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Smile at Me! Dogs Activate the Temporal Cortex Towards Smiling Human Faces

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ABSTRACT

Dogs use emotional cues from humans to guide their behavior. Happiness is a basic emotion that humans express and dogs can perceive and interpret. Here, we describe the brain correlates of perception of happy human faces in dogs by using functional magnetic resonance imaging (fMRI). Eight dogs participated: they were trained to remain awake, still, and unrestrained inside an MRI scanner. The visual paradigm included blocks of happy or neutral human faces, with gender matched to each dog's main caretaker. We found brain activity related to happy human faces mainly in the temporal cortex (including Sylvian Gyrus, Straight Gyrus, Proreus and Caudate). These results are consistent with studies in humans showing that the superior temporal cortex plays a key role in the perception of emotional faces. We suggest that perception of happy human faces plays a significant role in the attachment between dogs and humans. This is the first study that directly explores the cerebral correlates in dogs of perception of happiness in human faces.

Introduction

A smile is very powerful: it can cheer up our day and even modify our behavior. The human expression of happiness through smiling is not only universal, but also one of the basic emotions[1]. From a smile we can extract and interpret social cues that in turn help us to fit into our social environment. What is interesting is that we are not the only species capable of recognizing happiness in a human face —dogs can, too. Dogs are a special species, as they live in a rich social environment that includes humans, making the heterospecific relationship with them a challenge. Their ability to fit into their environment is strongly dependent on their capacity to communicate and interpret emotional cues from humans. For a dog, the ability to interpret happiness in humans and modulate its behavior could be helpful to adapt to human society[2].

Aside from common interaction with dogs, it is known from behavioral experiments that they are sensitive to expression of emotions, as evidenced by their longer observation of human emotional faces compared to neutral faces[3]. Furthermore, dogs gazed longer at their owners when they seemed happy (as owners viewed a cheerful movie) than when they seemed sad[4]. Considering that dogs glean a wealth of information from olfaction and other senses, it may seem impressive that dogs can perceive human happiness in pictures. Nonetheless, dogs and humans seem to share a similar mechanism to perceive emotional human faces, as they both present a bias to the left hemiface, and they both spend more time looking to the left hemiface of a face with a positive valence[5]. An interesting study showed that once dogs learn from images of their owners' faces to discriminate a smiling face from a neutral face, they can generalize their learning to other humans of the same gender as their owners[2]. An eye-tracking study[6] found that dogs use a conjunction of information from eyes, midface, and mouth (i.e., inner face) to process faces in general; however, when looking at a pleasant human face, dogs spend significantly more time looking at the eyes in comparison to the mouth. The same authors also found different gazing patterns when dogs looked at threating and pleasant human faces, but not between pleasant and neutral faces. A recent study[7] proved that dogs can discriminate emotions on faces (angry vs. happy) and not rely only on local cues. Said authors used an innovative paradigm with which they found that dogs trained with either the upper or the lower half of faces are able to discriminate the emotion in the non-trained part of the face. Moreover, a study using a cross-modal preferential looking paradigm suggested that dogs without training are able to discriminate positive faces and that they also possess representations of the emotional states (with the integration of visual and auditory cues), including positive emotions in humans[8].

Behavioral evidence, however, does not provide a clear prediction about the cerebral mechanisms that underlie processing of happy human faces in dogs. Understanding how these processes take place in the dog's brain can be helpful to create an integrative viewpoint on the perception of human happiness in dogs. Our goal is to describe the cerebral correlates of happy face perception in dogs. Eight trained and awake dogs participated. They remain still inside the scanner watching Happy and Neutral human faces in a block design (see (Fig. 1) while we acquire a functional magnetic resonance imaging (fMRI) sequence.This is the first time that the cerebral correlates of the perception of human happiness are directly evaluated in dogs.

