Jealousy in dogs? Evidence from brain imaging

Peter Cook[1,2], Ashley Prichard[1], Mark Spivak[3], & Gregory S. Berns[1]

[1] Department of Psychology, Emory University, Atlanta, Georgia
[2] Department of Psychology, New College of Florida, Sarasota, Florida
[3] Comprehensive Pet Therapy, Atlanta, Georgia

Abstract: Domestic dogs are highly social and have been shown to be sensitive not only to the actions of humans and other dogs but to the interactions between them. We used the C-BARQ scale to estimate dogs' aggressiveness, and we used noninvasive brain imaging (fMRI) to measure activity in their amygdala (an area involved in aggression). More aggressive dogs had more amygdala activation data while watching their caregiver give food to a realistic fake dog than when they put the food in a bucket. This may have some similarity to human jealousy, adding to a growing body of evidence that differences in specific brain activities correlate with differences in canine temperament. The amygdala response habituates when an interaction is observed repeatedly, suggesting that repeated exposures may be a useful behavioral intervention with potentially aggressive dogs.

Peter Cook is Assistant Professor of Psychology at the New College of Florida. He studies animal cognition and comparative neuroscience in a wide range of species. He is particularly interested in finding novel, ecologically valid approaches to studying the brain and behavior outside the traditional laboratory setting. **www.ncf.edu/directory/listing/peter-cook/**

Ashley Prichard is a doctoral student in Psychology at Emory University with primary research interests in the overlapping areas of animal cognition, neuroscience, and animal behavior. Her current work centers on similarities and differences in perceptual abilities in dogs compared to humans and other species. **sites.google.com/view/ashleyprichard**

Mark Spivak is President of Comprehensive Pet Therapy. He has trained pets professionally since 1992 and is a widely sought expert in legal cases. He has a special interest in managing dog aggression. **cpt-training.com/mark-spivak/**

Gregory S. Berns, Distinguished Professor in Psychology, Emory University, directs the Facility for Education & Research in Neuroscience. His research uses fMRI to study canine cognitive function in awake, unrestrained dogs. The goal is to map the perceptual and decision systems of the dog's brain non-invasively. He also uses diffusion tensor imaging (DTI) to reconstruct the white matter pathways of a wide variety of other mammals, including dolphins, coyotes, and the extinct Tasmanian tiger. **www.ccnl.emory.edu/greg/**
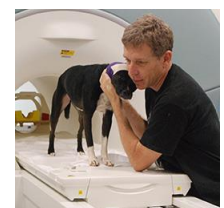
Introduction

Most dogs rely on humans for food, shelter, and companionship. Dogs are attentive and sensitive to human social signals, including tone of voice, posture, and facial expression (Topál et al., 1998; Schwab & Huber, 2006; Lakatos et al., 2012; Merola et al., 2012; Müller et al., 2015; Nagasawa et al., 2015; Kujala, 2017). The importance of the dog-human relationship suggests that dogs might use aggression to defend their access to human caregivers. There is an elevated level of dog-dog and dog-human aggression in social situations involving interactions between a caregiver and another dog or human (Wright, 1991; Casey et al., 2014). Harris and Prouvost (2014) had dogs observe their caregivers praising and interacting with a realistic animatronic dog as well as with socially irrelevant inanimate objects. When their caregivers interacted with the fake dog, dogs had increased behavioral arousal and showed aggression toward the fake dog. No such behavior was elicited by the socially irrelevant objects. The authors interpreted their findings as evidence of something like jealousy (or "proto-jealousy") in the domestic dog.

Described in humans as a set of negative emotional and behavioral responses when a rival receives something one wants for oneself (Hart, 2010), jealousy is a "complex" emotion sharing the brain and behavioral correlates of several primary emotions such as anger and sadness (Buss, 2014). Humans regularly attribute jealousy to dogs (Konok, Nagy & Miklosi, 2015; Morris, Doe & Godsell, 2008), but Harris and Prouvost's findings were the first to provide clear empirical evidence of domestic dogs "guarding" a "social resource" through aggression in response to a friendly interaction of their caregiver with another dog. More evidence is required to determine the extent to which dogs experience an emotion akin to human jealousy: anger is just one component of jealousy in humans. However, the evidence to date suggests that a form of social-resource guarding may contribute to aggressive behavior in domestic dogs.

Emotion in non-human animals can be illuminated by examining neurobiology (Panksepp, 2004). Animals cannot report their internal states to us verbally, but the physiological correlates of those states can be measured. Inclusion of physiological and neurobiological measures in dog emotion research may be particularly important to avoid anthropomorphic interpretations of behavior (Cook, 2017). The neurobiology of social-resource guarding in dogs might help predict which ones are more likely to be aggressive and may help in developing behavior management strategies.

Jealousy is not well-understood neurobiologically. For human jealousy, there is evidence of increased activation in subcortical regions, including the amygdala and hypothalamus; in interoceptive areas such as the insula; and in social/emotional regions of cortex, such as the posterior temporal sulcus (Harmon-Jones, Peterson & Harris, 2009). There seems to be a sex difference: men show more activation of limbic and visceral areas when jealous, whereas women show more activation in the socio-emotional regions of the cortex (Takahashi et al., 2006). In a positron emission tomography study in monkeys (Rilling, Winslow & Kilts, 2004), male monkeys watching a mate interact with another male also showed increased activation in the amygdala, insula, and superior temporal sulcus.

