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Canine emotions as seen through human social cognition

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Abstract: It is not possible to demonstrate that dogs (*Canis familiaris*) feel emotions, but the same is true for all other species, including our own. The issue must therefore be approached indirectly, using premises similar to those used with humans. Recent methodological advances in canine research reveal what dogs experience and what they derive from the emotions perceptible in others. Dogs attend to social cues, they respond appropriately to the valence of human and dog facial expressions and vocalizations of emotion, and their limbic reward regions respond to the odor of their caretakers. They behave differently according to the emotional situation, show emotionally driven expectations, have affective disorders, and exhibit some subcomponents of empathy. The canine brain includes a relatively large prefrontal cortex, and like primates, dogs have a brain area specialized for face perception. Dogs have many degrees of emotion, but the full extent of dog emotions remains unknown. Humans are a socially minded species; we readily impute mind and emotion to others, even to vegetables or rocks. Hence the experimental results need to be analyzed carefully, so the emotional lives of dogs are accurately estimated.

Keywords: *Canis familiaris*, domestic dog, emotion, psychology, social cognition, comparative cognition, neuroscience



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1. Introduction

Dogs are our age-old domesticated companions. Darwin (1872) considered dogs as a comparative example in his work on emotional expression across species. Sharing the living environment with us, dogs have developed remarkable social skills in inter-species communication (for the original articles, see Hare et al. 1998, Soproni et al. 2001, Call et al. 2003, Miklósi et al. 2003, Kaminski et al. 2009). Thus, it is no surprise that we have inherent interest in understanding dog experience, behavior, and cognition. However, proving that someone experiences something is an impossibility because experiences are subjective (Nagel 1974). We can never know that another person experiences the same thing as us. There are always subtle differences in the underlying psychology and physiology, although the larger-scale responses may be similar within a species. How, then, can we know anything about the inner lives of other species such as our companion dogs?

In human emotion research, “emotion” and “feeling” are often separated because emotion can be targeted for objective experimental study through behavioral and neurophysiologic observations, whereas feeling is subjective: What the emotion feels like and how it is interpreted by the subject can only be inferred indirectly. We can detect the behavioral and physiological correlates of both my happiness and your happiness, but they can be felt and interpreted very differently by each of us.

In this work, the topic of canine emotions is approached using the framework of Anderson and Adolphs (2014). They argue that the capacity for emotion can exist across phylogeny, but emotions may consist of a different set of parallel behavioral, somatic, physiological, and cognitive responses in different species. We begin by considering the effect of the human viewpoint. Canine emotions are examined both behaviorally and biologically, with a brief review of the neural basis for primary emotions and the respective structures in the dog brain. The neural basis for secondary emotions is also reviewed, followed by a discussion of the current research on dogs. Long-term moods and comparative aspects are also considered. The ultimate purpose of this target article is to stimulate discussion about the nature and extent of dog emotions and the need for this new field of research, as well as to provide groundwork for the approach from various scientific disciplines.

One of the difficulties in considering emotional states in dogs is the inconsistency in terminology across studies. Avoiding anthropomorphic terms has left many canine affective phenomena without a standardized terminology. Different researchers have used different terms for the same phenomenon, or similar terms for separate phenomena. This review attempts to integrate results across studies and disciplines.

2. Human social cognition affects perception of dog emotional states

The existence of emotions in dogs and the perception of dog emotions by the human caretakers are separate issues. Everyday life presents many possibilities for humans to misinterpret the mind behind a dog’s behavior. For example, guardians may misinterpret the dog’s affective state in separation-related anxiety (see Mendl et al. 2010a). According to the three-factor theory of anthropomorphism (Epley et al. 2007), behavioral interpretations that are often valid with other humans are also easily attributed to non-human animals such as

dogs. Thus, human, biologically tuned social perception is the starting point, as it filters our understanding of dog emotions.

People believe that animals such as dogs experience emotions (Morris et al. 2008, Morris et al. 2012, Walker et al. 2014). Humans are also quite consistent in classifying dogs' emotional behavior in different contexts (Pongrácz et al. 2005, Tami & Gallagher 2009, Walker et al. 2010, Buckland et al. 2014, Faragó et al. 2014, Lakestani et al. 2014). Humans friendly dog behavior most easily recognize, whereas aggression and fear are more difficult to identify (Tami & Gallagher 2009, Wan et al. 2012, Mirkó et al. 2013, Lakestani et al. 2014) — especially by children (Meints et al. 2010, Lakestani et al. 2014). Prior experience of dog behaviour and training, rather than mere guardianship, enhances the interpretation of canine behaviour from the whole-body cues (Kujala et al. 2012, Wan et al. 2012).

Although emotions are visible throughout dog bodily cues, human attention is generally drawn to the faces of both humans (Johnson et al. 1991) and dogs (Quinn et al. 2009). Humans can classify a dog's emotional valence (positivity-negativity) from the face irrespective of prior experience with dogs (Bloom & Friedman 2013, Schirmer et al. 2013). They can distinguish happiness (88% of the time) and anger/aggressiveness (70%) from a dog's face, but discrimination of other discrete expressions is less reliable (fear: 45%, sadness: 37%, surprise: 20%, and disgust: 13%; Bloom & Friedman 2013).

Perception of others is affected by many factors in the human mind. The human social mind is equipped with a presupposition of intentionality (for reviews, Blythe et al. 1999, Scholl & Tremoulet 2000, Urquiza-Haas & Kotrschal 2015), from which anthropomorphism can arise. Attributing intentionality or other human characteristics to non-living things is strengthened by personal connection (Kiesler et al. 2006), and mental attribution is found in people's descriptions of rocks (Kiesler & Kiesler 2005), computers (e.g., Nass et al. 1994), animations (Chaminade et al. 2007), robots (Gazzola et al. 2007, Imamura et al. 2015, Martini et al. 2016), or even vegetables (Vaes et al. 2016). Humans also project their views of themselves onto dogs much as they do with conspecifics, and their perceptions of dogs are similarly affected by stereotypes (Kwan et al. 2008). Thus, humans easily attribute mental and emotional states to companion dogs, and human interpretation of canine emotions is filtered by human psychological characteristics (Kujala et al. 2017).

