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Abstract

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Humans are well versed in perceiving and deciphering complex emotional states from facial expressions, and use this information to engage in emotionally intelligent behaviors. Previous neuroimaging studies have identified facial processing regions not only in the human brain but also in non-human primates and dogs. This face region has been well-localized within the canine brain, but the extent to which emotion-related information from facial expressions is extracted and interpreted is not well understood. Previous behavioral studies suggest that dogs may have the processing capabilities to interpret and react to human facial expressions. In this study, we provide neurological evidence for emotional affect in dogs. To measure the effect of two key emotional components of facial expressions, namely valence and arousal characteristics, we presented videos of dynamic and spontaneous emotional facial expressions to dogs during fMRI. Dogs were presented with a series of 5-second videos of these facial expressions. We found significant areas of increased activation along the inferior temporal gyrus in response to high arousal stimuli, and increased activation in the dog face area in response to negatively valenced stimuli. These findings are suggestive of a neural basis for emotional intelligence that spans across interspecies boundaries.

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1. Introduction

Humans are well versed in perceiving and deciphering complex affective states from facial expressions alone, and these discriminations help inform emotionally intelligent decision making [1,2]. However, neurological evidence for emotional intelligence in non-human animals has yet to be identified [3,4]. Emotional intelligence is conceived of as the ability to monitor one's own and others' feelings and emotions, to discriminate among them, and to use this emotional information to guide one's thinking and actions [5,6]. A dual-dependence between assessment and awareness of one's own emotions and awareness of others is implicated in emotional intelligence. To what extent emotional intelligence is conserved across species is a limited domain of research, as current understanding of emotion itself in non-humans is still developing.

Humans report observing a wide range of emotions in dogs, a domesticated non-human animal that lives within human social groups. These include a range of both primary emotions, such as fear, joy, and sadness, and secondary emotions like jealousy, guilt, and pride, amoung others [7,8]. Dogs, and subsequently their brains, have evolved in parallel to humans for millennia, and maintain more intimate social bonds with humans than most other non-human animals [9]. Dogs produce more salivary cortisol and engage in increased submissive and alert behaviors in response to infant crying, suggesting emotional contagion [10]. There is also behavioral evidence to suggest dogs appropriately understand the nuances of emotional valence, that is, the implications of positive and negative emotions [11]. However, we cannot say for sure whether this ability is innate or merely learned via conditioning. Understanding how non-human animals experience emotion will help us better understand how emotional intelligence is conserved across species, and working to demonstrate evidence that dogs interpret and experience emotion would also aid animal welfare movements' goal to develop better guidelines for animal research [12]. We must first establish a baseline of dogs' ability to discriminate emotions before we can draw conclusions about their emotional intelligence.

Most research on emotion in dogs is behavioral, due to the challenges of awake neuroimaging [13]. In one such study examining dogs' ability to discriminate faces, dogs were able to complete an identification task wherein they were required to identify positive or negative emotions from top or bottom halves of faces. Dogs took longer to learn to consistently identify negative emotions, and the possibility that these slower learning times were the result of a conflict between viewing an angry face and receiving a reward is discussed [11]. These may have been learned associations, although one could argue emotional interpretation is learned through association in humans as well.

Humans and dogs have developed close social bonds over the course of evolution, and the ability to communicate between species has been crucial to the success of this relationship over time [9]. Humans intuitively classify canine emotional valence. We understand play behavior and affection as a signal of positive emotion, and aggression and fear responses like snarling or cowering as negative ones. There is support for dogs' ability to determine the valence of human facial expressions and can make generalizations outside of their guardians [11,14]. The way dogs communicate with humans is different from the way they communicate within their own species, and will demonstrate similar behaviors with differing meanings depending on the intended recipient. For instance, rolling over to expose a belly is an act of submission between dogs, but is seen as a sign of trust between a human companion [15]. To consider emotional displays in a cross-species model, one recommendation is to define emotion as primarily a description of a behavioral pattern, breaking it down into four main components: behavioral, physiological, somatic, and cognitive [16,17]. Here, we chose to focus on one element of this emotional model, that of physiological facial expressions as a communicative tool.