The neural circuitry of social aggression has been studied more extensively than that of jealousy. Although aggressive behavior is complex, involving interactions between the environment, hormones, and a large number of brain regions, the basic mechanisms of impulsive aggression in the brain are fairly well-understood (Nelson & Trainor, 2007). The

hypothalamus, amygdala, bed nucleus of the stria terminalis, and periaqueductal gray have all been implicated in a brain network underlying anger and aggressive responses in rodents, non-human primates, and humans. Many lesion studies have shown the importance of this brain network in aggression. Rodent and human studies have also used functional brain imaging to measure the response of these brain regions to social aggression (Ferris et al., 2008; Coccaro et al., 2007). The roles of the hypothalamus and amygdala in driving aggressive behavior have been particularly well-studied. Lesions in either area reduce aggressive responses, and both areas respond to testosterone concentrations that modulate bodily arousal during social competition (Montoya et al., 2012). A study of sexual and emotional infidelity in humans, for example, found increased activation in the amygdala and hypothalamus, especially in men (Takahashi et al., 2006). The amygdala and hypothalamus are accordingly logical places to look for predictors of social aggression in canines – perhaps even below the threshold for any behavioral sign of overt aggression.

In previous work (Berns, Brooks & Spivak, 2012; see reviews: Cook et al., 2016a; Berns & Cook, 2016), we have measured fMRI in awake, unrestrained domestic dogs to examine the neurobiological underpinnings of prosocial behaviors. We train subjects with operant conditioning and positive reinforcement. Participation is always voluntary. This allows us to do human-style cognitive neuroscience with dogs, assessing brain responses in alert animals in a range of affective states. Work from our lab and others highlights the extent to which dogs are neurobiologically predisposed to respond to human social signals (Cuaya, Hernández-Pérez & Concha, 2016; Dilks et al., 2015; Andics et al., 2014). We have also found that brain responses can be strong predictors of future behavior. In a recent study, we found that dogs who showed greater striatal activation when they were expecting verbal praise than when they expected food were also likely to prefer interacting with their caregiver over the opportunity to eat a treat (Cook et al., 2016b). In addition, in a study with 50 dogs undergoing training for service work, amygdala and striatal activation patterns in response to hand signals were strong predictors of a dog's likelihood of successful placement in service (Berns et al., 2017). In certain cases, where behavioral responses may be affected by a wide range of uncontrolled factors, or are likely to emerge only in rare situations, neural responses can serve as a reliable indicator of behavioral inclinations.

Overt aggressive behavior clearly depends on a range of interrelated factors, including situation, training, prior experience, ability to inhibit, and strength of aggressive drive (O'Heare, 2017). Because many potentially aggressive dogs are not, in most situations, overtly aggressive, it may be difficult to predict behavior or assess risk until an actual incident. This might occur only upon exposure to a specific provocative stimulus or stimuli. Such provocation also raises ethical and safety concerns. An alternative to direct provocation, however, is to look at an individual's behavioral tendencies over time. The degree to which these are stable is classically termed "temperament" (Cloninger, Svrakic & Przybeck, 1993) and is frequently assessed in non-human animals (Reale et al., 2007). The Canine Behavioral Assessment & Research Questionnaire (C-BARQ) (Hsu & Serpell, 2003; van den Berg et al., 2010) is a validated and reliable measure of temperament in pet dogs. Caregivers rate their dog's behavior on a number of scales. These yield measures of the dog's propensity for attachment behaviors, aggression, anxiety, and a range of other factors. Our prior work has indicated that a dog's temperament, as measured by the C-BARQ, can be predictive of neurobiological responses to prosocial stimuli (Cook, Spivak & Berns, 2014). It is hence reasonable to use the same approach for studying potentially anti-social reactions to threats

to resources, as in jealousy.

Building on prior work by Harris and Prouvost (2014), we conducted an fMRI study with dogs aimed at assessing whether they would show neurobiological signs of arousal in response to a potential threat to their social resources. We predicted greater amygdala activation when dogs watched their caregivers give a food reward to a fake dog than when they put the food in a socially irrelevant object (a bucket). We also predicted that dogs with more aggressive temperaments, as assessed by the C-BARQ, would show more amygdala activation when their caregivers interacted with a fake dog.

Materials and Methods

Participants
Participants were 13 domestic dogs. All dogs and caregivers were volunteers from the Atlanta area. All dogs had previously completed one or more scans for the project and had demonstrated the ability to remain still during training and scanning (Berns, Spivak & Brooks, 2012; Cook, Spivak & Berns, 2014; Cook et al., 2016). This study was performed in accordance with the recommendations in the National Institutes of Health Guide for the Care and Use of Laboratory Animals. The study was approved by the Emory University IACUC (Protocol DAR-2002879-091817BA). All caregivers gave written consent for their dog's participation. Because the dogs were already skilled in the MRI process, no additional training for the current study was required. To protect their hearing during live-scanning, all participants wore MuttMuffs or ear plugs secured with vet wrap as in our prior experiments (see Berns, Brooks & Spivak, 2013).

Temperament Assessment
Each subject had previously received a C-BARQ assessment by their primary caregiver and handler (see Supplementary Table S1 for full profile of each dog.) All subjects in our studies received a C-BARQ assessment. Caregivers were not aware of any particular experimental use of these data at time of assessment. C-BARQ assessments yield multiple temperament factors. In the current study, we used the factor for dog-dog aggression, as our interest was specifically in our subjects' arousal in response to their caregiver providing something of value to another dog.

Imaging
All scans were acquired on a 3T Siemens Trio MRI. Scan parameters were similar to those in Cook, Spivak and Berns (2014). Functional scans used a single-shot echo-planar imaging (EPI) sequence to acquire volumes of 22 sequential 2.5-mm slices with a 20% gap (TE = 25 ms, TR = 1,200 ms, flip angle = 70 degrees, 64 × 64 matrix, 3-mm in-plane voxel size, FOV = 192 mm). A T2-weighted structural image was previously acquired during one of our earlier experiments using a turbo spin-echo sequence (25-36 2-mm slices, TR = 3,940 ms, TE = 8.9 ms, flip angle = 131 degrees, 26 echo trains, 128 × 128 matrix, FOV = 192 mm). Three runs of up to 800 functional volumes were acquired for each dog, with each run lasting 12 to 16 minutes.