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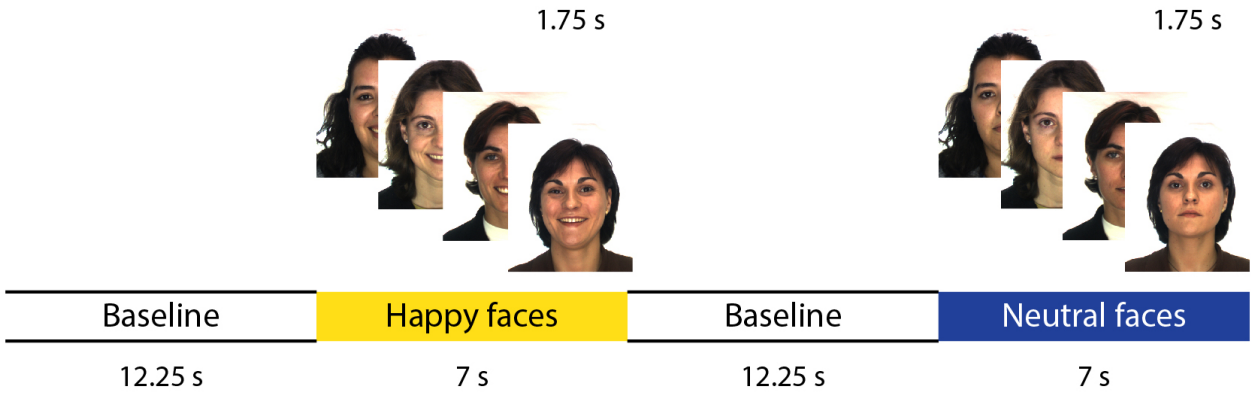

Figure 1. Visual stimulation paradigm. We used a block paradigm constituted by two types of blocks: Happy human faces and Neutral human faces. Each block was presented 5 times in each run in a pseudo-randomized order. A white screen with a cross was presented between blocks. The duration of each run was 192.5 s, and each dog experienced 5 runs in total. Each dog observed only faces of the same gender as their main caretaker. Photographs of faces were reprinted from the AR Face Database under a CC BY license, with permission from the author.

Results

To identify face-sensitive regions, we analyzed the cerebral activity resulting from viewing both happy and neutral faces in the contrast Faces > Baseline (Fig. 2). The results were overlaid on the Datta atlas[9]. We created a 5 mm radius sphere around the voxel with the largest z value within the resulting cluster; this voxel was located in the left occipital cortex (blue sphere in Fig. 2A. The activity related to both faces includes bilateral occipital cortex and left temporal cortex.

To describe the dog's brain correlates of perception of happy human faces, we contrasted BOLD activity between the two viewing conditions (i.e., Happy human faces > Neutral human faces). Similar to the previous analysis, we created a 5 mm radius sphere around the voxel with the largest z value located in the superior temporal cortex (purple sphere in Fig. 2B). The Fig. 2C shows BOLD signal response towards happy faces and neutral faces in the region more sensitive to faces in general (occipital cortex in blue) and in the region more sensitive to happy faces (temporal cortex in purple). The left occipital cortex responds in a similar way to both faces (blue bars), but the response in the temporal cortex is higher to happy faces than to neutral faces (purple bars).

The Fig. 3 shows the resulting cluster (25,327 mm^3 for the contrast Happy > Neutral faces, located in the right hemisphere, which included the temporal lobe and extended to the caudate nucleus. Due to the extension of the resulting cluster, we extracted the BOLD signal change from spheres of 5 mm radius centered at three local maxima of this cluster, located in the Sylvian (purple), Proreus (light blue), and Straight Gyri (green)[9]. The difference in BOLD signal change between happy and neutral faces in each sphere is shown to the right in Fig. 3. To explore the cerebral activity in the left hemisphere, we created 5 mm spheres centered at the corresponding anatomical locations (light bars in Fig. 3). We did not find any significant differences in the activity elicited by happy or neutral faces in the left hemisphere regions (paired t test, $p < 0.05$). The response in the Straight gyrus is the highest and least lateralized in comparison with the other structures. Coordinates, localization, and z value of local maxima are shown in Table 1. The opposite contrast (Neutral human faces > Happy human faces) showed no significant differences.

Local Maxima	z	x	y	z	Localization
Purple	2.85	184	126	135	Sylvian Gyrus
Light Blue	2.82	156	187	123	Proreus
Green	2.77	176	155	107	Straight Gyrus

Table 1. Local Maxima resulting from the contrast Happy Faces > Neutral Faces. Coordinates and location are given in mm according to the Datta atlas. Colors are matched with Fig. 3