There are several regions of cortex in humans and non-humans involved in face processing. In humans, the fusiform face area (FFA), occipital face area (OFA), and superior temporal sulcus (STS) all show sensitivity to face information [18-21]. The posterior superior temporal sulcus (pSTS) has also been identified as sensitive to visually presented social information [22]. The amygdala and fusiform gyrus are both implicated in the recognition of facial and bodily signals, while the STS, parietal lobes, and other subcortical structures aid in the representation of facial and bodily expressions [2]. In non-humans, the posterior temporal face patch in macaque and the dog face area (DFA) in canines are in topographically analogous regions to the FFA, both of which are sensitive to face information [23-25]. In addition, dogs have analogous brain morphology in many of these same areas as humans do, including the STS, pSTS, amygdala, fusiform gyri, and parietal lobes [26]. However, although this analogous morphology suggests the capability to discriminate amongst facial expressions, the extent to which emotional information is extracted from these within the canine brain is not well understood.

To further examine emotional processing in the canine brain, we use the Circumplex Model of Affect, a two-dimensional circular model that well describes emotional affect, wherein activation-deactivation is present on the vertical axis and pleasant-unpleasant on the horizontal axis (Figure 1) [27]. These scales account for a major proportion of variance in the judged similarity among emotional words, which can be arranged on these axes [28]. Benefits of this model include non-specific methods of classifying attributes of emotions, without the need to assign specific emotional patterns to non-specific emotion words. The original paper discusses that rather than considering how each emotion is produced by its own unique neural pathway, that placing emotions along an arousal-valence two-dimensional graph is a more intuitive way to conceptually categorize emotion. Valence is a dimension of positivity or negativity in emotional quality. In both humans and primates, emotional valence is associated with the mesolimbic dopamine system (Figure 2) [29,30]. Several studies have also suggested that uneven activation between the left and right prefrontal cortices is associated with certain positive or negative emotions [31-33]. Arousal is a dimension of strength and salience, associated with activation in the amygdala and reticular formation [34-36]. It is thought that neural representations of

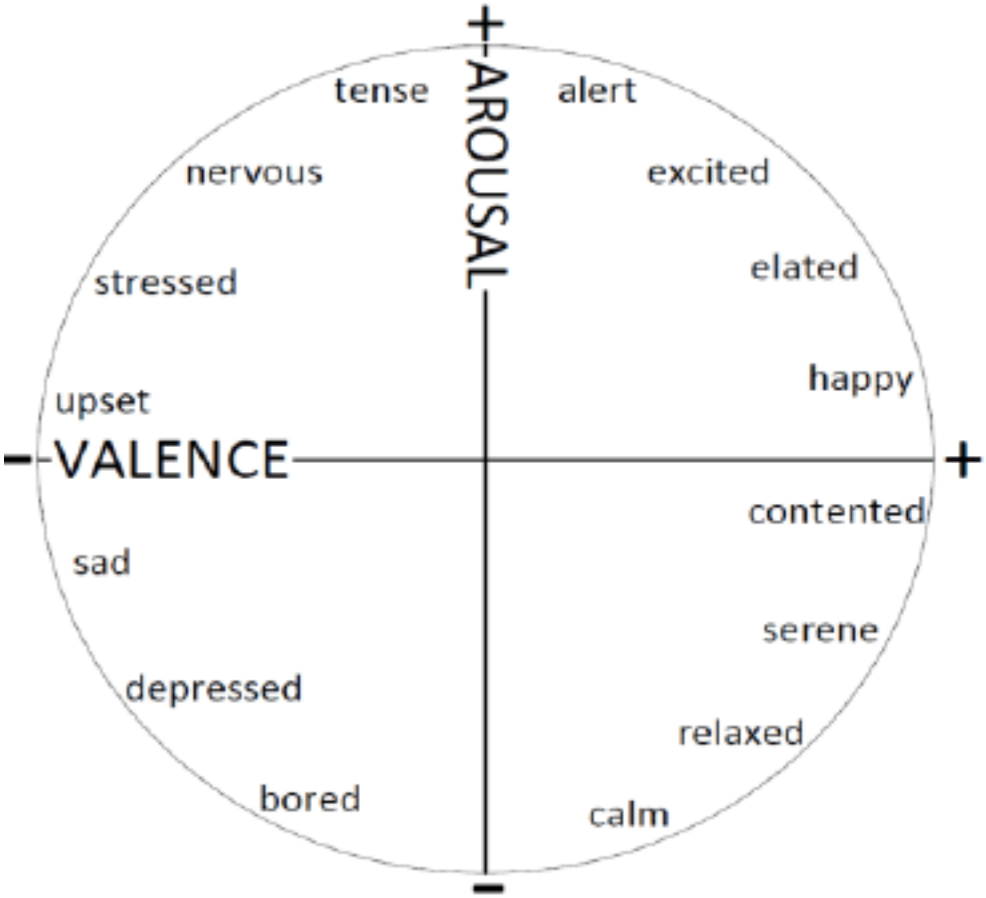

Figure 1. The Circumplex Model of Affect. A graphical representation of the circumplex model of affect with the horizontal axis representing the valence dimension and the vertical axis representing the arousal or activation dimension [58].