Experimental Design
There were three trial types: (1) dog gets food; (2) fake-dog gets food; and (3) food is deposited in a bucket. The dog gets food condition was not analyzed but served two purposes: (i) Regular feeding keeps the dogs in the scanner for longer. (ii) Because each piece of food is a potential reward, the dogs may pay greater attention to the caregiver's interactions with the bucket and fake dog. Dogs were stationed in the scanner in the "sphinx" position, in a custom-made chin rest facing out the back of the scanner bore (described in detail in Berns, Brooks & Spivak, 2012). The fake dog (Sandicast Large Life Size Yellow Labrador) was to the subject's right, placed on a table at eye level, approximately 6 feet from the subject's head. The fake dog (Figure 1), approximately the size of a real-life Labrador retriever, was made of painted ceramic. It did not move. It had been rubbed with a blanket used by a dog unfamiliar to all subjects. To receive the food, a plastic tube was affixed behind the fake-dog's muzzle, out of view of the subject in the scanner. A red, plastic, 2.5-gallon bucket was placed on the same table, at the same distance, but to the subject's left. The dog's primary handler was present and in view for the entire experiment, stationed just at the end of the scanner bore, approximately three feet from the subject's head.
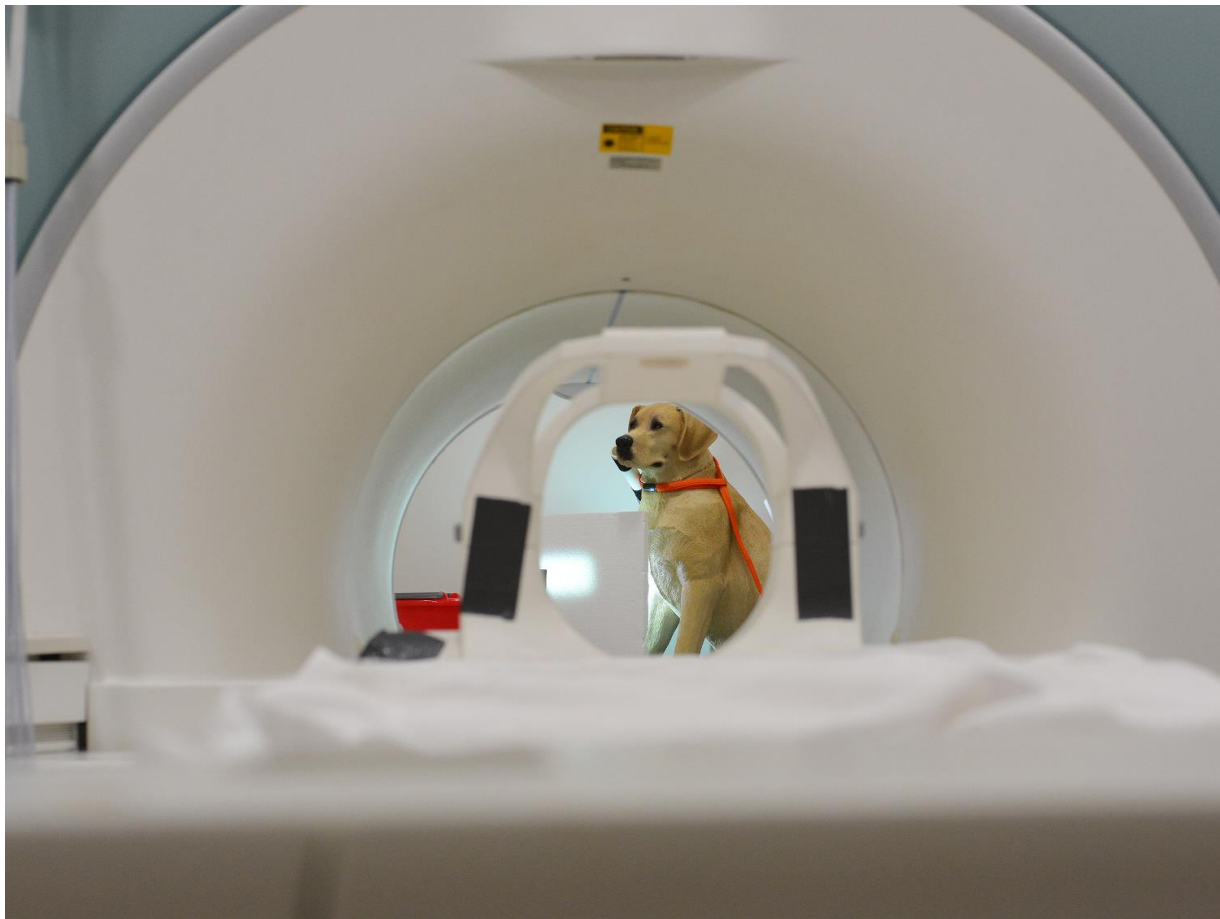

Figure 1. View of the fake dog through the scanner bore. To "feed" the fake dog, the caregiver placed food in a tube behind the dog's muzzle.

Each trial began with the presentation of an object on the end of a wooden stick for 6 to 7 s. These were cues that denoted the beginning of each of the three trial types. Dogs were not exposed to the three objects prior to scanning. The objects were presented from the side of the scanner bore, by an experimenter who was always out-of-sight. Handlers were instructed to maintain neutral expressions during testing and not to make eye contact with their dog except when feeding them directly. Then, depending on the trial type, the caregiver picked up a piece of food from a dish at the end of the scanner bore (about two feet from the subject's head) and either fed the subject dog; put the food in a small, hidden pouch attached to the fake-dog's mouth; or put the food in the bucket. The subject dog in the scanner was able to see these outcomes (Figure 1). Each of the three runs contained 30 trials of each type in random order.