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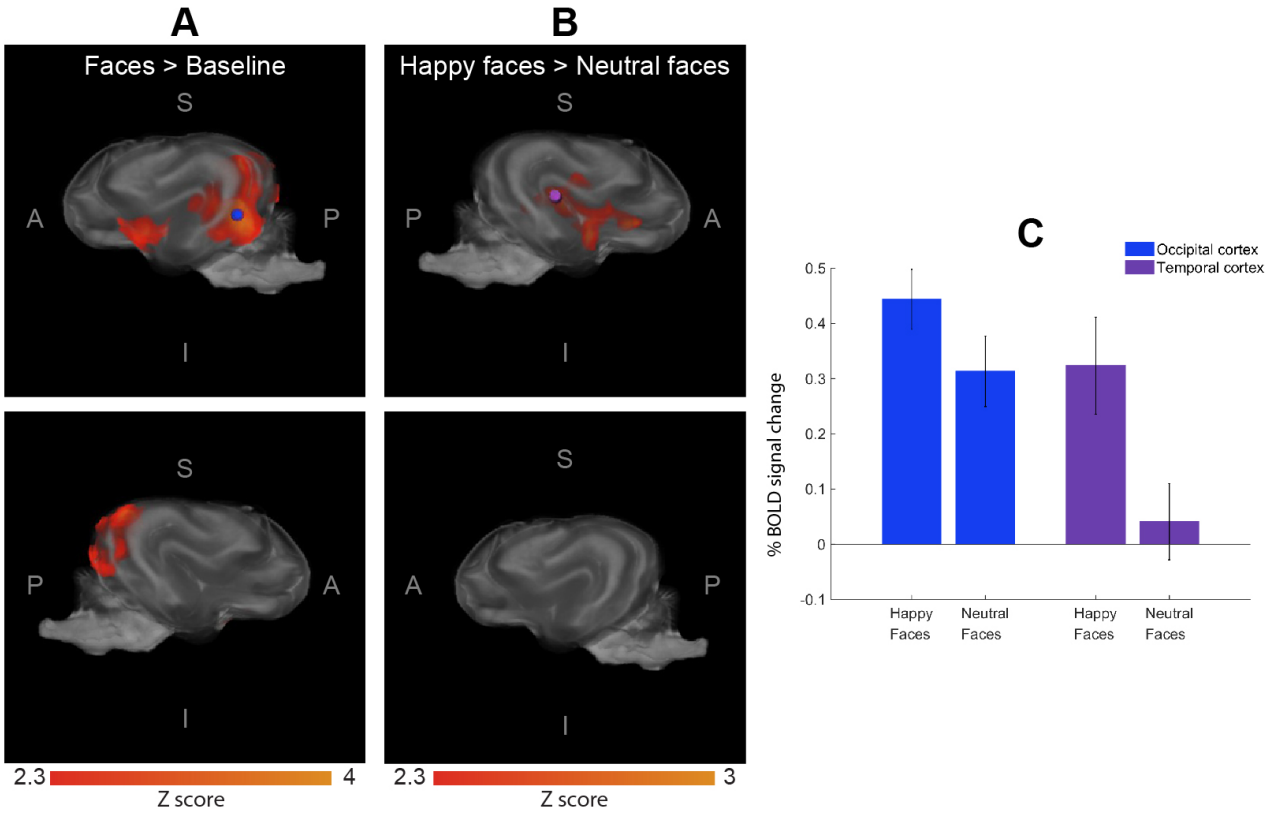

Figure 2. Differences in the cerebral response to happy vs. neutral faces in occipital and temporal cortex (n = 8). Volume rendering in lateral views, showing resulting clusters overlaid on the Datta atlas[9]. **A.** Faces (happy and neutral faces) > Baseline; the blue sphere indicates the voxel with largest z value located in the occipital cortex. **B.** Happy > Neutral faces; the purple sphere is centered at the voxel with maximum z value, located in the temporal cortex. **C.** BOLD signal change between happy faces and neutral faces in the spheres of the local maxima in both contrasts. Vertical lines represent standard error. S = Superior, I = Inferior, L = Left, R = Right, P = Posterior, and A = Anterior.

Discussion

We provide direct evidence of the cerebral processing of happy human faces in dogs through fMRI. We found cerebral activity related to the processing of happy faces in the right hemisphere, mainly in the temporal cortex. Previous studies found that the perception of human faces (vs. objects) elicits a strong response in the ventral temporal cortex[10,11], and our current study extends said findings, showing that the strongest response to happy faces is located in the superior portion of the temporal lobe. Both results are remarkably similar to reports with humans[12,13]. In humans, the superior temporal sulcus (STS) is crucial for social communication because it is related to the processing of biological motion, including the dynamic aspects of face perception like emotional expressions[12–15]. We suggest that in dogs the superior temporal cortex could play a similar role in the processing of dynamic aspects present in a happy human face. There is evidence suggesting that STS plays a key role in the integration of emotional information, as this region increases its activity with bimodal emotional stimuli[16], and the right STS shows an additive response to stimuli with congruent facial and vocal emotion[17]. In humans, STS decodes patterns in faces that express a specific emotion[18], regardless of the specific sensory cues[19]. In line with the role of STS in human emotion processing, activity of the superior temporal cortex in dogs could be involved in processing of happiness in general, and not necessarily be restricted to happiness related to human faces.