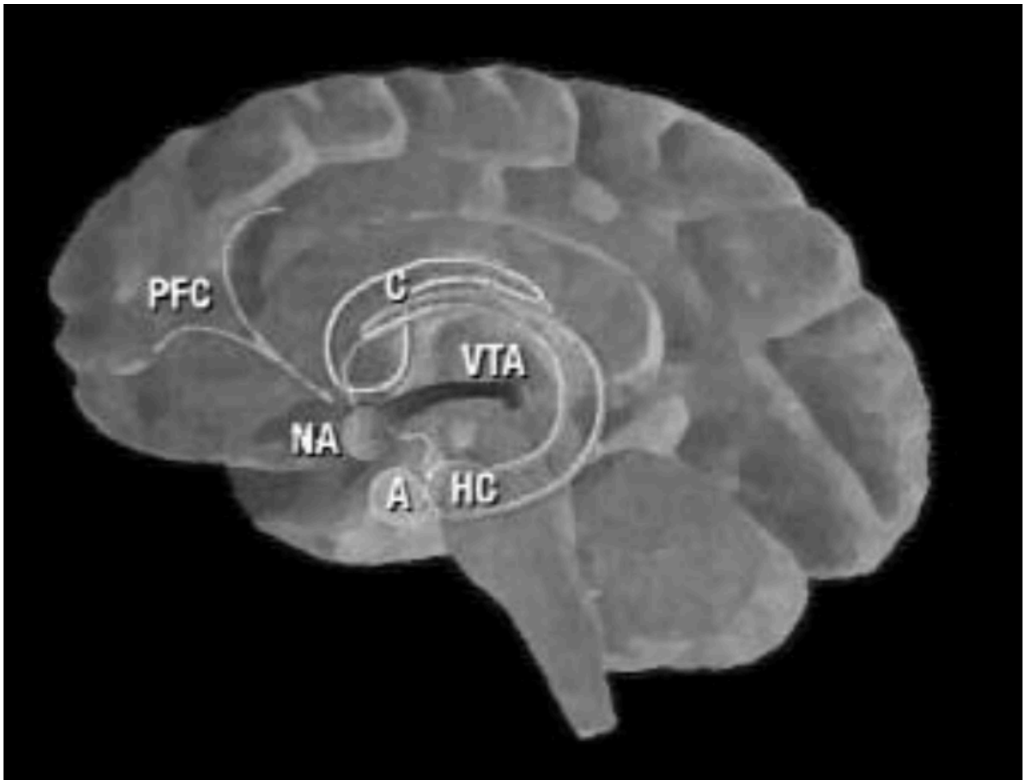

Figure 2. The mesolimbic system. The ventral tegmental area (VTA) projects to the nucleus accumbens (NA) via dopaminergic projections. The NA also projects to the amygdala and prefrontal cortex, as well as other regions.

emotional significance are a role of the amygdala, wherein assessment of emotional arousal are relayed to the reticular formation. It appears the prefrontal cortex integrates these two systems into active awareness of these emotional states, utilizing prior context [37]. We use this model to define our variables, valence and arousal, for this study.

Using fMRI, we localized regions of the canine brain that differentially respond to aspects of valence and arousal displayed on human facial expressions, as defined by the Circumplex Model of Affect. Since non-humans are unlikely to conceptualize emotion in terms of language the way humans do, we use this model as a tool to effectively examine these emotional affects in dogs, removing the complicating aspect of language. We took video stimuli from the DynEmo database, which allows for full onset and offset of candid emotional displays

[38]. Additionally, certain regions of cortex, such as the pSTS, are preferentially activated by moving stimuli rather than static stimuli, so we opted to use these video stimuli to optimize salience [39,40]. Dogs passively viewed these facial expressions, removing the challenge of learning, where we can observe the spontaneous neural response to novel stimuli. If dogs possess the capability to discriminate between aspects of emotion, then we would expect to find differential activation in certain regions of cortex in response to these scales of valence and arousal. We aim to understand which, if any, of these aspects are more salient to a dog.

