean that the images necessarily represent their real-world counterparts to the dog.

81 Research in canines and other nonhumans that utilize pictures share an underlying
82 assumption that, like humans, dogs perceive 2D stimuli such as faces as similar to real 3D faces.

83 Dogs do behaviorally differentiate pictures, as they can discriminate between pictures of
84 human facial expressions and between pictures of familiar and strange dogs or humans (Autier-
85 Derian et al. 2013; Barber et al. 2016; Huber et al. 2013; Muller et al. 2015; Pitteri et al. 2014;
86 Somppi et al. 2012), and following substantial training, dogs show the ability to follow
87 commands presented by humans through video projection (Pongracz et al. 2003). One study
88 reported dogs' use of duplicates of the objects or miniature versions as referents to retrieve the
89 corresponding objects, concluding that dogs can use iconic representations (Kaminski et al.
90 2009). However, the same dogs did not perform well using pictures versions of the
91 corresponding objects. Despite this widespread use of 2D visual stimuli in canine cognition,
92 studies have not shown that dogs use 2D stimuli as referents for real world stimuli.

93 The ability to abstract from 2D to 3D versions of objects is not uniquely human. Many
94 nonhuman species show evidence of behavioral transfer from pictures or videos to objects,
95 pictures of food, or conspecifics following substantial training (Bovet and Vauclair 2000;
96 Johnson-Ulrich et al. 2016; Wilkinson et al. 2013). This means that there is little evidence for 2D
97 to 3D transfer happening naturalistically in a nonhuman species. Nor does recognition between
98 pictures mean that the animal has abstract knowledge of objects, that they have formed a
99 mental representation, or that they equate pictures and real world objects (Jitsumori 2010;
100 Weisman and Spetch 2010).

101 Using functional magnetic resonance imaging (fMRI), regions of the primate brain have
102 been identified as selective for processing specific types of visual stimuli, including the fusiform
103 face area (FFA) for processing faces or the lateral occipital complex (LOC) for processing objects
104 (Beauchamp et al. 2004; Durand et al. 2007; Eger et al. 2008; Janssen et al. 2018; Kourtzi and

105 Kanwisher 2000; Kriegeskorte et al. 2008). Yet these fMRI studies have a similar caveat: they
106 too rely on 2D visual stimuli as proxies for real-world stimuli and use subjects who are overly
107 familiar with pictures.

108 There is some evidence that object processing regions of the human brain respond
109 differently to 2D and 3D versions of stimuli. An fMRI study that directly compared neural
110 activation within the LOC to real world objects and 2D versions of the same objects found that
111 the LOC does not respond to the two versions of stimuli in the same way (Snow et al. 2011). In
112 behavioral studies, real objects also prompt greater attention and memory retrieval than 2D
113 images, and elicit goal-directed actions whereas 2D images do so to a lesser degree (Gomez et
114 al. 2018; Snow et al. 2014). Goal directed actions, such as grasping, are difficult to generalize to
115 2D versions of objects because 2D versions lack the same binocular cues or proprioceptive
116 feedback (Freud et al. 2018; Gallivan and Culham 2015; Hutchison and Gallivan 2018).

117 As in human studies of vision, fMRI can be used to elucidate the neural mechanisms
118 underlying dogs' perception of objects. FMRI studies of awake dogs have increased in
119 complexity and duration, paralleling human fMRI studies. Canine studies show that stimulus-
120 reward associations acquired prior to or during scanning are learned at different rates due to
121 neural biases within the reward-processing regions of the brain, such as the caudate and
122 amygdala (Cook et al. 2016; Prichard et al. 2018a). Dogs also process familiar human words
123 associated with objects in similar language-processing regions of humans, like the temporal-
124 parietal junction, and show greater activation to novel words versus familiar words (Prichard et
125 al. 2018b). As in human imaging, functional localizers have also revealed areas of dogs' occipital
126 cortex selective for processing human and dog faces (Cuaya et al. 2016; Dilks et al. 2015; Szabo

127 et al. 2020; Thompkins et al. 2018). Together these studies show that activation within areas of
128 the dog brain can be used to predict perceptual or behavioral biases when processing visual
129 stimuli.