The cerebral response to happy faces in dogs was present beyond the superior temporal cortex (Fig. 3), and it included the ventral temporal cortex, anterior regions (Proreus), and caudate. This result is consistent with the model of the distributed human neural system for face perception[12] that proposes a hierarchical structure of face perception with a core system and an extended system. The core system includes the occipital and temporal cortex (Fig. 2) with the STS related to the changeable aspects of faces (like emotional expressions), in contrast to other face-sensitive regions like the occipital cortex, which is not modulated by emotional facial expressions (Fig. 2C). The processing system extends further, with the participation of other

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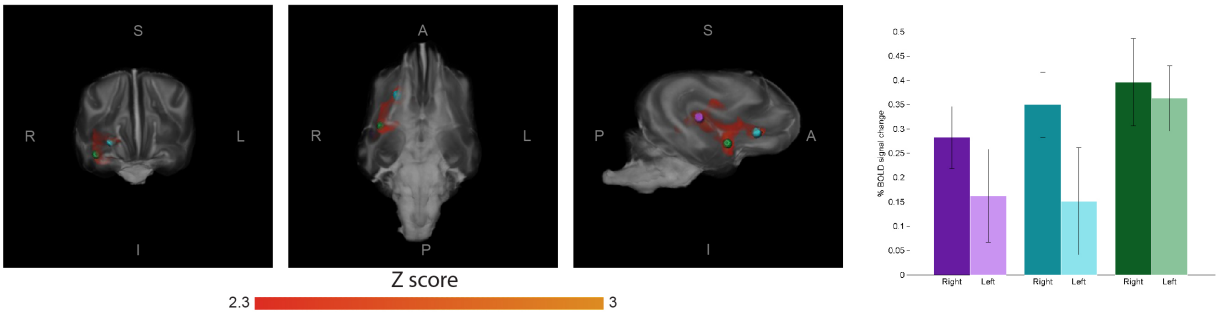

Figure 3. Happy human faces > Neutral human faces (n = 8). Volume rendering shown in frontal, inferior, and right views overlaid with the resulting statistical map. BOLD activity was extracted from spherical regions centered around three local maxima (5 mm radius) within the large resulting cluster in the right hemisphere. Similar spherical regions were evaluated on the left hemisphere at the same locations. The right-most panel shows the difference in the BOLD signal change between happy and neutral faces derived from these spherical regions (dark and light bars for right and left hemispheres, respectively). Vertical lines represent standard error. S = Superior, I = Inferior, L = Left, R = Right, P = Posterior, and A = Anterior.

cortices beyond the occipitotemporal visual extrastriate cortex. We interpret our results as analogous to those seen in humans, namely that activity seen in the anterior regions (Proreus) and caudate are evidence of the participation of these structures as part of an extended system for face perception in dogs (Fig. 3).

All brain activity related to happy faces appeared only in the right hemisphere, yet we believe that this is an effect of the statistical threshold used, because the left hemisphere also shows activity related to happy faces (Fig. 3). Our results, nonetheless, suggest a slight advantage in the right hemisphere to process happy human faces in dogs. This inter-hemispheric asymmetry was most evident in the activity of the right superior temporal cortex, highlighting its key role in the positive emotional processing in dogs. Although face processing in humans involves both hemispheres, it has been reported that the right STS is more actively involved in facial emotion recognition[20,21]. Our results showed greater activity within the right hemisphere during processing of happy human faces in dogs, supporting the Right Hemisphere Model, which posits that processing of emotional stimuli -including positive stimuli- occurs in the right hemisphere[22]. The right hemisphere in dogs has been related to novelty detection, to processing of emotions and human commands with intonational salience[23–27], and to processing of emotional -including happy- human faces[28]. In our paradigm, we can rule out that the activity found in the right hemisphere was due to novelty because both neutral and happy faces were unfamiliar to participants. Therefore, we propose that activation of the right hemisphere is due to the facial expression of happiness. Future studies could address the effect of other human emotions, including negative ones, to understand how a dog's brain processes emotions.