2. Materials and Methods

2.1 Participants

Participants were dogs (N=4) from the Atlanta community. 9 dogs participated in the experiment, though data were only retained for 4 of them following preprocessing procedure (see Methods 2.5). These four dogs included 2 females and 2 males, all spayed/neutered, ranging in age from 7 to 12 years old. This sample included 1 boxer mix, 1 Boston terrier mix, 1 lab-golden mix, and 1 pit mix. Prior to this experiment, all dogs had completed a training program that prepared them to be comfortable within the scanner environment and had participated in prior scan sessions. Two dogs had participated in previous fMRI studies involving video stimuli and demonstrated an ability to lie awake and unrestrained during scanning while viewing stimuli on a projection screen, while two dogs were new to these kinds of stimuli.

2.2 Stimuli

To operationalize aspects of valence and arousal, stimuli were taken from the DynEmo database, which contains video content of dynamic and spontaneous emotional facial expressions

[38]. These subjective affective states were rated by both the expresser and unbiased observers. Affective states were rated by the emotion expressed (amusement, irritation, etc.) and the salience of that emotion (1-6 Likert scale; 6 most salient, 1 least salient). In this way, we categorized positive valence with “amusement,” “satisfaction,” and “surprise” emotion categories, and negative valence with “irritation,” “disgust,” and “fright” emotion categories. We categorized stimuli with salience scores of 4, 5, and 6 as high arousal, and lower arousal with salience scores of 1, 2, and 3. We used these measures to create four video conditions that represent the four quadrants defined by the Circumplex Model of Affect (positive/negative valence, high/low arousal) [27]. Each clip represented only one of the four quadrant conditions. All were novel to participants.

2.3 Experimental design

During runs, dogs viewed video stimuli projected on a translucent screen positioned towards the end of the scanner bore. Stimuli were presented via the PsychoPy software [44]. A mixed block experimental design was utilized. Dogs were presented with a series of randomized clips of five seconds each, with varied length breaks of 2-4 seconds between clips. Each clip was manually triggered by an experimenter while dogs lay down in a sphinx position to watch stimuli. A food reward was given as needed to maintain attention. Each run contained 40 blocks and lasted approximately six and a half minutes. Each dog completed two runs, except for one who completed only one and was later removed due to preprocessing protocol (Methods 2.5).

2.4 MRI scan acquisition

The scanning protocol for dogs in this study was consistent with previous dog fMRI studies [42,43]. All scans were obtained using a Siemens 3T Trio whole body scanner. The dogs' functional scans were obtained using a single-shot echo-planar imaging (EPI) sequence that acquired volumes of 22 sequential slices of 2.5 mm with a 20% gap (echo time (TE) = 25 ms, repetition time (TR) = 1260 ms, flip angle = 70°, 64 × 64 matrix, 2.5 mm in-plane voxel size). Approximately 200-500 functional volumes were obtained for each dog over two runs. Slices were oriented dorsally to the brain with the phase-encoding direction right-to-left.

2.5 Preprocessing

Analysis of Functional NeuroImages (AFNI) (National Institutes of Health) was used to preprocess and analyze the functional data [44,45]. Preprocessing of the fMRI data included motion correction, censoring, and normalization. Censoring was performed based on both signal intensity and motion. Volumes with either more than 2.0 mm of scan-to-scan movement or more than 1% of voxels flagged as outliers were censored from further analysis. To improve signal-to-noise ratio, the remaining data were spatially smoothed with a 6 mm Gaussian kernel. Additionally, a mask was drawn in functional space for each dog in the cerebellum, which was used to censor the data further by removing volumes where the beta values extracted from the cerebellum were assumed to be beyond the physiologic range of the BOLD signal (|signal change| > 3%) for each trial. Of the 9 dogs that completed the study, 4 had at least 66% of their data retained for all runs. This criterion was set so that there was ample reliable data to compare between all conditions for each dog.

Task related regressors for each experiment were modeled using AFNI's dmUBLOCK and stim_times_IM functions and were as follows: (1) positive valence; (2) negative valence; (3)

high arousal; (4) low arousal. This function created a column in the design matrix for each trial, allowing for the estimation of beta values for each trial. Data were censored for outliers as described above for our contrasts of interest. A series of these contrasts were pre-planned to assess the main effects within valence and arousal conditions, respectively. The contrasts were performed to identify regions that differentially respond to aspects of valence and arousal.