Humans can also deny humanity in other humans (for reviews, Leyens et al. 2000, Haslam 2006). They consistently attribute more complex emotions to their in-group than out-group members (see Leyens et al. 2000). In a human brain imaging study, the observation of images of extreme out-group members (such as drug addicts or the homeless) failed to produce the medial prefrontal cortex activation connected with social cognition (Harris & Fiske 2006). Thus, the human mind is affected by various social factors, with the judgments sometimes representing more the judge's own ideology than the reality. Likewise, when humans attempt to decipher canine emotions, dog guardians can underestimate their dogs' aggressiveness (Mirkó et al. 2013).

Attributing minds to others is innate in humans, and the human brain appears remarkably flexible regarding the source of the other mind. Human empathy generalizes to other species (Ascione 1992, Paul 2000, Taylor & Signal 2005, Norring et al. 2014, Westbury Ingham et al. 2015, Kujala et al. 2017) and affects our interpretation of dog behavior (Meyer & Forkman 2014, Meyer et al. 2014). Empathy (Westbury Ingham et al. 2015) and the attribution of mental states (Harrison & Hall 2010) to non-human animals varies with their

phylogenetic relatedness to humans. Mental attribution to both human and non-human species is connected to the temporoparietal junction associated with human theory-of-mind abilities (Cullen et al. 2014). Human brain responses to dogs can also be strikingly similar to responses to human conspecifics, whether observing dogs' facial expressions (Spunt et al. 2016), pain (Franklin et al. 2013), or social interaction (Kujala et al. 2012). Human brains seek other minds and emotions, and dog emotional behaviour is filtered through the same machinery.

3. Neural support for the basic (primary) canine emotions

It is generally agreed that basic emotional states such as anger, happiness, and fear are evolutionarily adaptive (Ekman 1992, Izard 1992, Panksepp 1998, Plutchik 2001), and they have universal facial expression patterns in humans (Ekman & Friesen 1971). Basic emotional states are associated with neural structures within the limbic system and its connections to the neocortex in mammals (Damasio 1994; LeDoux 1996; Rolls 1999). Specific basic emotions are associated with specific chemical neurotransmitter balance in the brain (Panksepp 1998).

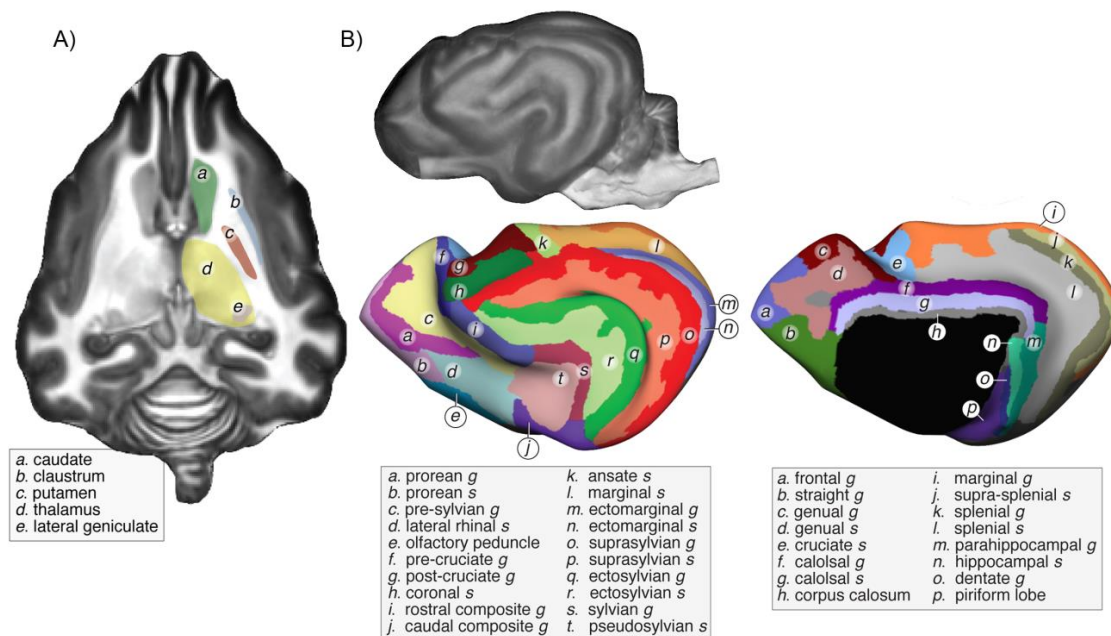


Figure 1. Key areas of the dog brain. (A) Some key subcortical areas shown on the axial magnetic resonance imaging slices (dog's nose pointing upwards; top = anterior, bottom = posterior, left = left hemisphere, and right = right hemisphere) and (B) the cortical surface of the dog brain, with the sulci opened and the nomenclature overlaid below. The cortical surface is shown laterally from the left hemisphere (dog's nose pointing left; left = anterior, right = posterior, top = dorsal, and bottom = ventral); the image has been magnified with standard digital image processing to show the gyri and sulci. Modified, under the terms of the Creative Commons Attribution License, from figures <http://dx.doi.org/10.1371/journal.pone.0052140.g002> and <http://dx.doi.org/10.1371/journal.pone.0052140.g003> (Datta et al. 2012).