The cluster related to viewing happy human faces included the caudate. Other fMRI studies with dogs have also shown activation of this structure because it has been related to reward[29] and to familiarity of scents[30]. Our group also found greater caudate activity related to neutral human faces than to objects[10]. Considering that all stimuli used were unfamiliar to dogs, we suggest that the caudate activity reflects that a happy human face is intrinsically processed as a reward. In a study in which dogs were trained to discriminate between happy or angry faces both groups learned to discriminate facial emotions, but the group trained to identify happy faces learned significantly faster[7]. While the authors of said study suggested that dogs recognized an angry face as an aversive stimulus, the inverse is just as likely, with dogs showing accelerated learning due to the rewarding nature of happy faces. Moreover, a recent neuroimaging study found that the caudate is functionally connected to the auditory regions only when dogs listen to verbal praise with meaning and positive intonation[31]; the intonational information was not enough to recruit the caudate. Therefore, it is possible that happy human faces not only worked on dogs as rewarding stimuli, but they also represented meaningful stimuli, consistent with the importance of emotions to dogs, a social species.

An interesting possible interpretation of our results is that the activity of the superior temporal cortex also reflects that our participants paid more attention to happy faces. In humans it has been reported that attention is necessary for the response of STS to emotional faces[32], and activity of the right STS increases with attention to emotional faces, but not with attention to faces per se[21]. Although we cannot determine the degree of attention that dogs paid to our stimuli, this interpretation is compatible with the fact that happy faces are salient for dogs. Several behavioral studies in dogs have not found differences between happy and neutral human faces[5,6,28,33], yet we found differences in brain activity related to these two types of stimuli. Our results suggest that the specific brain activity to happy human faces reflects that these stimuli are important for dogs.

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Happy human faces appear to play a major role in establishing inter-species attachment. In recent years, oxytocin has been highlighted as a key player in this process. Morisaki, Takaoka, and Fujita[4], found that dogs spontaneously look longer at their owners when they express positive feelings and that gazing promotes a release of oxytocin in dogs[34,35]. This is similar to the enhancing effects of oxytocin on emotion recognition in humans[36–38]. While we did not directly investigate the role of oxytocin in human face perception, said findings are suggestive of our current results may be associated to this hormone.

The small sample (n = 8) is a limitation of this study, secondary to the challenges intrinsic to training dogs for the acquisition of functional images. Moreover, imaging sessions had to be kept as short as possible to ensure dogs' attention and compliance. Also, BOLD signal is inherently noisy in humans but more so in dogs, and it may be crucial to develop coils tailored to the anatomy of dogs[39]. Future studies will be needed to replicate and expand our results; for example, studies that explore a more extensive repertoire of emotions and sensory modalities.

In conclusion, this study gives the first evidence that a happy human face generates a broad activity in the dog's brain, and it implies that dogs can discriminate at the brain level between happy and neutral faces. Finally, due to the caudate's activity, we suggest that seeing a happy human face is rewarding for dogs. So let us keep smiling at our dogs!

Methods

Participants. Eight healthy dogs participated in the study. All were medium breeds (six Border Collies, one Labrador, and one Golden Retriever) ranging in age from 18 to 53 months. The sample included four neutered males, one neutered female, and three unneutered females. All dogs were pets, lived with human families, and were well socialized with humans and other dogs. During the study the dogs lived with their human families without changes in their routine aside from the training and imaging protocols described herein. All procedures were performed in compliance with Association for the Study Animal Behavior (ASAB) guidelines, and the Bioethics Committee of the Institute of Neurobiology of the Universidad Nacional Autónoma de México approved the study. The main caretaker of each dog gave informed consent.

Of the eight dogs included in this study, seven had previously participated in an fMRI experiment and had been trained to remain still inside a scanner (in a sphinx position) while watching images projected during the acquisition of fMRI. Those dogs did not require additional training. The new participant (Molly) was trained using the same procedure as the other seven dogs[10].