The contrast [positive valence—negative valence] was performed to identify regions that differentially respond to positively valenced emotional facial expressions versus negatively valenced emotional facial expressions. Similarly, the contrast [high arousal—low arousal] was performed to identify regions that differentially respond to highly salient emotional facial expressions versus lower salient emotional facial expressions.

3. Results

Contrast	*Area*	*p-value*	*Dogs*	*Betas (β)*	*Beta Means ($\overline{\beta}$)*	*Beta SD (SD_β)*
[positive valence–negative valence]	DFA	0.03*	Bhubo Daisy Eddie Koda	0.372075 -0.958339 -2.36651 -1.30816	-1.0652335	0.564920051
[positive arousal–negative arousal]	ITG	0.03*	Bhubo Daisy Eddie Koda	2.06996 0.254508 2.05759 -0.217404	1.0411635	0.59821708

Table 1. *Regions of interest statistics.*

Regions of interest (ROIs) were defined from the contrasts [positive valence—negative valence] and [high arousal—low arousal]. To allow for comparison between dogs, we warped the dogs' individual data into a group atlas and overlaid each contrast individually onto the group mean image in AFNI, referred to as groupspace [46]. We then varied the voxel threshold ($p < 0.05$) of the statistical map in groupspace until one or two clusters remained that were 75–150 voxels, with a voxel size of 1mm^3. Clusters lying along the perimeter of the brain were discarded as motion artifacts. We used regression analysis to estimate beta coefficients of the clusters in each dog [Table 1]. To determine the strength of these correlates in groupspace, we calculated the average regression slope for all dogs per condition.

In 3 of 4 dogs, we identified a region of cortex that exhibited increased activation with negatively valenced facial expressions in the dog face area (DFA), according to high-resolution canine brain atlases ($p = 0.03$, $\overline{\beta} = -1.07$, $SD_\beta = 0.56$) [26,47]. In 3 of 4 dogs, we also identified a region of cortex in area composita posterior lateralis I that exhibited increased activation with high arousal facial expressions, a region anatomically analogous to the inferior temporal gyrus (ITG) in humans ($p = 0.03$, $\overline{\beta} = 1.04$, $SD_\beta = 0.60$) (Table 1, Figures 3,4). These regions were approximately 75 and 115 voxels each, respectively.

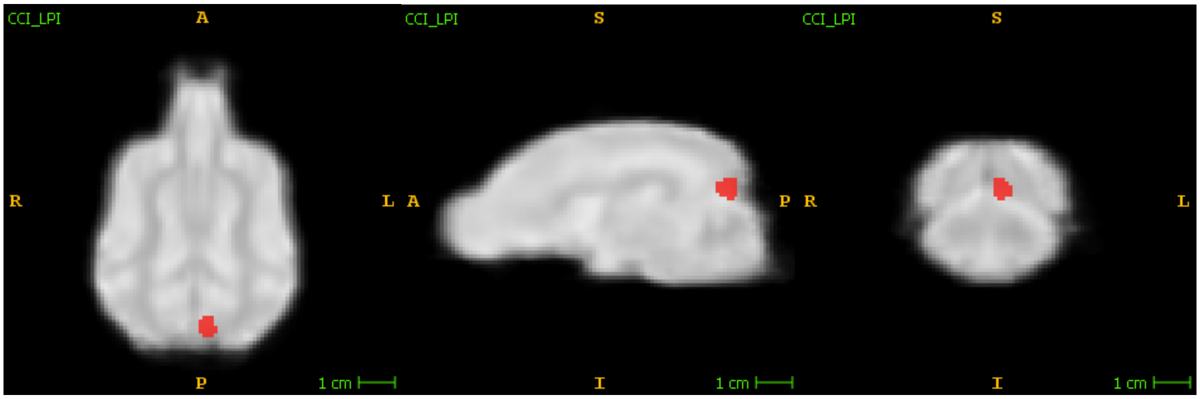

Figure 3. Valence contrast. Greater activation in the DFA was found in response to more negatively valanced emotions.