The domestic dog, as a member of mammalian order Carnivora and the Caninae family, has a brain that includes all the major structures and connections supporting basic emotional functions (Jensen 2007, de Lahunta & Glass 2009, Evans & de Lahunta 2013). Dog brains include, bilaterally, the limbic system with the nucleus accumbens; the amygdala with its sensory and cortical connections; the cingulate cortex; and the sensory-motor cortices and the insula, deep within the pseudosylvian fissure (in humans, the Sylvian fissure occupies the topologically equivalent position). Dogs also have a relatively large prefrontal cortex that is not directly associated with motor functions (see Figure 1, Palazzi 2011, Datta et al. 2012, Evans & de Lahunta 2013).

The corresponding structures in humans have been studied extensively in recent decades regarding their roles in social and emotional function (for reviews, see e.g., Bush et al. 2000, Damasio et al. 2000, Adolphs 2002, Leppänen & Nelson 2009, Etkin et al. 2011, Schilbach et al. 2013). For dogs, the research is more scattered. Some dog brain function is also inferred from neurological experiments with cats (*Felis catus*) and the homologues between the brain anatomies of the two species. Many functions of the subcortical nuclei (e.g., the septal area or hypothalamus) and the finer neurophysiologic details, as well as visual cortical organization, are inferred from cat studies (King 1987, de Lahunta & Glass 2009, Sjaastad et al. 2010). Utilization of the methodology for studying human brain function has facilitated the study of dog brains. A recent study showed that dogs' nucleus accumbens is activated by the odor of familiar humans, highlighting the possibilities of methodological advances in examining dog emotions (Berns et al. 2015).

Dog and human brains also have important differences. The association areas (brain areas not directly responsible for sensomotor functions) cover about 20% of the dog neocortex but 85% of the human neocortex (Evans & de Lahunta 2013). The rhinencephalon, devoted to processing olfactory signals, covers a relatively large area in dog brains (Evans & de Lahunta 2013). The existence of limbic and cortical structures in dogs is consistent with having the basic emotions, although dogs' qualia – what it feels like to be a dog (Nagel 1974) — no doubt differ from our own.

4. Emotional reactivity and affective-behavioral disorders in dogs

Research on dog emotions has traditionally concentrated on the problems dog behavior causes for the human guardians, which is why we know more about dog fear and aggression. Dog emotionality has been studied to predict general emotional reactivity (Goddard & Beilharz 1986, Sforzini et al. 2009), aggression (Netto & Planta 1997, van den Berg et al. 2003, van der Borg et al. 2010), behavioral disorders (van der Borg et al. 1991), and differences among dog breeds (Scott & Fuller 1965) from puppies to adulthood. Dog aggressiveness is tested by presenting provocative stimuli, such as an unfamiliar barking dog (Netto & Planta 1997, van den Berg et al. 2003) or staring the dog in the eyes (Sforzini et al. 2009). Guardian questionnaires are also used (Netto & Planta 1997, Hsu & Serpell 2003, Duffy et al. 2008). Similarly, testing a dog's fearfulness can include presenting a sudden loud noise, a novel object, a falling bag, or a gunshot (Melzack 1952, Beerda et al. 1998, King et al. 2003, Hydbring-Sandberg et al. 2004, Morrow et al. 2015).

Both fearful and aggressive behaviors in dogs are associated with some physiological or autonomic responses. Stimuli eliciting fearful behavior in dogs increase their cortisol (Beerda et al. 1998, King et al. 2003, Hydbring-Sandberg et al. 2004, Dreschel & Granger 2005, Morrow et al. 2015) or progesterone levels (Hydbring-Sandberg et al. 2004), heart rates (King et al. 2003, Hydbring-Sandberg et al. 2004, Ogata et al. 2006), and body temperatures (Ogata et al. 2006). Aggressive behaviors are associated with reduced serotonergic function (Reisner et al. 1996).

The most common affective-behavioral clinically treated disorders in dogs are related to fearful or aggressive behavior and may be induced by separation anxiety, noise sensitivity (for review, Sherman & Mills 2008), and dominance/competitive aggression (see e.g., Beaver 1983, Wright & Nesselrote 1987, Cameron 1997, Reisner 1997, Haug 2008). Treatments for these conditions usually include behavior modification, often combined with neuropharmacological medication as in human psychiatric disorders (Overall 2000).

Taken together, aggression and fear are the most studied emotions in dogs, but research on other emotional states is scarce. An exception among the positive emotions is dog play behavior, which is well-documented (Bekoff 1974a, Bekoff 1974b, Bekoff 1995, Rooney et al. 2000, Horvath et al. 2008, Ward et al. 2008, Horowitz 2009a, Palagi et al. 2015).

5. Production and perception of facial expressions

Faces and facial expressions convey delicate and meaningful information about emotional states to conspecifics in humans (for reviews, Adolphs 2002, Calder & Young 2005, Hari & Kujala 2009, Leppänen & Nelson 2009) as well as in many non-human species (for reviews, Tate et al. 2006; Leopold & Rhodes 2010). Facial expressions of emotion in dogs were discussed by Darwin (1872); they characterized in great detail since the 1960s, noting similarities in the emotional expressions for aggression and happiness between dogs, other carnivores, and primates (Bolwig 1964, Fox 1970). A precise coding of human facial expressions based on the movement of facial muscles — a facial action coding system (FACS) — was developed in the 1970s (Ekman & Friesen 1978). The system has since been applied to many other primate species (Vick et al. 2007, Parr et al. 2010, Waller et al. 2012, Caeiro et al. 2013), horses (*Equus caballus*, Wathan et al. 2015), cats (<http://www.catfacs.com/>), and dogs (Waller et al. 2013). Deviating from the human-FACS, the non-human-FACS often includes the movement of ears.