Design and Stimuli. We used images of human faces as stimuli and used a block design (see Fig. 1). There were two types of blocks: faces with neutral expressions and faces with happy expressions. Each block was presented for 7 s with an inter-trial period of 12.25 s used to estimate baseline activity (during which they observed a white screen with a small cross). Each fMRI acquisition (run) had a duration of 192.5 s and included 5 blocks of happy faces and 5 blocks of neutral faces. Blocks were presented in a pseudo randomized order, and the same type of block was never presented two consecutive times. In total, each dog experienced 5 runs (each run had a different order of blocks). Dogs experienced only 1-3 runs with rest periods between them in each imaging session, and different sessions occurred on different days. We decided to use short runs to maximize the attention that dogs pay to the stimuli and minimize the possibility of a dog falling sleep. Thus, fMRI acquisition was completed throughout 2-3 non-consecutive days for each dog. Visual stimulus presentation was controlled by PsychoPy2[40]. The lights in the MRI suite were turned off during paradigm presentation, and the stimuli were projected onto a screen in front of the dogs at a distance of 1.5 m.

Four different photographs of faces composed each block. All images were extracted from the AR Face Database[41], so all stimuli were of persons not familiar to the dogs. We presented the same persons with neutral and happy expressions. Each image was presented only once during each run to avoid habituation to the images. In order to have closer natural stimuli, all images were in color, presented in a frontal view, and the size of the projected images was similar to that of a real face (15 cm x 20 cm), as this size has been used in other studies[2,10,42]. The gender of the faces presented to each participant was the same as the main caretaker: four dogs (one male dog and three female dogs) saw female faces and the other four participants saw male faces. We decided to show a specific gender to each dog, as dogs show lower accuracy in a behavioral task when probed with an unfamiliar face of a person of the opposite gender of their main caretaker[2].

Data acquisition. All images were acquired at the National Laboratory for Magnetic Resonance Imaging in the Institute of Neurobiology of the Universidad Nacional Autónoma de México. We used a 3 T Philips Achieva TX scanner and a two-channel SENSE Flex Small coil, which was attached to the dogs with Velcro. To help the dogs maintain the sphinx position, we used a chin rest to support their heads. Dogs were fitted with ear muffs to provide noise protection during scanning. During the acquisition one experimenter remained inside the scanner room (out of the dog's sight) and visually monitored the dogs to make sure they were awake and attentive. The dogs could leave the session at any time.

For anatomical reference and registration of each dog we acquired a standard T1-weighted structural image with a turbo spin echo sequence with 1 x 1 x 1 mm^3 covering the whole brain with 75 slices. Blood-oxygen-level dependent (BOLD) images covered the whole brain and were acquired with a gradient-echo-planar imaging (EPI) sequence (28 coronal slices, 3 mm thickness, no gap; TR = 1.75 s; TE = 30 ms; flip angle = 90°; FOV = 224 x 240 mm^2; acquisition matrix 112 x 120; spatial

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resolution 2 x 2 x 3 mm^3; 110 volumes and 5 dummy scans). The acquired data during the current study are available from the corresponding author.

Image Analysis. The brain was extracted from each run using manual segmentation. All functional analyses were done with FSL[43] version 4.19. Images were preprocessed for temporal correction, and spatial smoothing was performed using a Gaussian kernel with FWHM = 5 mm. Motion correction was performed using MCFLIRT, and runs showing motion greater to head rotation than 1° or translation greater than 3 mm were discarded (if a run was discarded, a new acquisition was obtained until each dog had five good-quality runs). As maintenance of the sphinx position requires muscle tone, loss of which would result in major head movement, the criteria used for motion correction of imaging data further guaranteed that the dogs remained awake. Functional images were spatially normalized to an anatomical image of each dog and to a digital atlas of the dog's brain[9].

We used the General Linear Model for the statistical analyses, including the stimuli vectors of happy and neutral faces as regressors. Each run was analyzed individually in a first level. Regressors were convolved with the canonical hemodynamic response function modeled as a Gamma function. The five runs of each participant were first analyzed using a fixed effect analysis. A random effects analysis was used to study common activations within the eight participants. To describe the cerebral regions involved in the perception of happy faces, we analyzed the contrast happy faces vs. neutral faces in the entire brain. The resulting statistical parametric maps were corrected for multiple comparisons using random field theory[44] (cluster-forming threshold $z > 2.3$ and $p < 0.05$). To localize and label the cerebral structures and report the coordinates, we used the digital atlas of Datta et al.[9]. We created a sphere of 5 mm radius around the voxel with the local maxima that resulted from the contrast Happy faces > Neutral faces to extract the BOLD signal change.

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Author contributions statement

All authors conceived the experiment, L.V.C and R.H.P. conducted the experiment, All authors analyzed the results. All authors reviewed the manuscript.

Additional information

Competing financial interests. The authors declare no competing financial interests.