130 In two separate studies, we used fMRI to measure activity in dogs' brains in response to
131 both objects and pictures of the objects. In Study 1, 15 dogs were split into two groups; dogs in
132 the first group were trained on two 3D objects, and dogs in the second group were trained on
133 two pictures of the objects. One stimulus was associated with reward and the other with
134 nothing. During the fMRI session, dogs from both groups were presented with both the picture
135 stimuli and object stimuli. If hedonic mechanisms facilitate abstraction from 2D to 3D (and vice-
136 versa), then dogs should show greater neural activity in the caudate for the trained reward
137 stimulus than the no reward stimulus, regardless of whether they were trained on objects or
138 pictures. In Study 2, we developed a functional localizer for object processing regions analogous
139 to LOC. If dogs equate 2D and 3D stimuli, then they should show no difference in neural activity
140 between the object and the picture in these regions.

141 **MATERIALS AND METHODS**

142 *Participants*

143 Participants for both studies were 15 pet dogs volunteered by their Atlanta owners for
144 fMRI training and fMRI studies (Prichard et al. 2018a) (Table 1). Each dog had previously
145 completed two or more scans for the project and had demonstrated the ability to participate in
146 MRI scans.

147 *General Experimental Design*

148 The experimental design was similar to previous dog fMRI studies that examined
149 preference using visual stimuli associated with food or social reward (Cook et al. 2016). Briefly,
150 dogs entered and positioned themselves in custom chin rests in the scanner bore. All scans took
151 place in the presence of the dog's owner, who stood out of view of the dogs throughout the
152 scan near the opening of the scanner bore and delivered all rewards (hot dogs) to the dog. An
153 experimenter was stationed next to the owner, out of view of the dog, where the experimenter
154 controlled the presentation of stimuli to the dogs. The onset and offset of each stimulus were
155 timestamped by the simultaneous press of a four-button MRI-compatible button box by the
156 experimenter.

157 *Imaging*

158 Scanning was conducted with a Siemens 3 T Trio whole-body scanner using procedures
159 described previously (Berns et al. 2013; Berns et al. 2012; Prichard et al. 2018a; Prichard et al.
160 2018b). The functional scans used a single-shot echo-planar imaging (EPI) sequence to acquire
161 volumes of 22 sequential 2.5 mm slices with a 20% gap (TE = 25 ms, TR = 1260 ms, flip angle =
162 70°, 64 x 64 matrix, 2.5 mm in-plane voxel size, FOV = 192 mm). Slices were oriented dorsally to
163 the dog's brain (coronal to the magnet, as in the sphinx position the dogs' heads were
164 positioned 90 degrees from the prone human orientation) with the phase-encoding direction
165 right-to-left. Four runs of up to 400 functional volumes were acquired for each subject, with
166 each run lasting about 9 minutes. Following functional scans, a T2-weighted structural image of
167 the whole brain was acquired using a turbo spin-echo sequence (25-36 2mm slices, TR = 3940
168 ms, TE = 8.9 ms, flip angle = 131°, 26 echo trains, 128 x 128 matrix, FOV = 192 mm).

169 *Preprocessing*

170 Preprocessing was the same as described in previous studies (Berns et al. 2013; Prichard
171 et al. 2018a). Briefly, preprocessing of the fMRI data included motion correction, censoring, and
172 normalization using AFNI (NIH) and its associated functions. A hand-selected reference volume
173 for each dog that corresponded to their average position within the magnet bore across runs
174 was used for two-pass, six-parameter rigid-body motion correction. Aggressive censoring
175 removed unusable volumes from the fMRI time sequence because dogs can move between
176 trials and when consuming rewards. Data were censored when estimated motion was greater
177 than 1 mm displacement scan-to-scan and also based on outlier voxel signal intensities. A mask
178 was drawn in functional space for each dog in the cerebellum, which was used to censor the
179 data further by removing volumes where the beta values extracted from the cerebellum were
180 assumed to be beyond the physiologic range of the BOLD signal ($> |3$ percent signal change |)
181 for each trial. Smoothing, normalization, and motion correction parameters were identical to
182 those described in previous studies (Prichard et al. 2018a). EPI images were smoothed and
183 normalized to %-signal change with 3dmerge using a 6mm kernel at full-width half-maximum.
184 The Advanced Normalization Tools (ANTs) software was used to spatially normalize the mean of
185 the motion-corrected functional images (Avants et al. 2011) to the individual dog's structural
186 image. We also performed a nonlinear transformation from each dog's structural image to a
187 high-resolution canine brain atlas, developed from a previous study of Labrador retrievers
188 (Berns et al. 2017).