Behavioral and brain responses during the perception of facial expressions have been studied in non-human primates and sheep for decades (see Tate et al. 2006). As a second non-primate species after sheep (Kendrick & Baldwin 1987), dogs have been shown to possess a distinguishable face-processing region in the temporal cortex, separating brain responses to faces from the responses to objects (Figure 2) (Dilks et al. 2015, Cuaya et al. 2016). The response profiles are roughly comparable with those of the human fusiform face area (Kanwisher et al. 1997), although the cortical region seems to be more variable in dogs. In humans, face processing continues from the fusiform to the inferotemporal cortex and the superior temporal sulcus, with the extraction of identity- and emotion-specific information (for review, Haxby et al. 2000).

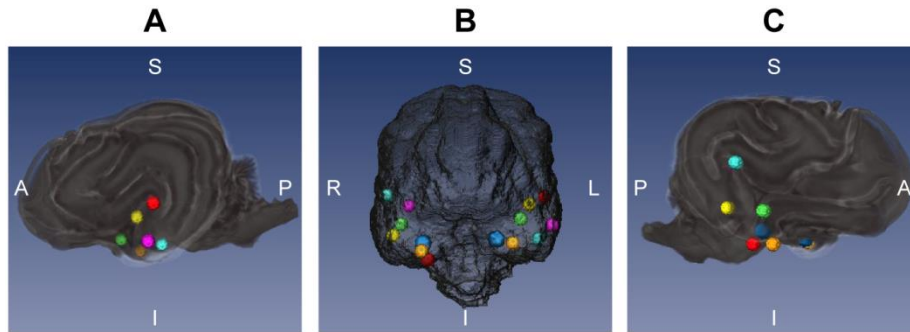


Figure 2. Stronger brain responses from dogs for faces versus objects. Images show the focus of brain activation during non-invasive functional magnetic resonance imaging in seven dogs for faces versus objects with contrast, overlaid on a digitally produced glass brain to reveal foci located within the sulci. (A) Lateral view from left hemisphere, (B) rostral view from front, and (C) lateral view from right hemisphere. A = anterior, P = posterior, S = superior (or dorsal), I = inferior (and ventral), L = left, and R = right. Modified, under the terms of the Creative Commons Attribution License, from figure <http://dx.doi.org/10.1371/journal.pone.0149431.g005> (Cuaya et al. 2016).

While direct information on dogs' brain processing of emotional expressions is missing, a growing body of behavioral and eye-tracking research supports the ability of dogs to distinguish negative and positive facial expressions in both humans and dogs, and to respond appropriately according to the valence of faces (Nagasawa et al. 2011, Racca et al. 2012, Müller et al. 2015, Barber et al. 2016, Somppi et al. 2016) (Figure 3).

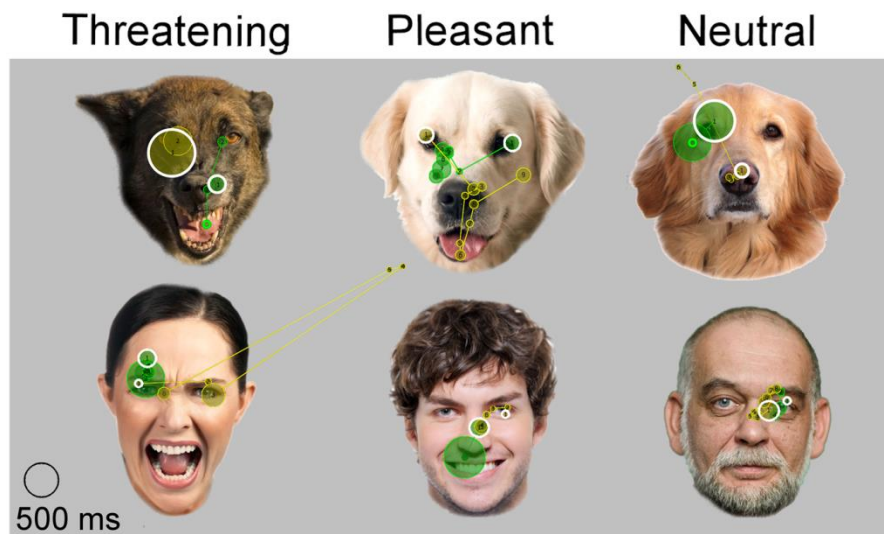


Figure 3. Gaze fixations (circles) and scanning paths (lines between the circles) of two dogs (shown in light and dark green) for facial expressions of dogs and humans. White circles represent the targets of the first fixations; dogs tend to gaze first into the eyes of both humans and dogs. Figure from <http://dx.doi.org/10.1371/journal.pone.0149431.g005> (Somppi et al. 2016), reprinted under the terms of the Creative Commons Attribution License.

Dogs associate emotional vocalizations of both humans and dogs with the corresponding facial expressions, showing multisensory processing of emotional expressions (Albuquerque et al. 2016). Like human infants, dogs use human emotional expressions for social referencing, as a source of approach/avoid information for novel objects (Merola et al. 2012b, Merola et al. 2012a, Buttelmann & Tomasello 2013, Merola et al. 2014, Turcsán et al. 2015). Furthermore, they appear to generalize the valence information of facial expressions across human individuals (Müller et al. 2015, Somppi et al. 2016) rather than responding only to guardians' expressions — in contrast to cats, who respond mainly to the valence of their guardians' facial expressions (Galvan & Vonk 2016).

Human cross-cultural studies could provide some useful clues for studying emotions in dogs. The basic emotions are remarkably similar around the world (Ekman & Friesen 1971). Facial expressions and their recognition, situations provoking emotions, and the organization of emotions on the valence-arousal dimensions are consistent across cultures (Shaver et al. 1992). However, the perception of emotional intensity differs across cultures (Ekman et al. 1987), and the decoding and encoding of emotion in the cultural in-group appears more accurate (for meta-analysis, Elfenbein & Ambady 2002). Similarly to the cultural differences in humans, differences in breeds or environment may affect the expression or perception of emotion in dogs (for review, Mehrkam & Wynne 2014).