Trial events (onset and offset of object presentations) were recorded by an observer out-of-sight of the subject via a four-button MRI-compatible button-box. A computer running PsychoPy (Peirce, 2009) was connected to the button-box via a USB port, and recorded both the button-box responses by the observer and scanner sequence pulses.

Analysis
Data pre-processing included motion correction, censoring and normalization using AFNI (Cox, 1996) and its associated functions. Two-pass, six-parameter affine motion correction was used with a hand-selected reference volume for each dog. Scan censoring (i.e., removing bad scan volumes from the fMRI time sequence) was used because dogs can move between trials and when consuming rewards. Data were censored when estimated motion was greater than 1 mm displacement scan-to-scan and based on outlier voxel signal intensities. Smoothing, normalization, and motion correction parameters were identical to those described previously (Cook et al., 2016). A high-resolution canine brain atlas (Datta et al., 2012) was used as the template space for individual spatial transformations. The Advanced Normalization Tools (ANTs) software was used to spatially normalize the statistical maps of the contrasts of interest to the template brain using affine and symmetric normalization (SyN) nonlinear transformations (Avants et al., 2011).

Each subject's motion-corrected, censored, smoothed images were analyzed within a General Linear Model (GLM) for each voxel in the brain using 3dDeconvolve (part of the AFNI suite). Nuisance regressors included the six motion parameters. A constant and linear drift term were included for each run to account for baseline shifts between runs as well as slow drifts unrelated to the experiment. Task-related regressors were modeled using AFNI's GAM function with 3-s duration and were as follows: (1) onset of trial cue; (2) feeding of the fake-dog (the moment the food was placed in the pouch); and (3) food in bucket. These were modeled separately for each run so that we could measure any sensitization or habituation that occurred across runs. The outcome of feeding the subject dog was not modeled because those volumes were censored due to excessive motion during the consumption of the food.

To identify the neural response associated with a realistic dog receiving a treat but controlling for the fact that the subject didn't get the expected treat, we formed one contrast of interest: [fake-dog – bucket]. In theory, this isolated the social saliency of the fake dog, above and beyond its mere presence.

Because our main hypothesis centered on the role of the amygdala in social saliency, we extracted mean beta values for this contrast from the left and right amygdala after spatial normalization to the atlas (Figure 2). Using a mixed-effect model in SPSS (v. 23, IBM), with

identity covariance structure and maximum-likelihood estimation, we tested for the following fixed-effects: sqrt(run-1), C-BARQ dog-directed aggression score, and the interaction of sqrt(run-1) with dog-directed aggression score. The rationale for including the run number was to control for any sensitization or habituation effects that might occur from repeated presentations of a stimulus; using sqrt(run-1) allowed for a presumed curvilinear relationship to the run number. The inclusion of C-BARQ dog-directed aggression tested for the relationship between this behavioral trait and amygdala reactivity to the salience of the fake-dog, while the interaction with the run number controlled for potentially different rates of habituation with different temperaments.

Results

The mixed-effect model showed a significant relationship of amygdala activity to the dog-directed aggression score [$t(76) = 3.35$, $p = 0.001$] as well as an interaction with sqrt(run-1) [$t(76) = -2.33$, $p = 0.023$] (Table 1). The negative coefficient of the interaction of sqrt(run-1) × dog-aggression indicated that dogs with higher aggression not only had a higher amygdala activation to the fake-dog, but also had a greater amount of habituation over the 3 runs. Because activation and habituation were correlated, we also ran the analysis on run 1 only (Figure 2 & Table 2). This confirmed the relationship of amygdala activation to dog-aggression [$t(26) = 2.58$, $p = 0.016$].

Table 1. Estimates of fixed effects for amygdala and contrast: [fake-dog – bucket]

Effect	Estimate	SE	df	t	Significance
Intercept	-0.26	0.15	76	-1.77	0.081
Sqrt(Run-1)	0.11	0.15	76	0.70	0.484
Dog-Directed Aggression	0.53	0.16	76	3.35	0.001
Sqrt(Run-1) × Dog-Directed Aggression	-0.37	0.16	76	-2.33	0.023

Table 2. Estimates of fixed effects (Run 1 only) for amygdala and contrast: [fake-dog – bucket]

Effect	Estimate	SE	df	t	Significance
Intercept	-0.27	0.19	26	-1.42	0.167
Dog-Directed Aggression	0.53	0.20	26	2.58	0.016