189 *Experimental Design*

190 **Study 1: 2D vs. 3D**

191 In each session, dogs were presented with two objects (a stuffed giraffe and a stuffed
192 whale) and two life-sized cut-out pictures posted on foamboard of the objects (Fig 1). Each
193 stimulus was attached to a three-foot dowel that the experimenter used to present the stimuli
194 to the dog while inside the scanner bore. Neither object had been encountered before by the
195 dogs. Dogs were semi-randomly split into two groups prior to scanning, 8 in the object group
196 and 7 in the picture group. Prior to the first run, dogs were trained on the stimulus-reward
197 associations (10 reward, 10 no-reward) based on their assigned group. Dogs were also
198 refreshed on the stimulus-reward associations between runs (5 reward, 5 no-reward).
199 Following each run, dogs would exit the scanner and rest or drink water.

200 Dogs in the object group were trained on object stimuli and were semi-randomly
201 assigned the whale or giraffe as the reward stimulus. The presentation of the reward object
202 (giraffe or whale) was immediately followed by the delivery of a food reward, and presentation
203 of the other object was immediately followed by nothing. In the picture group, dogs were
204 trained on picture stimuli and were semi-randomly assigned the whale or giraffe as the reward
205 stimulus. The presentation of the reward picture (giraffe or whale) was immediately followed
206 by the delivery of a food reward, and the other picture was immediately followed by nothing.
207 Training on the conditioned stimuli occurred prior to each run when the dog was positioned in
208 the scanner bore, but before scan acquisition. During scan acquisition, no stimuli were followed
209 by the delivery of a food reward, so that dogs could not discriminate between objects and
210 pictures based solely on food reward. To maintain general motivation to stay in the scanner,

211 food rewards were presented by the owner randomly throughout the scan session between
212 presentations of the stimuli.

213 An event-based design was used, consisting of trained reward and trained no-reward
214 trial types, as well as symbolic reward and symbolic no-reward trial types. Trained reward and
215 trained no-reward trials consisted of the two conditioned stimuli associated with food reward
216 prior to scanning (e.g. objects for half of the dogs, pictures for the other half). Symbolic reward
217 and symbolic no-reward trials consisted of the two untrained stimuli (e.g. pictures for dogs
218 trained on objects, and objects for dogs trained on pictures). On all trials, a stimulus was
219 presented for a 5 s duration, followed by nothing. Trials were jittered to randomize
220 presentation order and were separated by a variable inter-trial interval. Each dog received the
221 same trial sequence.

222 A scan session consisted of 4 runs, lasting approximately 9 minutes per run. Each run
223 consisted of 25 trials (5 trained reward, 5 trained no-reward, 5 symbolic reward, 5 symbolic no-
224 reward, and 5 food rewards delivered at random), for a total of 100 trials per scan session. No
225 trial type was repeated more than 4 times sequentially, as dogs could habituate to the
226 continued presentation of a stimulus.

227 *Analyses*

228 Each subject's motion-corrected, censored, smoothed images were analyzed within a
229 general linear model (GLM) for each voxel in the brain using 3dDeconvolve (part of the AFNI
230 suite). Task related regressors for each experiment were modeled using AFNI's dmUBLOCK and
231 stim_times_IM functions and were as follows: (1) trained reward stimulus; (2) trained no-
232 reward stimulus; (3) symbolic reward stimulus; (4) symbolic no-reward stimulus. This function

233 created a column in the design matrix for each trial, allowing for the estimation of beta values
234 for each trial. Data were censored for outliers as described above for the contrasts of interest.

235 A series of contrasts were pre-planned to assess main effects related to the acquisition
236 of trained associations and whether they generalized between 2D and 3D versions. Acquisition
237 of the trained stimulus-reward association was probed with the contrast [trained reward—
238 trained no reward]. Transfer of the trained reward and no-reward association to the untrained
239 stimuli was probed with the contrast [symbolic reward—symbolic no reward]. A direct
240 association between the trained and untrained reward stimuli was tested with the contrast
241 [trained reward – symbolic reward]. The contrast [all_3D—all_2D] was performed to test for
242 perceived differences between all 3D and all 2D stimuli, regardless of training. The average
243 difference between trained stimuli and symbolic stimuli was assessed with the contrast
244 [(trained reward + trained no-reward)—(symbolic reward + symbolic no-reward)]. Finally, the
245 interaction between reward and no reward stimuli and symbolism was measured with the
246 contrast [(trained reward — trained no reward)—(symbolic reward —symbolic no reward)].

247 *Region of Interest (ROI) Analysis*

248 *Caudate*

249 As our interest was based on the dog's response to trained stimuli versus symbolic
250 stimuli, quantitative analyses based on the imaging results used activation values in the canine
251 brain area previously observed to be responsive to reward stimuli (Cook et al. 2016).