It appears unquestionable that dogs can both produce and process emotions through facial expression, but the question is to what extent? One remaining question concerns what part of recognizing human facial expressions by dogs is innate and what is learned through association and experience. Also, the research addressed mainly the positive-negative valence information of faces rather than the more diverse, discrete expressions of emotion (e.g., happiness, sadness, surprise, fear, disgust, anger: Ekman & Friesen 1971), so information on dogs' ability to discriminate or respond to discrete expressions of emotion is lacking. Are there universal facial expressions of emotion in dogs as there are in humans (Ekman & Friesen 1971) — and if so, what are they?

6. Fundamental basis for secondary (social) emotions

Secondary emotions — generated through the interpretation of social situations and requiring some sense of another's mind — are less likely than basic (primary) emotions to be attributed to dogs by people, but 22 to 94% of people believe that dogs do have secondary emotions such as shame or guilt (Morris et al. 2008, Morris et al. 2012). As adult humans, we effortlessly attribute secondary emotions to other people. Without knowledge of the differences among minds across species, we can just as easily attribute the emotions to non-humans, including dogs. However, dogs may be incapable of experiencing the more complex social emotions, or their experiences may be qualitatively very different from ours. The reason the dog is human's best friend may be the apparently missing canine capacity for secondary emotions such as contempt or Schadenfreude (the joy in others' misfortune).

The secondary emotions seem to require some sense of the self (Leary 2003). Having self-awareness complicates the emotional experience in many ways — allowing imagined experiences with no basis in reality. Leary (2003) clarifies the effect of self on emotional experience through five points: "Specifically, having a self permits people to (1) evoke emotions in themselves by imaging self-relevant events, (2) react emotionally to abstract and

symbolic images of themselves in their own minds, (3) consciously contemplate the cause of their emotions, (4) experience emotions by thinking about how they are perceived by other people, and (5) deliberately regulate their emotional experience” (p. 775). As he also points out, animals do not need a concept of self in order to have a basic emotion. Humans often attempt to suppress self-referential emotional thought in various ways (e.g., by drinking alcohol) since such thoughts can cause increasing distress. In children, self-awareness appears to arise roughly concurrently with the ability to take another’s perspective (Lempers et al. 1977); early studies suggest similar co-occurrences in other species (Gallup & Suarez 1986). To date, the level of dogs’ self-awareness is not known — for example, they have not passed Gallup’s (1986) mirror self-recognition test, but they do spend less time inspecting their own urine markings than those of others (Bekoff 2001).

The brain regions responsible for secondary emotions include a network comprising the medial orbitofrontal cortex, the temporal pole, and the superior temporal sulcus in humans (Moll et al. 2002, Burnett & Blakemore 2009). In principle, homologues of these regions may also be present in the brains of dogs, in the temporal and frontal association areas. Homologues in cortices are difficult to verify because the brain functions of these cortical regions cannot be localized anatomically, thus functional brain imaging is needed. Nevertheless, the cortical association areas, associated with secondary emotions in humans, are larger in humans than in dogs (20% of the cortex in dogs and 85% in humans; Evans & de Lahunta 2013).

The brain areas responding to secondary emotions are also strongly connected to areas of the limbic system, and the connections alter the level of cognitive evaluation of the emotional states (Berridge 2003). The connections between the cortex and the limbic system are so different in magnitude between humans and other mammals that cortical lesions having minimal effects on other mammals may cause drastic changes in human function (Berridge 2003). For example, a cat without a cortex may still move and behave like a cat, whereas a human without a cortex, if alive, lies in a hospital bed completely unresponsive. Thus, it is possible that the re-representation of emotions that human encephalization produces with the interconnections to the limbic system may be the source of secondary emotions. In other words, as humans we have the potential to be angry, realize that we are angry, ponder the causes of our anger, notice that the anger momentarily affects our ability to work or cooperate, try to suppress our anger, think about how our anger appears to our companions and how it affects our relationships, and try to modify the source of the anger. If the cerebral-limbic interconnections are the source of this emotional re-representational ability in humans, the overall capacity of dogs for secondary emotions, with less encephalization than humans, may be dramatically different from ours.

7. Do dogs display guilt — or merely appeasement?

Guilt is an example of a secondary emotion often attributed to dogs, but according to current research, it fits the dog mind poorly. Horowitz (2009b) first recorded canine behavior and gestural cues in a situation where dogs could disobey the guardian’s command and eat a forbidden treat. By manipulating the guardian’s belief about what happened in the situation, she showed that dogs’ gestures were not different whether or not they obeyed. Instead, the gestures commonly associated with dog “guilt” — for example, avoiding eye contact, wagging

the tail low and quickly, holding one's ears or head down — were evident when the guardians scolded their dogs, regardless of the dog's actual behavior in the experiment. This strongly suggested that the dogs responded to the guardian's behavior with submissive gestures interpreted by dog guardians as "guilt," rather than displaying remorse for a misdeed with the "guilty" gestures (Horowitz 2009b). After a dog has learned the association between a certain unwanted behavior (e.g., stealing food) and the guardian's punishment later, they may display the submissive behavior in a similar situation even before the guardian's scolding (Horowitz 2009b). This does not require remorse or an "understanding" of violating a norm, but a simple learned association between two successive situations. When dogs display "guilt" behavior, guardians are likely to scold their dog less, which suggests that "guilt" behavior may function as learned appeasement (Hecht et al. 2012).

In a recent work, pet dogs' heart rates were measured during the "forbidden treat" experiment, and dogs who took the forbidden treat had a higher heart rate than dogs who did not (Torres-Pereira & Broom 2014). This suggests a learned association between eating the treat and a possible consequent scolding. To ensure that the rise in heart rate was not merely a function of sympathetic nervous system activation in the active condition (eating a forbidden treat), a similar result should be obtained with dogs eating a treat that they were allowed. Alternatively, as both positive and negative stress can increase sympathetic nervous system activation, the treat-stealing dogs may just be more excited by the treat. Nevertheless, even representation of the causality of the action plus an anticipatory response to the consequence does not require a sense of guilt.