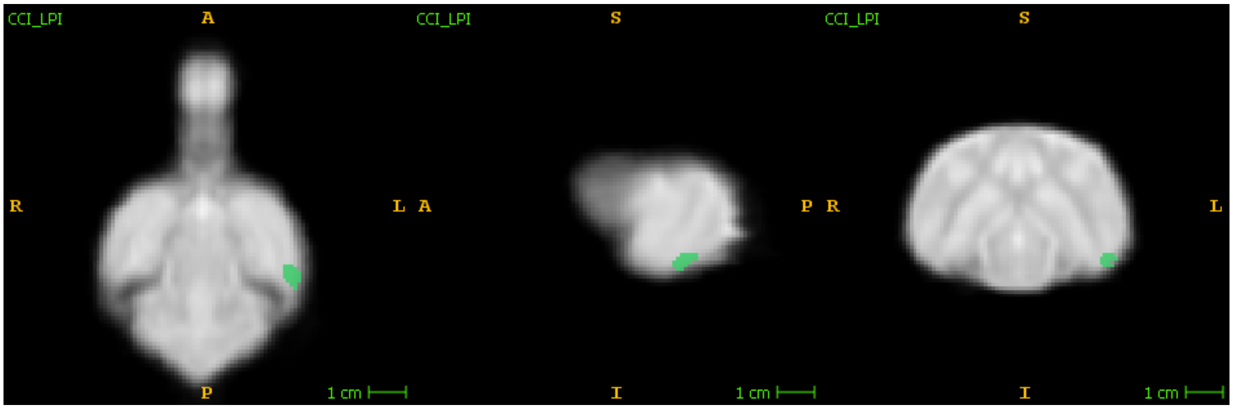

Figure 4. Arousal contrast. Greater activation along the posterior inferior temporal gyrus was found in response to more highly salient, arousing emotions.

4. Discussion

In summary, we examined the neural basis of emotion processing in dogs and found activation in early visual areas that varied in response to aspects of emotional affect. For more negatively valenced expressions of emotion, activation in the DFA significantly increased from that in more positively valenced conditions. Behavioral evidence from human studies suggests attention is moderated differently by positive and negative emotions, an effect that could be observed here in a non-human species [48]. For higher arousal stimuli, activation along the inferior temporal gyrus significantly increased from that in lesser arousal stimuli, an area implicated in the processing of both emotion and face information in other non-human animals, namely macaque and Rhesus monkeys [49-51]. Previous research reveals extensive connections between the ITG and limbic areas, further implicating the amygdala and its role in arousal [49-51].

Neuroimaging studies in humans examining the Circumplex Model of Affect have implicated several brain regions that exhibit activation to measures of valence and arousal. Negative affect is demonstrated to incite greater activation in areas of the prefrontal cortex. In addition to the amygdala complex, the prefrontal cortex is also implicated in measures of arousal

[52,53]. Due to distortion of images caused by the interference of air pockets in the proximal sinuses of dogs, it is challenging to localize regions of activation in the prefrontal cortices of the canine brain, which is perhaps why we did not find regions of interest in this location in our study. However, the connection between the amygdala and ITG is of particular interest to our findings, as this has not yet been localized in the context of arousal in dogs. Touching on the effect negative valence has on activation in the DFA, it may be that dogs are more attentive to negative stimuli that could precede punishment, such as an angry face, and less so attentive to positive or neutral faces. These novel findings in dogs expand our understanding of the canine brain, its processing of emotion, and the aspects of emotion that are more salient to a dog.

Given that face stimuli were novel, this research provides evidence that dogs spontaneously discriminate visual expressions of emotion from unfamiliar faces. These findings further suggest that dogs have a sense of facial expression subserved by similar neural mechanisms to those in humans. Dogs draw cues from human facial expressions in relation to aspects of positivity, negativity, and arousal, basic aspects of emotions categorized by the Circumplex Model of Affect, and differentiate between them. This ability to discriminate expression is applied to novel faces, suggesting it is not merely limited to learned familiar faces, such as that of an owner, but generalized to the human face itself.

Anatomical differences are a primary source of variability in brain imaging studies. Previous neuroimaging studies examining suitability for assistance work in a group of 49 labrador/golden retriever mixes found size variations in brain mass up to 30% [54]. Thus, although there was variability in the specific location of each dog’s ROIs, this is unsurprising given the different breeds and small sample size in the present study [55].

Whether dogs are born with a neural mechanism to interpret human facial expressions, or if they simply learn through conditioning mechanisms, cannot be determined from this study alone. Our subject sample consisted of older dogs who perhaps had more experience with interpreting facial expressions than a younger dog would have. Comparing the strength of these study's effects across a larger age span would prove insightful into the ways this mechanism develops over the lifespan. The method that these expressions were presented in is also worth considering. In a previous functional imaging study, we determined that video stimuli are less salient, but still effective, than live stimuli used in dog studies [56]. However, the spontaneity by which the emotions of the DynEmo database faces were elicited contributes an element of candidness that outweighed this concern for this experiment. A comparison could be made between live actors producing non-candid facial expressions to determine the effects of live versus video in regards to the salience of emotional affect to dogs.