252 Anatomical ROIs of the left and right caudate nuclei were defined structurally using each dog's
253 T2-weighted structural image. ROI-based analyses were performed in individual, rather than
254 group space.

255 Beta values for the contrasts comparing the change in activation to reward and no
256 reward stimuli for trained (20 reward trials, 20 no-reward trials) and symbolic stimuli (20
257 reward trials, 20 no-reward trials) were extracted from the caudate ROIs in the left and right
258 hemispheres. Beta values greater than an absolute four percent signal change were removed
259 prior to analyses (assuming that these were beyond the physiologic range of the BOLD signal).
260 The remaining beta values were analyzed using the mixed-model procedure in SPSS 24 (IBM)
261 with fixed-effects for the intercept, group, hemisphere (left or right), and contrast type, identity
262 covariance structure, and maximum-likelihood estimation.

263 *Whole Brain Analysis*

264 Each subject's individual-level contrast from the GLM was normalized to the Labrador
265 Retriever atlas space via the ANTs software. Spatial transformations included a rigid-body mean
266 EPI to structural image, affine structural to template, and diffeomorphic structural to template.
267 These spatial transformations were concatenated and applied to individual contrasts from the
268 GLM to compute group level statistics. 3dttest++, part of the AFNI suite, was used to compute a
269 t-test across dogs against the null hypothesis that each voxel had a mean value of zero. All
270 contrasts from the GLM mentioned above were included. The average smoothness of the
271 residuals from each dog's time series regression model was calculated using AFNI's non-
272 Gaussian spatial autocorrelation function 3dFWHMx -acf. The acf option leads to greatly
273 reduced FPRs clustered around 5 percent across all voxelwise thresholds (Cox et al. 2017).
274 AFNI's 3dClustsim was then used to estimate the significance of cluster sizes across the whole
275 brain after correcting for familywise error (FWE). Similar to human fMRI studies, a voxel
276 threshold of $p \leq 0.005$ was used, and a cluster was considered significant if it exceeded the

277 critical size estimated by 3dClustsim for a FWER ≤ 0.05 , using two-sided thresholding and a
278 nearest-neighbor of 1.

279 ***Study 2: Object Localizer***

280 To identify object-processing regions, dogs were presented with 3-s color movie clips
281 projected on a screen in the bore of the magnet. Videos included human faces, novel objects
282 (toys), familiar objects, and scram-bled objects (a 15 by 15 box grid with spatially rearranged
283 movie frames.) Stimuli were presented using Python 2.7.9 and the Psychopy Experiment library.
284 A blocked fMRI design was used where each block was 21 s with seven movie clips for each
285 category. Each run contained two sets of four consecutive stimulus blocks in palindromic order.
286 Stimulus blocks had a delay of 10 s, where dogs were fed intermittently between blocks, such
287 that each run was approximately 7 minutes. On average, each dog completed three runs.

288 *Analyses*

289 As in Study 1, a general linear model was estimated for each voxel using AFNI's
290 3dDeconvolve. Task related regressors were: (1) faces, (2) novel objects, (3) trained objects, and
291 (4) scrambled objects. Individual object-specific regions, such as LOC, were identified with the
292 contrast [novel objects—faces]. Each dog's object-specific region was defined by the voxel
293 threshold of the statistical map for the [novel objects—faces] contrast until the number of
294 voxels in each ROI was approximately 40 voxels or less (Aulet et al. 2019). Beta values from the
295 contrasts of interest mentioned in Study 1 were extracted from the object-specific region of
296 each dog to examine potential differences in neural activation between 2D and 3D objects from
297 the contrasts mentioned above.

298

RESULTS

299 **Study 1: 2D vs 3D Results**

300 *Caudate ROI Analyses*

301 There was differentiation of the reward and no-reward stimuli in the caudate ROIs for
302 the trained stimuli, regardless of whether dogs were trained on objects or pictures. There was
303 also a significant interaction of training x [Reward – No Reward] ($F(1,45) = 11.29, p = 0.002$) (Fig
304 2). This indicates that the trained reward association did not transfer to the symbolic stimuli.