8. Fairness or unequal treatment of conspecifics

Another example of dog affective representations closer to the secondary emotions is inequity aversion (Figure 4). In studies of primate social cooperation, unequal treatment of individuals is related to negative responses (for review, de Waal & Suchak 2010). In humans, the feeling of inequality is characterized by a negative response to the violation of fairness (for reviews, see Fehr & Rockenbach 2004, Fehr & Camerer 2007). A degree of inequity aversion was reported in capuchin monkeys (*Cebus apella*, Brosnan & De Waal 2003) and chimpanzees (*Pan troglodytes*, Brosnan et al. 2005), and a few studies have investigated the phenomenon in dogs (Range et al. 2009, Horowitz 2012, Range et al. 2012, Brucks et al. 2016). In a situation where a conspecific partner was rewarded for a task and canine subjects were not, they refused to perform the task or hesitated longer (Range et al. 2009, Brucks et al. 2016).



Figure 4. Testing dog inequity aversion; both dogs are asked to give the paw in turn. Figure from <http://dx.doi.org/10.1371/journal.pone.0153799.g001> (Brucks et al. 2016), reprinted under the terms of the Creative Commons Attribution License.

The phenomenon does not qualify as a simple extinction of a learned behavior because the canine subjects refused to obey earlier after witnessing a partner receive a reward for obeying, compared to being alone (Range et al. 2009, Range et al. 2012, Brucks et al. 2016). They also tended to refuse earlier in the unequal situation than in the situation where neither dog received rewards (Range et al. 2009, Range et al. 2012). Dogs also shared their food and interacted less with partners after unequal situations, showing that the negative experience of unequal treatment, or not being rewarded for one's efforts, diminishes subsequent cooperation and tolerance of company (Brucks et al. 2016).

Humans and some other primates can resist unequal treatment (i.e., refuse to cooperate) either when they gain less than the partner or when they gain more (Brosnan et al. 2010, Blake & McAuliffe 2011). In contrast, dogs do not resist the inequity when they are more rewarded than their companions (Horowitz 2012).

Taken together, dogs are sensitive to conspecific company in the inequity aversion test. They refuse earlier to perform the task in situations when they receive fewer rewards than their partner, compared to when they are alone, but unlike some primates, they do not resist gaining more than the partner. Although dogs behave differently toward the companion and experimenter after unequal and equal conditions (Brucks et al. 2016), this could also reflect the negative overall mood created by not being rewarded. The data to date suggest that dogs have the capacity for inequity aversion, but future work is needed with more conditions such as varying food quantities and the direction of the inequality, learning through a social model, expectation violation, negative situations affecting subsequent behavior, and individual factors such as personality or breed.

9. Resource competition as a precursor of jealousy?

Another case of possible secondary emotions in dogs is jealousy. Dog guardians report behaviors related to jealousy as often as behaviors related to the basic emotion of anger (Morris et al. 2008). However, this also illustrates anthropomorphic misunderstandings: Couples may report that “On the rare occasion that we have a cuddle he’ll start barking and whining.” But hugging is not in dogs’ natural behavior repertoire, so people cuddling can appear to dogs as a threat between pack members, to which they react by whining or trying to separate the “fighting pack members.” In humans, jealousy usually concerns romantic relationships and extends to imaginary situations of a rival threatening a significant relationship (Leary 2003). A precursor of jealousy in dogs may exist in a situation of defending a previously gained resource such as a human companion.

In a recent behavioral study where dog guardians ignored their dogs and attended to realistic toy dogs or other objects, the dogs exhibited significantly more behaviors such as going between the guardian and the target of their attention, or pushing/touching the guardian or the target, when the target was a realistic toy dog rather than an object (Harris & Prouvost 2014). Similarly, human infants showed more negative responses when a mother’s attention was directed towards a life-like doll than an object like a book (Hart et al. 1998, Hart & Carrington 2002).

Although the current data are consistent with the possibility of situation-based resource defense being a precursor of jealousy, the evidence for envy or jealousy in dogs is inconclusive and more rigorous research is required. Unfortunately, the behaviors associated with dog jealousy can also appear in dogs as replacement behaviors, when the dog is confused as to how to react.

10. Divisions of empathy

The neuroscientific study of human empathy exploded in the beginning of the 2000s (see Singer et al. 2004, Jackson et al. 2005, Gazzola et al. 2006, Saarela et al. 2007), revealing that the emotional aspect of empathy is processed in the limbic system, insula, and anterior cingulate cortex. Similar patterns may be also possible in the canine brain. Although simple forms of non-human empathy had been studied in previous decades (Church 1959, Rice & Gainer 1962, Masserman et al. 1964, Watanabe & Ono 1986), interest in animal and human empathy grew with the study of non-human primates (for reviews, Preston & de Waal 2002, de Waal & Ferrari 2010), and also extended to non-primates, including rats (*Rattus norvegicus*, Ben-Ami Bartal et al. 2011).

In humans, empathy has three components: emotional empathy, cognitive empathy, and the separation of the self from the other (see Decety & Jackson 2004). Emotional empathy can be further divided into emotional contagion/self-distress and empathic concern: emotional contagion originates from automatically triggered responses to others’ emotions, and empathic concern includes expressing a worry about others’ wellbeing (Davis 1980). Emotional contagion is important for compassion, but at high levels it may lead to anxiety and passivity or aggression and antisociality rather than helping behavior (Roberts & Strayer 1996). Cognitive empathy involves a theory-of-mind-like meta-representation of another’s emotional state. To highlight the difference between emotional and cognitive empathy, the

latter can be fully preserved in humans diagnosed with psychopathic tendencies, whereas this population shows much less emotional contagion and empathic concern (Blair 2005), possibly due to altered limbic function (Birbaumer et al. 2005).