There are several limitations to our study. Firstly, our small sample size is a typical result of the challenge of dog functional neuroimaging. The ability to lie awake and unrestrained in the loud, stimulating, and confined environment of an MRI proves challenging to dogs, and significant training is needed to create a subject pool suitable for these types of experiments. Our retention ratio for this study was just under 50%, and further research could attempt to replicate these results with a larger sample size. In addition, this was an exploratory study that examined just one aspect of emotional expression humans engage in. Humans express emotion not just through use of facial expressions, but also through a combination of body language, spoken language, pheromones, etc. [57]. Looking into the salience of these other aspects of emotion could help garner a better understanding of how various emotional components are concatenated into the canine brain to form an understanding of the emotions of heterospecifics.

Consistent with recent evidence for emotional capabilities in non-human species, the present work provides evidence for a baseline of emotion processing in the canine brain, beyond the scope of relationships with their owners. It also suggests that more salient facial expressions, such as a wide smiling face or a scrunched angered face, are more imperative to a dog's ability to discriminate between expressions. In summary, our findings provide evidence that emotion systems are conserved across species, from which we can now further explore the implications of emotional intelligence outside of our own species.

5. Conclusion

The present work provides evidence for emotion processing abilities in a non-primate mammal. It also suggests similar functionality of the inferior temporal gyrus in emotional face processing across conspecifics, the moderating effect on activity that emotion has in face processing regions, and implicates a basic but established baseline of emotional understanding that may have helped cultivate dog and human's close parallel evolution. More work should be done to foster a greater understanding of emotional processing in non-humans to develop insight into emotional intelligence across species.

Appendix A: References

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Appendix B: Tables and Figures

Table 1. Regions of interest statistics.

Contrast	*Area*	*p-value*	*Dogs*	*Betas* (β)	*Beta Means* ($\overline{\beta}$)	*Beta SD* (SD_β)
[positive valence–negative valence]	DFA	0.03	Bhubo Daisy Eddie Koda	0.372075 -0.958339 -2.36651 -1.30816	-1.0652335	0.564920051
[positive arousal–negative arousal]	ITG	0.03	Bhubo Daisy Eddie Koda	2.06996 0.254508 2.05759 -0.217404	1.0411635	0.59821708

Figure 1. The Circumplex Model of Affect.