305 *Whole Brain Analyses*

306 We found neural evidence for the differentiation of stimuli as an effect of the
307 dimensionality of the training stimuli. Whole brain analysis of the contrasts of interest revealed
308 significant activation for three contrasts (Table 2). The [trained reward—symbolic reward]
309 contrast and the contrast comparing activation to the trained stimulus dimensionality versus
310 the untrained stimulus dimensionality [trained reward + trained no-reward)—(symbolic reward
311 + symbolic no-reward)] revealed a region in the posterior parietal lobe with greater activation
312 toward the trained dimensionality of stimuli than the untrained dimensionality (Fig 3A). The
313 contrast comparing the reward associations for the untrained dimension of stimuli [symbolic
314 reward— symbolic no-reward] revealed a region in the right anterior parietotemporal cortex
315 (Fig 3B).

316 **Study 2: Object Localizer Results**

317 *Individual Object Regions*

318 Three dogs (Velcro, Rookie, and Zoey) failed to complete three runs of the object
319 localizer task such that there was insufficient data to localize object-specific regions in the

320 brain. Twelve dogs had object selective regions defined by the contrast [novel_objects—faces]
321 in overlapping regions in either the left or right hemisphere (Fig. 4). We further examined these
322 object regions for differences between 3D and 2D versions of the objects from the contrasts in
323 Study 1. However, there were no statistically significant results for any of the contrasts in the
324 object-specific regions across dogs.

325 DISCUSSION

326 Our fMRI results provide the first evidence for neural differences in the occipital and
327 parietal cortices of the dog brain for the processing of two- and three-dimensional objects. The
328 main finding is that dogs' perception of 2D and 3D objects is influenced by their experience with
329 either stimulus dimension. Activation within reward processing regions was greater for the
330 dimensionality of the trained reward stimulus. Whole-brain analyses revealed a left posterior
331 parietal region selective for the trained dimension of stimuli over the untrained dimension.
332 Taken together, these findings suggest that the neural representation of objects depends on
333 dogs' familiarity with two- and three-dimensional objects.

334 *Object Regions*

335 In humans, viewing real objects as well as images of objects activates similar networks,
336 particularly the lateral occipital complex along the lateral and ventral convexity of occipito-
337 temporal cortex (Snow et al. 2011; Todd et al. 2012). However, in a human fMRI study that
338 presented real objects and pictures of the objects, the LOC in particular was sensitive to visual
339 differences between the two, such that LOC did not code the real (3D) and pictorial (2D)
340 versions of a shape as equivalent (Snow et al. 2011). Because real objects afford specific
341 actions, including the graspability of an object or if it is within reach of the dominant hand,

342 object-specific actions may have a unique effect on neural responses to the different versions
343 of the same object stimuli (Gallivan et al. 2009; Gallivan and Culham 2015; Gallivan et al. 2011;
344 Snow et al. 2014). Unlike humans, we found little difference in dogs' neural activation in
345 individual object regions between 2D and 3D versions of object stimuli associated with reward.
346 Our finding of similar neural activation in object regions of the dogs' brains to 2D and 3D
347 versions of object stimuli could be due to dogs forming an abstract object concept that is
348 invariant to the dimensionality of the object. However, as the object-reward pairings were
349 acquired using a passive viewing task, dogs had little experience interacting with the objects or
350 picture versions of the objects. The dogs' lack of action-associations with either object may
351 therefore have made both objects and pictures of objects equivalent to the dog as neither was
352 actionable. It is also possible that the study was insufficiently powered to detect potentially
353 smaller effect sizes in dogs than in humans.

354 *Dimensionality Regions*

355 As most studies of canine cognition rely on visual stimuli, we examined whether dogs
356 use hedonic neural mechanisms to generalize from pictures of objects to real world objects. In
357 the interaction contrast, we found that dogs show greater activation within the caudate
358 nucleus to the trained dimension of stimuli relative to the untrained dimension (e.g. dogs
359 trained on pictures of objects had greater activation to pictures relative to real world objects),
360 suggesting hedonic neural mechanisms are biased toward the dimensionality of stimuli with
361 which they are more familiar. Additional brain regions selective for stimulus dimensionality
362 included a left posterior parietal region across dogs where there was greater activation to the
363 trained dimensionality of stimuli than to the untrained dimensionality, which appeared in the

364 same region but opposite hemisphere as the LOC defined in each dog in the object localizer
365 study. Multi-voxel pattern analysis (MVPA) of human imaging data supports these findings, as
366 patterns in object regions can be different for object exemplars from the same category that
367 vary based on viewpoint or size, as well as between 2D and 3D versions of the same objects
368 (Eger et al. 2008; Snow et al. 2011). Consistent with human imaging studies, the left posterior
369 region also showed greater activation to objects relative to faces across dogs and appeared in
370 regions of the canine brain similar to the primate LOC (Freud et al. 2017; Freud et al. 2018).