11. From emotional contagion to prosocial behavior in dogs

Although long recognized by some (see e.g., Bekoff 2007), the capability of dogs to empathize has been receiving more scientific attention recently. Anecdotal reports of dogs apparently consoling conspecifics or humans are abundant, but the topic has been thoroughly examined only in a few experiments.

Most research on dogs' empathy-related behavior toward conspecifics concerns behavior that resembles consolation, that is, reconciliation or post-conflict affiliation. In cooperative species, aggression toward conspecifics may be costly for the whole group. An important mechanism for managing the effects of aggression is post-conflict affiliative behavior between the former opponents (reconciliation), sometimes through mediation by a third party (de Waal & van Roosmalen 1979). Both reconciliation behavior and third-party post-conflict affiliation are present in group-living dogs and wolves in heightened greeting; sitting or lying down together; and sniffing, playing, or licking the victim of aggression (Cools et al. 2007, Palagi & Cordoni 2009, Cordoni & Palagi 2015). Emotional contagion across dogs was recently studied by playing familiar and unfamiliar conspecific whines to dogs and examining their behavior during the playback and reunion with the familiar dogs (Quervel-Chaumette et al. 2016). When exposed to dog whines (recorded when the dog was left alone), the canine subjects were more alert and exhibited more stress-related behaviors compared with exposure to acoustically matched control sounds (Quervel-Chaumette et al. 2016). Additionally, exposure to familiar dog whines triggered more comfort-offering behaviors toward the partner dogs in reunion, resembling post-conflict affiliative behavior observed in natural groups (Cools et al. 2007, Palagi & Cordoni 2009, Cordoni & Palagi 2015). Post-conflict affiliation highlights the possibility of emotional contagion or empathic concern in dogs, although its mechanisms are unknown.

Across-species affiliative interaction between a dog and their caretaker (e.g., guardian petting the dog) can cause hormonal and physiological synchronization, lowering cortisol levels and increasing oxytocin and dopamine levels in both species (Odendaal & Meintjes 2003, Miller et al. 2009, Nagasawa et al. 2009, Handlin et al. 2011, Nagasawa et al. 2015). This across-species emotional synchronization suggests a possible physiological mechanism for the emotional contagion both in humans and dogs. In a similar example related to the stress response, cortisol levels in both humans and dogs increased significantly after listening to a crying human infant compared with a babbling infant or white noise (Yong & Ruffman 2014).

Dogs may also act prosocially, pulling a rope that delivers a partner dog a reward even when the puller dogs themselves are not rewarded, but only if the recipient dog is familiar (Quervel-Chaumette et al. 2015). Similar helping behavior from dogs to humans was previously found (for review, Bräuer 2015). These results show the possibility of dogs' altruistic behavior. More studies on the extent of this kind of behavior. Overall, the studies show emotional contagion from humans across species to dogs, as well as from dogs to their conspecifics, although the underlying mechanisms of contagion are currently not clear.

12. Yawning contagiousness in dogs: Empathy or social relaxation?

Contagious yawning is not used as a measure of empathy in human psychology, since well-validated questionnaires (e.g., Mehrabian & Epstein 1972, Davis 1980, Lawrence et al. 2004, Dadds et al. 2008) can be combined with either behavioral studies (especially in children, see e.g., Eisenberg & Miller 1987, Eisenberg & Fabes 1990, Roberts & Strayer 1996, Eisenberg et al. 1999) or brain imaging studies (for reviews, Decety & Jackson 2004, Bernhardt & Singer 2012) to show a correspondence between self-reported reactivity and behavioral or physiological changes. Early studies reported diminished contagiousness of yawning in children with Autism Spectrum Disorders (ASD) (Senju et al. 2007, Giganti & Esposito Ziello 2009, Helt et al. 2010), which prompted speculation regarding the possible relation of contagious yawning to empathy. Newer studies have reported the capacity for contagious yawning in children with ASD (Senju et al. 2009, Usui et al. 2013) and the independence of yawning contagiousness from empathy (Bartholomew & Cirulli 2014). However, since the inaugural study showing yawn contagion across species from humans to dogs (Joly-Mascheroni et al. 2008), a range of studies has explored the possible connection of contagious yawning and empathy in canines (O'Hara & Reeve 2011, Silva et al. 2012, Madsen & Persson 2013, Romero et al. 2013, Silva et al. 2013, Buttner & Strasser 2014, Romero et al. 2014).

Yawning is a somewhat problematic measure in dogs because the canine yawn serves as a tension-releasing stress response (see e.g., Beerda et al. 1998). Nevertheless, many studies found a higher frequency of canine yawning after observing or hearing a human yawn (Joly-Mascheroni et al. 2008, Silva et al. 2012, Madsen & Persson 2013, Romero et al. 2013). Some studies also reported stronger yawn contagiousness in dogs after perceiving a familiar rather than non-familiar person yawning (Silva et al. 2012, Romero et al. 2013). This effect of social connectedness was also demonstrated within wolves (Romero et al. 2014).

In humans, the tendency to yawn after witnessing another person's yawn is negatively correlated with amygdala activation (Schürmann et al. 2005). Thus, higher amygdala activation, which may occur naturally in unknown company as vigilance for a threat (e.g., Whalen 1998, Hart et al. 2000), acts against yawning contagion. If a similar connection existed in canids, familiarity would increase contagious yawning merely as a function of the individual's level of social relaxedness. The yawn contagiousness in dogs, however, adds to the possibility of interspecific emotional synchronization and contagion in relaxation (Odendaal & Meintjes 2003, Miller et al. 2009, Nagasawa et al. 2009, Handlin et al. 2011, Nagasawa et al. 2015).