Discussion

In 13 domestic dogs cooperatively scanned with awake-fMRI, aggressive temperament was positively correlated with bilateral amygdala activation when viewing their caregivers providing food to a realistic-looking fake-dog relative to dropping the food in a bucket. Because dogs were rewarded with food on one third of the trials, both the bucket and dog conditions involved loss of the potential reward and were differentiated only by the end-point for those rewards.
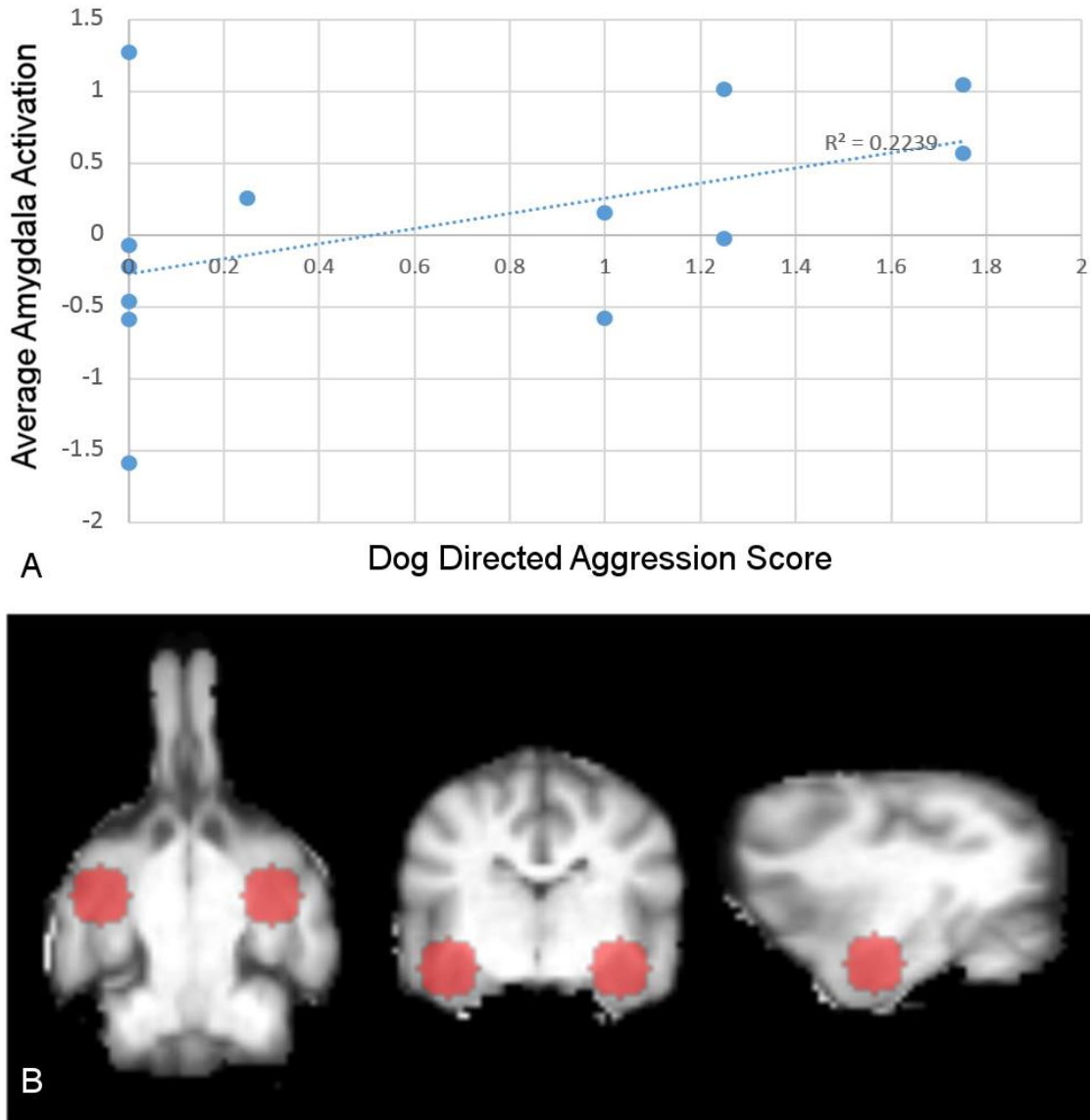
Figure 2. Relationship of amygdala activation to dog-directed aggression. A: Amygdala activation vs. dog-directed aggression score. Average differential amygdala activation during run 1 for each dog, plotted as a function of the dog-directed aggression score. There is a significant, positive correlation between the differential activation in the amygdala for [fake-dog – bucket]. B: Anatomically defined, spherical, bilateral amygdala regions of interest (ROIs) used to determine amygdala activation, shown in the transverse, coronal, and sagittal planes.

From both human and non-human studies, activation in the amygdala has been linked with a range of affective states, including anxiety, anger, fear, and even jealousy. As such, amygdala activation should not be equated with specific emotions; it should be more broadly interpreted as a neurobiological indicator of high arousal. Depending on the context, such arousal may serve as a prelude to overt aggressive behavior (LeDoux, 2003).

Dog-dog and dog-human aggression is troublingly common and the results can be

serious (Overall & Love, 2001). Although folk theories are rampant, there is little prior scientific knowledge on the biological and neurobiological underpinnings of aggression in domestic dogs. Our findings suggest that dogs with a temperamental inclination toward dog-dog aggression (as assessed by the C-BARQ) may show increased arousal (as indexed by amygdala activation) when their caregivers interact with other dogs in a food context. This finding is consistent with prior work in humans and non-human animals (Nelson & Trainor, 2007; Ferris et al., 2008). It is of course important to further validate our findings and those of other authors using fake-dogs to elicit social responses.

None of our subjects left the scanner or showed any overt signs of aggression when food was provided to the fake dog or at any other point during imaging. In addition, even the most temperamentally aggressive dogs were well-trained and relatively well-mannered in the context of the MRI. Together, these facts suggest that covert arousal can be increased in aggressive dogs in certain situations even without overt behavioral manifestations. Importantly, each of our subjects had extensive training to remain still and under control in the scanner environment. This training may have tempered the manifestation of aggression in the scanner context. Even so, actual aggressive behavior is likely to be preceded by covert arousal, and there may be covert arousal in many situations when no actual aggression occurs. Interaction between a dog's caregiver and another dog may be a dangerous trigger for aggression in certain dogs, even if, in most cases, aggression does not occur. As discussed by Cook, Spivak and Berns (2016), dogs with poor inhibitory control and high degrees of covert aggression might be most at risk.

We also found significant habituation of the amygdala response across experimental sessions — but only in the aggressive dogs: the ones who had amygdala activation in the first place. Notably, this activation was maximal in the first run but effectively nonexistent in the second and third runs. Whether the decrease in amygdala response is due to habituation or desensitization is difficult to determine, but a decreased physiological response following repeated exposure is consistent with the classical definition of habituation (Groves & Thompson, 1970). This suggests that behavioral interventions involving controlled exposure to interactions between their caregiver and other dogs might be an effective therapy for dogs prone to aggressive behavior in these contexts. Exposure-based interventions may also prove effective for dogs who show aggression in other contexts. There is a robust literature indicating the value of exposure therapy in humans with anxiety and other high-arousal disorders (Davis, 2002; Hofmann, 2008). More data are needed on pharmacological treatment of aggression before making specific recommendations for dogs, but serotonin agonists and vasopressin antagonists have shown some promise in humans (Ferris et al., 2008). Importantly, in our scanning context, we could not rule out the potential contribution of satiation, and thus reduced motivation, to the decrement in amygdala activation over the course of the experiment.