371 There was also greater activation to the untrained reward versus no reward stimuli in a
372 right parietotemporal region across dogs (e.g. dogs trained that the 2D giraffe was the reward
373 stimulus had greater activation to the 3D giraffe than the 3D whale in this region). Greater
374 activation to the untrained reward stimulus in this region provides some evidence that dogs use
375 hedonic neural mechanisms to generalize a stimulus-reward association from the trained
376 reward stimulus to the untrained stimulus. However, we do not know what features, such as
377 color or shape, that the dog may use to facilitate this representation. In human fMRI, the right
378 primary visual cortex (V1) and right inferior temporal gyrus also showed greater activation to
379 2D versions of objects versus 3D objects (Snow et al. 2011). Our results also suggest that dorsal
380 regions of the dog brain may process abstract features of object stimuli that include, but are
381 not limited to, actions (Freud et al. 2017).

382 There were several limitations to our studies, the foremost being that only a subset of
383 dogs participated in both the localizer study and the 2D-3D study. Some dogs were unavailable
384 for both studies, and some dogs were unable to remain still while viewing video stimuli in the
385 MRI. Further, we limited the number of objects to two or three items, which allowed for a

386 simple controlled design with many trials per item but may limit the generalizability of our
387 findings to all objects that a dog may encounter. Unlike human imaging studies, we did not
388 include more abstract stimuli that were composed only of lines or were limited in color to black
389 and white. To address these concerns, future research could confirm the selectivity of object
390 processing regions for each dog using novel stimuli.

391 *Conclusions*

392 Our fMRI results provide evidence for dedicated object processing regions in the
393 occipital and parietal cortices in dogs. Although real objects and pictures of the same objects
394 share a degree of visual similarity, they differ fundamentally in the actions associated with
395 them and require experience with either dimension. Further, even children at age 4 can show
396 confusion about the properties of pictures and the objects they depict and the consequences of
397 actions on pictures and objects (Ganea et al. 2009). We have begun to understand how dogs
398 perceive their world through brain imaging, as this offers direct insight from the participant
399 about the neural mechanisms underlying perception. Our studies reveal that there are
400 potentially shared neural mechanisms underlying dogs' and humans' visual perception of
401 objects, and that neural biases may in turn affect perception and behavior. These studies
402 provide insight into the question of whether pictures are an appropriate proxy for real world
403 stimuli for dogs and for fMRI.

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521 **Table 1. Dogs (N=19) and participation in experiments.**

Dog	Breed	Sex	Object		S+
			Localizer	2D to 3D	
Caylin	Border collie	F	1	1	3D Giraffe
Daisy	Pitbull mix	F	1	1	3D Giraffe
Eddie	Labrador Golden mix	M	1	1	2D Whale
Kady	Labrador	F		1	3D Whale
Koda	Pitbull mix	F	1	1	2D Giraffe
Libby	Pitbull mix	F	1	1	3D Whale
Mauja	Cattle dog mix	F		1	2D Whale
Ohana	Golden Retriever	F	1	1	3D Whale
Oliver	Border collie Beagle mix	M	1	1	2D Whale
Pearl	Golden Retriever	F	1	1	2D Giraffe
Tallulah	Carolina dog	F	1	1	2D Whale
Truffles	Pointer mix	F	1	1	3D Giraffe
Tug	Portuguese Water dog	M		1	3D Giraffe
Zen	Labrador Golden mix	M	1	1	2D Giraffe
Zoey	Goldendoodle	F	1	1	3D Giraffe
N			12	15	

522 Dog's names, breed, sex, and participation in experimental studies (indicated by 1) are listed. Grey denotes a dog
 523 participated in all 3 studies.

524 **Table 2. Cluster size and threshold significance for 2D and 3D object processing regions**

2D3D Contrast	Region	Voxel threshold	Cluster Size (1 mm ³ voxels)
trained reward – symbolic reward	Left posterior parietal	.005	454 (p<.02)
symbolic reward— symbolic no-reward	Right parietotemporal	.005	248 (p=.05)
(trained reward + trained no-reward)— (symbolic reward + symbolic no-reward)	Left posterior parietal	.005	528 (p<0.01)