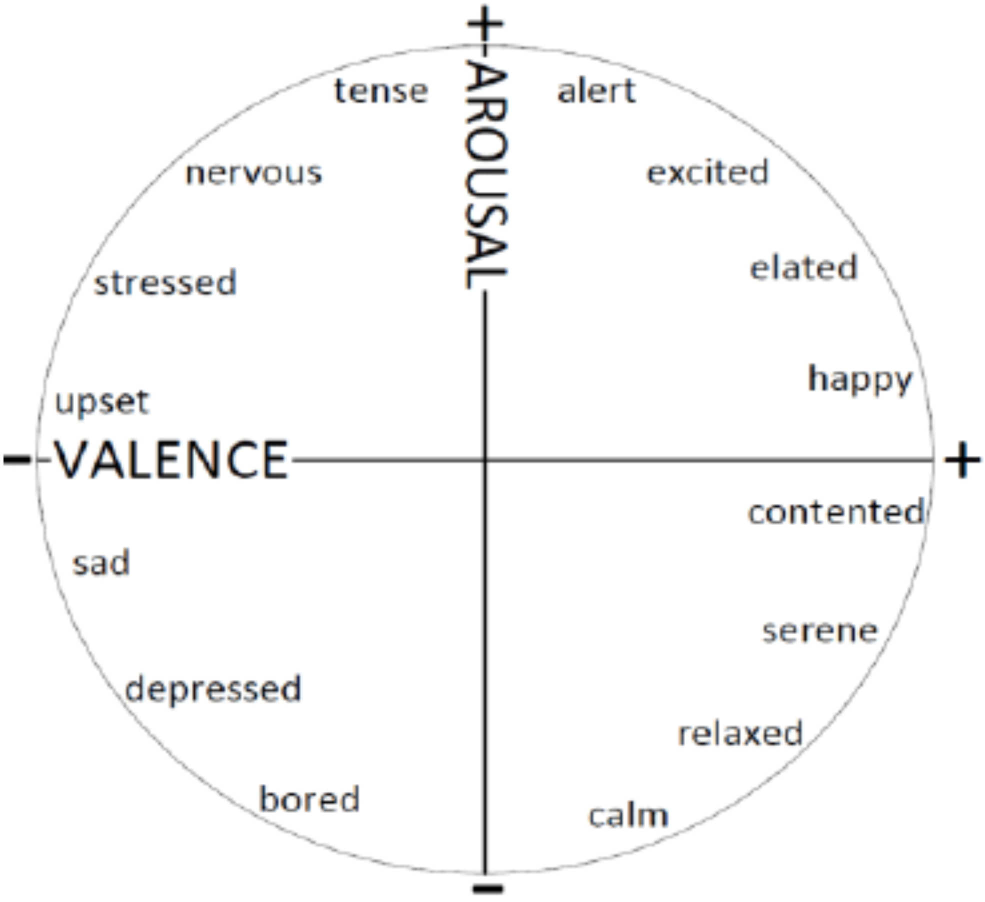

Figure 2. The mesolimbic system.

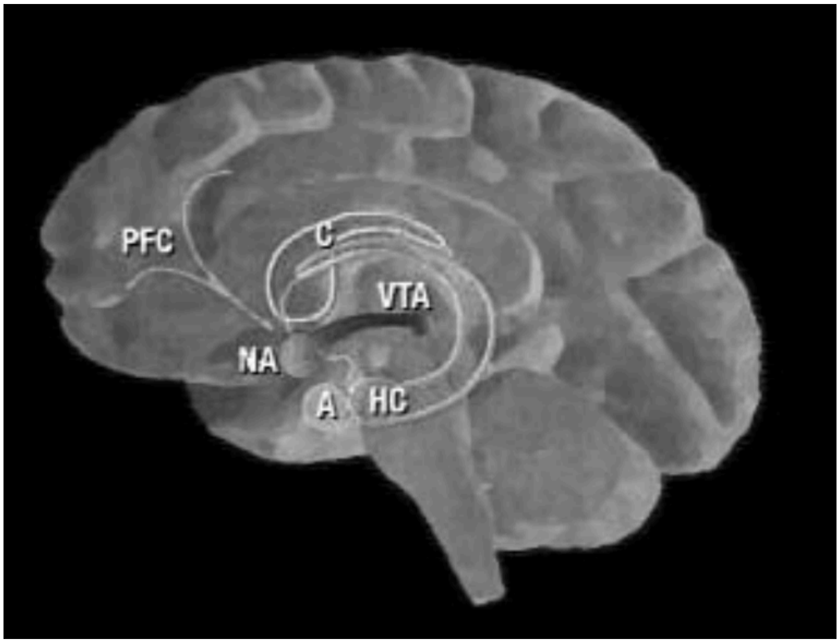

Figure 3. Valence contrast.

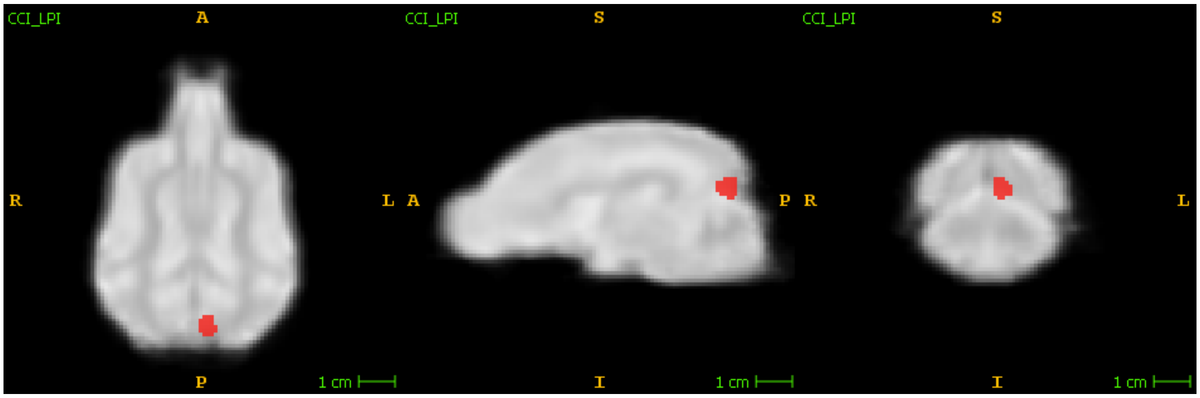

Figure 4. Arousal contrast.