Our findings may also be relevant to social-resource guarding in dogs. Recent behavioral evidence indicates that dogs show a tendency toward aggressive behaviors when their caregivers show affection toward a fake-dog as opposed to a neutral inanimate object (Harris & Prouvost, 2014)*.* This has been likened to human jealousy. The bond between the caregiver and dog is certainly central to the socioecology of domestic dogs. A number of other social species have been shown to be covetous of attention and access to conspecifics (Panksepp, 2010). In previous research, we have shown that some dogs show ventral caudate activation (which is associated with reward anticipation) in response to receiving praise

(Cook et al., 2016). Many domestic dogs value caregiver attention highly and may desire to protect their access to it. Such an inclination may be similar to a desire to guard and protect social and sexual partners within their own species.

In addition to responding to a potential social threat, our dogs might also have been responding to the simple receipt of reward by a conspecific, regardless of the role the caregiver played in providing it. As with primates (Brosnan & DeWaal, 2003), dogs have also shown some sensitivity to "reward inequity," that is, they react negatively when a conspecific receives a greater reward than they do (Range et al., 2009; Range, Leitner & Viranyi, 2012). Although the reward was balanced between the subject and the fake-dog in our study, all dogs in the study were accustomed to being fed in the imaging context and may have viewed the fake dog as an interloper. Importantly, whether it was something like proto-jealousy or reward inequity that drove the observed amygdala response, there was a clear difference when the reward was deposited in a bucket, suggesting that the aggressive subjects were sensitive to the target of human attention or food reward, not just to the loss of a potential treat. Interestingly, recent evidence suggests that eliciting a response to reward inequity in dogs may require that a human be the one providing the rewards (Brucks et al., 2017). This might be taken to suggest that there is an element of social-resource guarding in canine reward inequity.

In the current study, we could not rule out a related (but not mutually exclusive) interpretation of our findings. It may be that aggressive dogs show increased amygdala activation any time they attend to a conspecific, regardless of context. Although the fake-dog was present throughout the imaging sessions, and was always fully visible to the subjects, having the human deliver a food reward to the fake dog probably increased attentional focus on the fake dog. Future work might seek to disentangle this by finding other, non-social ways to direct attention to the fake dog. This may prove difficult, however, considering that the MRI will always be an environment in which the MRI-dogs are accustomed to receiving food and attention.

The complexities of the scanning environment necessitated our using a fake-dog rather than a real one. Fake-dogs have also been used in behavioral studies (Harris & Provoust, 2014), but they have typically been animatronic, moving and/or making noise. Our dog was simply a realistic-looking statue. We did observe apparently social reactions (e.g., growling, sniffing) to our fake dog in pilot work with dogs who did not participate in this imaging study, but studies with real conspecifics would be more valid ecologically (Prato-Previde et al., 2018). Determining how to control the behavior of a real dog during testing so as to avoid experimental confounds is paramount. With real dogs, the neurobiology of social status can also be studied, which might answer questions about the effect of status and relationship dynamics on affiliative behavior, jealousy, or aggression.

Dog-dog, and dog-human aggression affects millions of people world-wide. Our findings highlight the potential mediating factor of covert arousal, and the compounding roles of temperament and human attention. Studying and understanding covert aggression may yield valuable information for pet caregivers and society as a whole. Pet caregivers often cite that their dog "gave no warning" prior to an attack. The onset of amygdala activation might be an advance warning. Further study might help detect a visible correlate of amygdala activation in changes in facial countenance or body language. Our findings also suggest that covert arousal may habituate with exposure. Behavioral and pharmacological interventions with aggressive dogs may be able to build on this.

Competing Interests
G.B. and 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. M.S. is the president of Comprehensive Pet Therapy (CPT) but no CPT technology or IP was used in this research.

Author Contributions
P.C., M.S, and G.B. designed the research; all authors collected data; P.C and G.B. analyzed data; and all authors wrote the paper.

References

Andics A, Gácsi M, Faragó T, Kis A, Miklósi, Á. Voice-sensitive regions in the dog and human brain are revealed by comparative fMRI. *Current Biology*, 2014; 24(5):574-78.

Avants BB, Tustison NJ, Song G, Cook PA, Klein A, Gee JC. A reproducible evaluation of ANTs similarity metric performance in brain image registration. *Neuroimage*, 2011 Feb 1; 54(3):2033-44.

Berns GS, Brooks A, Spivak M. Replicability and heterogeneity of awake unrestrained canine fMRI responses. *PLOS ONE*, 2013 Dec 4; 8(12):e81698.

Berns GS, Brooks AM, Spivak M. Functional MRI in awake unrestrained dogs. *PLOS ONE*, 2012 May 11; 7(5):e38027.

Berns GS, Brooks AM, Spivak M, Levy K. Functional MRI in awake dogs predicts suitability for assistance work. *Scientific Reports*, 2017; 7:43704.

Berns GS, Cook PF. Why did the dog walk into the MRI? *Current Directions in Psychological Science*, 2016 Oct; 25(5):363-69.

Brosnan SF, De Waal FB. Monkeys reject unequal pay. *Nature*, 2003 Sep 18; 425(6955):297-99.

Brucks D, Marshall-Pescini S, Essler JL, Mcgetrick J, Huber L, Range F. What are the ingredients for an inequity paradigm? Manipulating the experimenter's involvement in an inequity task with dogs. *Frontiers in Psychology*, 2017; 8:270.