526

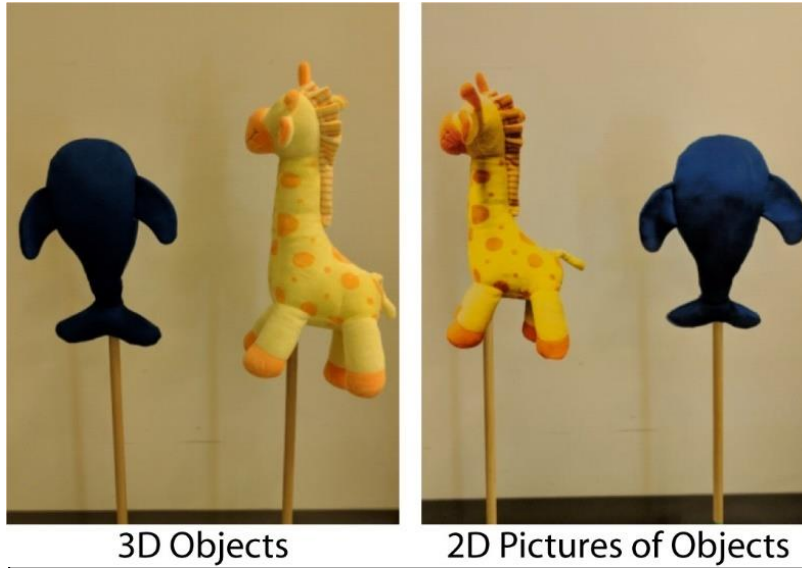


Figure 1. 2D & 3D Stimuli. **Left)** 3D whale and 3D giraffe objects attached to 2.5-foot dowels for presentation of stimuli to dogs while in the scanner. **Right)** Pictures of the whale and giraffe 3D objects were printed to create 2D color-matched versions of the 3D stimuli and pasted to foam board and 2.5-foot dowels for presentation of 2D stimuli to dogs while in the scanner

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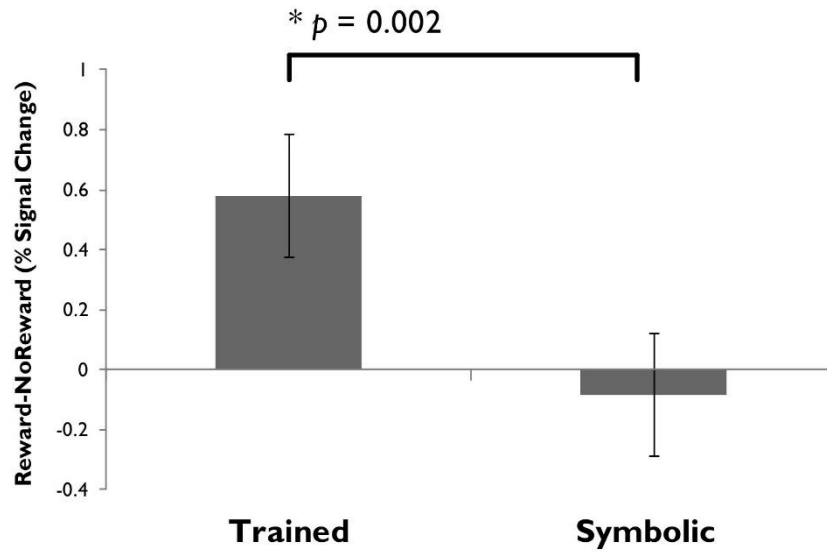


Figure 2. Average beta values (Percent signal change) in individual dogs' caudate nucleus for the contrast of Reward—No Reward separated by training and testing (symbolic) stimuli. Changes in brain activation were extracted from contrasts in the 2D to 3D study. In the caudate there was a significant interaction of training x [Reward – No Reward] ($F(1,45) = 11.29, p = 0.002$)

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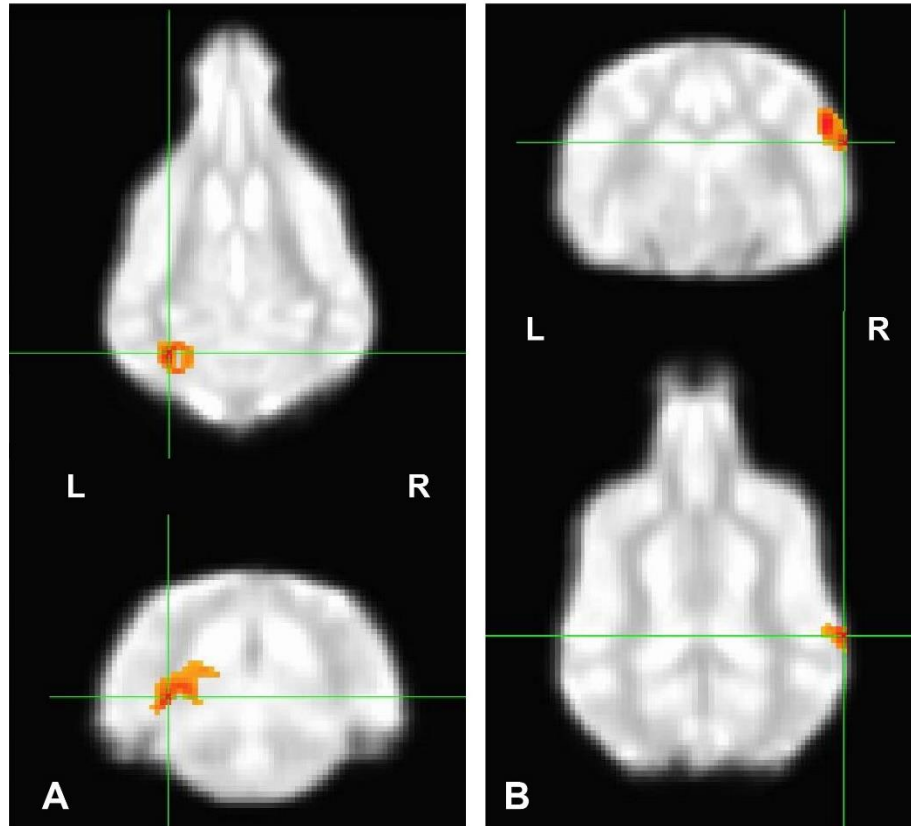


Figure 3. Regions important for the discrimination of dimensional object stimuli. Whole brain analysis of the contrasts of interest revealed significant activation only for three contrasts that survive a voxel threshold of 0.005. **A) The contrast comparing the trained S+ to the corresponding untrained dimension [trained reward—symbolic reward]** (454 voxels) revealed a region in the left posterior parietal lobe with greater activation toward the trained dimensionality of stimuli. **B) The contrast comparing the untrained dimension of stimuli [symbolic reward—no-reward]** (248 voxels) produced a region in the right anterior parietotemporal cortex.

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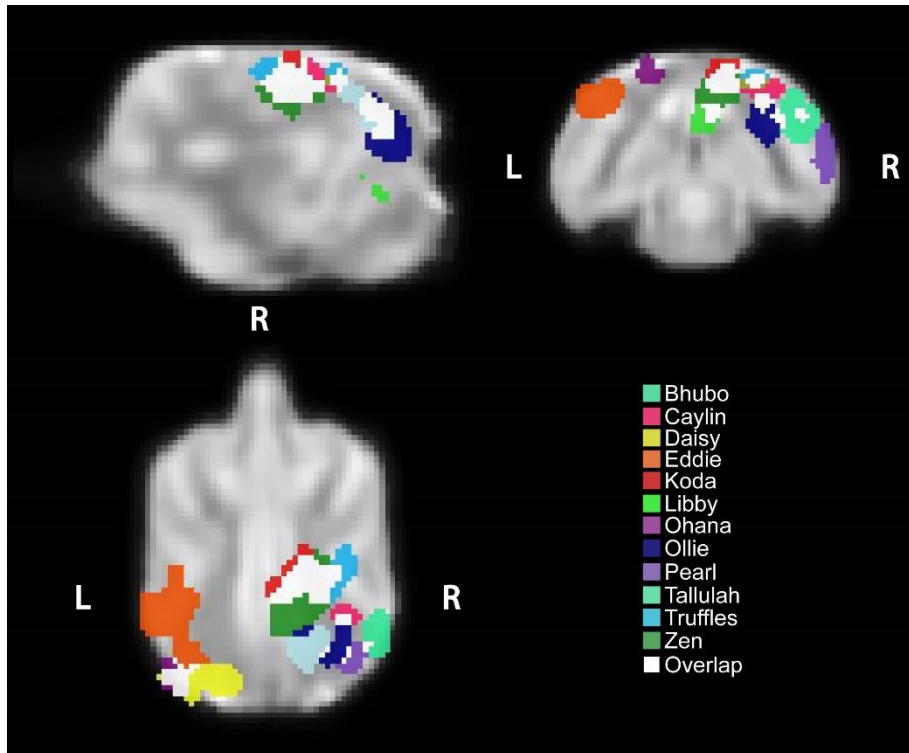


Figure 4. Individual Dog Object Regions. Sagittal, transverse, and dorsal sections. Regions were defined using the objects-faces contrast of video stimuli for each dog. Colors represent individual dogs; white represents overlap between two or more dogs.