Buss DM. Comment: Evolutionary criteria for considering an emotion "basic": Jealousy as an illustration. *Emotion Review,* 2014*;* 6(4):1–3.

Casey RA, Loftus B, Bolster C, Richards GJ, Blackwell EJ. Human directed aggression in domestic dogs (Canis familiaris): Occurrence in different contexts and risk factors. *Applied Animal Behaviour Science*, 2014 Mar 31; 152:52-63.

Cloninger, CR, Svrakic, DM, Przybeck, TR. A psychobiological model of temperament and character. *Archives of General Psychiatry*, 1993; 50(12):975-90.

Coccaro, EF, McCloskey, MS, Fitzgerald, DA, Phan, KL. Amygdala and orbitofrontal reactivity to social threat in individuals with impulsive aggression. *Biological Psychiatry*, 2007; 62(2):168-78.

Cook, PF. (2017). Studying dog emotion beyond expression and without concern for feeling. *Animal*

Sentience 14(15).

Cook PF, Brooks A, Spivak M, Berns GS. Regional brain activations in awake unrestrained dogs. *Journal of Veterinary Behavior: Clinical Applications and Research*, 2016 Nov 1; 16:104-12.

Cook PF, Prichard A, Spivak M, Berns GS. Awake canine fMRI predicts dogs' preference for praise vs. food. *Social Cognitive and Affective Neuroscience*, 2016 Aug 12; 11(12):1853-62.

Cook PF, Spivak M, Berns G. Neurobehavioral evidence for individual differences in canine cognitive control: An awake fMRI study. *Animal Cognition*, 2016 Sep 1; 19(5):867-78.

Cook PF, Spivak M, Berns GS. One pair of hands is not like another: Caudate BOLD response in dogs depends on signal source and canine temperament. *PeerJ*, 2014 Sep 30; 2:e596.

Cox RW. AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, 1996; 29(3):162-73.

Cuaya LV, Hernández-Pérez R, Concha L. Our faces in the dog's brain: functional imaging reveals temporal cortex activation during perception of human faces. *PLOS One*, 2016; 11(3):e0149431.

Cubicciotti DD, Mason WA. Comparative studies of social behavior in *Callicebus* and *Saimiri*: Heterosexual jealousy behavior. *Behavioral Ecology and Sociobiology*. 1978 Sep 1; 3(3):311-22.

Datta R, Lee J, Duda J, Avants BB, Vite CH, Tseng B, Gee JC, Aguirre GD, Aguirre GK. A digital atlas of the dog brain. *PLOS ONE*, 2012 Dec 20; 7(12):e52140.

Davis M. Role of NMDA receptors and MAP kinase in the amygdala in extinction of fear: clinical implications for exposure therapy. *European Journal of Neuroscience*. 2002 Aug 1; 16(3):395-98.

Dilks DD, Cook P, Weiller SK, Berns HP, Spivak M, Berns, GS. Awake fMRI reveals a specialized region in dog temporal cortex for face processing. *PeerJ*, 2015; 3:e1115.

Dodman NH, inventor; Trustees of Tufts College, assignee. Veterinary method for clinically modifying the behavior of dogs exhibiting canine affective aggression using preferential/discriminatory serotonin reuptake inhibitors. *United States patent* US 5,762,960. 1998 Jun 9.

Ferris CF, Stolberg T, Kulkarni P, Murugavel M, Blanchard R, Blanchard DC, Febo M, Brevard M, Simon NG. Imaging the neural circuitry and chemical control of aggressive motivation. *BMC Neuroscience*, 2008; 9(1):111.

Groves PM, Thompson RF. Habituation: A dual-process theory. *Psychological Review*, 1970; 77(5):419-450.

Harmon-Jones E, Peterson CK, Harris CR. Jealousy: Novel methods and neural correlates. *Emotion*, 2009; 9(1):113–17.

Harris CR, Prouvost C. Jealousy in dogs. *PLOS ONE*, 2014 Jul 23; 9(7):e94597.

Hart SL. The ontogenesis of jealousy in the first year of life: A theory of jealousy as a biologically-based dimension of temperament. In S. L. Hart & M. Legerstee (Eds.), *Handbook of jealousy: Theory, research, and multidisciplinary approaches*. Wiley-Blackwell, 2010; 57-82.

Hofmann SG. Cognitive processes during fear acquisition and extinction in animals and humans: Implications for exposure therapy of anxiety disorders. *Clinical Psychology Review*, 2008 Feb 29; 28(2):199-210.

Horowitz A. Attention to attention in domestic dog (*Canis familiaris*) dyadic play. *Animal Cognition*, 2009 Jan 1; 12(1):107-18.

Hsu Y, Serpell, JA. Development and validation of a questionnaire for measuring behavior and temperament traits in pet dogs. *Journal of the American Veterinary Medical Association*, 2003; 223(9):1293-1300.

Konok V, Nagy K, Miklósi Á. How do humans represent the emotions of dogs? The resemblance between the human representation of the canine and the human affective space. *Applied Animal Behaviour Science*, 2015; 162:37-46.

Kujala, MV. (2017). Canine emotions as seen through human social cognition. *Animal Sentience* 14(1).

Lakatos G, Gácsi M, Topál J, Miklósi Á. Comprehension and utilisation of pointing gestures and gazing in dog–human communication in relatively complex situations. *Animal Cognition*, 2012 Mar 1; 15(2):201-13.

LeDoux J. The emotional brain, fear, and the amygdala. *Cellular and Molecular Neurobiology*, 2003; 23(4-5):727-38.

Merola I, Prato-Previde E, Marshall-Pescini S. Social referencing in dog-caregiver dyads?. *Animal Cognition*, 2012 Mar 1; 15(2):175-85.

Montoya ER, Terburg, D, Bos PA, Van Honk J. Testosterone, cortisol, and serotonin as key regulators of social aggression: A review and theoretical perspective. *Motivation and Emotion*, 2012; 36(1):65-73.

Morris PH, Doe C, Godsell E. Secondary emotions in non-primate species? Behavioural reports and subjective claims by animal caregivers. *Cognition and Emotion*, 2008 Jan 1; 22(1):3-20.

Müller CA, Schmitt K, Barber AL, Huber L. Dogs can discriminate emotional expressions of human faces. *Current Biology*, 2015 Mar 2; 25(5):601-05.

Nagasawa M, Mitsui S, En S, Ohtani N, Ohta M, Sakuma Y, Onaka T, Mogi K, Kikusui T. Oxytocin-gaze positive loop and the coevolution of human-dog bonds. *Science*, 2015 Apr 17; 348(6232):333-36.

Nelson RJ, Trainor BC. Neural mechanisms of aggression. *Nature Reviews Neuroscience,* 2007; 8(7):536-46.

Netto WJ, Planta DJ. Behavioural testing for aggression in the domestic dog. *Applied Animal Behaviour Science*, 1997 Apr 1; 52(3-4):243-63.

O'Heare J. *Aggressive behavior in dogs: A comprehensive technical manual for professionals*. Dogwise Publishing, 2017.

Overall KL, Love M. Dog bites to humans—demography, epidemiology, injury, and risk. *Journal of the American Veterinary Medical Association*, 2001 Jun 1; 218(12):1923-34.

Palmer R, Custance D. A counterbalanced version of Ainsworth's Strange Situation Procedure reveals secure-base effects in dog–human relationships. *Applied Animal Behaviour Science*, 2008 Feb 29; 109(2):306-19.

Panksepp J. *Affective neuroscience: The foundations of human and animal emotions*. Oxford University Press, 2004.

Panksepp J. *The evolutionary sources of jealousy.* In SL Hart & M Legerstee (Eds.), *Handbook of jealousy: Theory, research, and multidisciplinary approaches*. Wiley-Blackwell, 2010; 101-20.

Peirce JW. PsychoPy—psychophysics software in Python. *Journal of Neuroscience Methods*, 2007 May 15; 162(1):8-13.

Prato-Previde, E., Nicotra, V., Pelosi, A., & Valsecchi, P. *Pet dogs' behavior when the owner and an unfamiliar person attend to a faux rival. PLOS ONE,* 2018; 13(4):e0194577.

Range F, Horn L, Viranyi Z, Huber L. The absence of reward induces inequity aversion in dogs. *Proceedings of the National Academy of Sciences*, 2009 Jan 6; 106(1):340-45.

Range F, Leitner K, Virányi Z. The influence of the relationship and motivation on inequity aversion in dogs. *Social Justice Research*, 2012 Jun 1; 25(2):170-94.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. Integrating animal temperament within ecology and evolution. *Biological Reviews*, 2007; 82(2):291-318.

Rilling JK, Winslow JT, Kilts CD. The neural correlates of mate competition in dominant male rhesus macaques. *Biological Psychiatry*, 2004 Sep 1; 56(5):364-75.

Schwab C, Huber L. Obey or not obey? Dogs (*Canis familiaris*) behave differently in response to attentional states of their caregivers. *Journal of Comparative Psychology*; 2006 Aug; 120(3):169.

Takahashi H, Matsuura M, Yahata N, Koeda M, Suhara T, Okubo Y. Men and women show distinct brain activations during imagery of sexual and emotional infidelity. *NeuroImage*, 2006; 32(3):1299-1307.

Topál J, Miklósi Á, Csányi V, Dóka A. Attachment behavior in dogs (*Canis familiaris*): A new

application of Ainsworth's (1969) Strange Situation Test. *Journal of Comparative Psychology*, 1998 Sep; 112(3):219.

Van den Berg SM, Heuven HC, van den Berg L, Duffy DL, Serpell JA. Evaluation of the C-BARQ as a measure of stranger-directed aggression in three common dog breeds. *Applied Animal Behaviour Science*, 2010; 124(3):136-41.

Wright JC. Canine aggression toward people: Bite scenarios and prevention. *Veterinary Clinics of North America: Small Animal Practice*, 1991 Mar 1; 21(2):299-314.

Call for Commentary: *Animal Sentience* publishes Open Peer Commentary on all accepted target articles. Target articles are peer-reviewed. Commentaries are editorially reviewed. There are submitted commentaries as well as invited commentaries. Commentaries appear as soon as they have been reviewed, revised and accepted. Target article authors may respond to their commentaries individually or in a joint response to multiple commentaries.

Instructions: animalstudiesrepository.org/animsent/guidelines.html

---

Supplementary Material

Table S1 – C-BARQ values for all dogs. Scores are listed for each dog for each dimension of temperament assessed by the C-BARQ. These values were calculated from rank scores each dog's primary handler selected while filling out the standard C-BARQ assessment. The 14 subscales are as follows: Train = Trainability; StrDirAgg = Stranger-Directed Aggression; OwnDirAgg = Caregiver-Directed Aggression; DogDirAgg = Dog-Directed Aggression; FamDogAgg = Familiar Dog-Directed Aggression; DogDirFear = Dog-Directed Fear; StrDirFear = Stranger-Directed Fear; NonSocFear = Non-Social Fear; TouchSen = Touch Sensitivity; SepRelProb = Separation-Related Problems; Excite = Excitability; AtcAtnSeek = Attachment/Attention Seeking; Chasing; Energy.

Table S2 – Percent BOLD change for the [FakeDog – Bucket] contrast is listed for each dog in the left and right amygdala ROIs by experimental run. Dog-Directed Aggression scores from the C-BARQ are also listed for each dog.