Altogether, the studies of empathy show that at least emotional contagion is possible in dogs. Studies on canine post-conflict affiliative behavior and prosociality also suggest some empathic concern. A recent study on canine prosocial tendencies (Quervel-Chaumette et al. 2015) also reported situation-dependent perspective-taking. The extent of empathic capacity in dogs is unknown, however (for discussion, see also Silva & de Sousa 2011). There are probably limits to the cognitive component of empathy in dogs: They lack meta-representational and self-representational skills because their brains have less encephalization and connectivity than humans. However, coupled with the rudimentary theory of mind hypothesized by Horowitz (2011), empathic responding may not be an all-or-none function but an ability that occurs to various degrees across social species.

13. Long-term moods: A “cognitive judgment bias” test

The effects of rearing environment on emotional response in animals were noted in the 1950s by psychologists such as Hebb (1955). Raising dogs in a restricted environment affected their subsequent emotional responses (Melzack 1954). Fifty years later, the work was extended into the field of animal welfare, and the effect of the environment on the positive or negative affective states in animals was studied using an emotional judgment bias test (Harding et al. 2004). The effect is called “cognitive judgment bias” or “cognitive bias” in the animal sciences (Mendl et al. 2010a, Rygula et al. 2015), although human psychology has a multitude of different cognitive biases (see e.g., Tversky & Kahneman 1974, Haselton et al. 2005). This expectation-related “cognitive bias” is also based on studies of humans in which the phenomenon is widely known as affective congruence (e.g., Bower 1991, Fazio 2010): anxious or depressed people tend to interpret ambiguous stimuli negatively (Eysenck et al. 1991, Wright & Bower 1992, MacLeod & Byrne 1996, Gotlib & Krasnoperova 1998). Non-human animals may also be biased in their expectations after negative or positive experiences (Mendl et al. 2010b).

The basic test is simple: animals are first trained that one stimulus (e.g., a black card) signals a positive event (reward, e.g., food), and another (a white card) signals a negative event (a punishment). After such training, they are presented with ambiguous, intermediate signals (e.g., a grey card), and their reactions (e.g., time of approaching the stimulus) to the ambiguous signals are recorded. In dogs, a food bowl is placed in one corner of a room and an empty bowl in another corner (Mendl et al. 2010a). When dogs learn to discriminate the two locations, a bowl is placed between them. In the test trials, approach time to the ambiguous locations is measured: a quick approach indicates anticipation of food, an “optimistic” judgment, and a slow approach indicates a “pessimistic” judgment (Mendl et al. 2010a).

Dogs with higher separation-related anxiety approach the ambiguous bowl locations more slowly, showing a negative cognitive bias (Mendl et al. 2010a). Anxiolytic medication with the human anti-depressant fluoxetine combined with behavioral modification diminishes the bias (Karagiannis et al. 2015). However, leaving dogs alone for a brief time does not generate negative expectations (Müller et al. 2012), suggesting that it is a prolonged emotional state that induces negative bias in dogs (Mendl et al. 2010a). Likewise, briefly searching for treats prior to testing was not enough to induce positive bias in dogs (Burman et al. 2011), whereas administering oxytocin prior to testing caused positive bias (Kis et al. 2015).

To date, it seems that the cognitive bias test measures long-term tendencies, expectations, and moods rather than sudden emotions. Inducing the positive or negative expectations experimentally has proven tricky, leaving room for further investigation.

14. Emotional and social data across species: Emotional evolution?

Although direct data on dog emotions are currently quite rare, there are more studies on dog skills in interspecific cooperative-communicative social tasks. In these tasks, parallel experiments in dogs and other canids, carnivores, and non-human primates have been extremely informative. Regarding evolutionary changes in emotion leading to changes in social cognition, Hare (2007) has suggested that “dogs’ specialized social-problem-solving skills may have first appeared after systems mediating fear and aggression were altered” (p. 62). In the long-term studies on experimental domestication of foxes, selective breeding for low levels of fear and aggression toward humans were associated with changes in foxes’ limbic systems (Trut 2001), and as a side-effect, their social cognitive abilities (Hare et al. 2005). This Emotional Reactivity Hypothesis (Hare & Tomasello 2005) was recently tested with dogs and wolves by Range, Ritter, and Viranyi (2015). In a cooperative situation, wolves were not more aggressive towards conspecifics than dogs. Thus, the modified Canine Cooperation Hypothesis is that dog-human cooperation might have originated from wolf-wolf tolerance and cooperation (Range & Viranyi 2014, Range et al. 2015).

The suggestion that there is interplay between emotional and social skills in dogs is intriguing, and merits a closer examination of the brain circuitries involved.

15. Methodological advances and future directions

Human and nonhuman emotions have a long history of being studied using different methods (Berridge 2003). Therefore, using comparable methods in humans and dogs should provide valuable new insights (for example, Racca et al. 2012, Andics et al. 2014, Törnqvist et al. 2015, Yong & Ruffman 2016). Methodological advances include non-invasive brain imaging usually used with humans, such as functional magnetic resonance imaging (Berns et al. 2012, Andics et al. 2014, Jia et al. 2014, Berns et al. 2015, Dilks et al. 2015, Cuaya et al. 2016) and surface-electroencephalography (Howell et al. 2012, Kujala et al. 2013, Törnqvist et al. 2013, Kis et al. 2014). These can now be used with dogs together with positive operant-conditional training. Thermographic imaging also appears promising for detecting emotionally-stimulated changes in body surface temperature (Travain et al. 2015, Riemer et al. 2016, Travain et al. 2016). All these new techniques require careful experimentation to avoid the possible confounds reported for human research (importantly, see Bennett et al. 2009, Kriegeskorte et al. 2009, Poldrack & Mumford 2009, Vul et al. 2009).

Numerous topics, such as theory of mind in dogs, and possible emotional lateralization or gender effects, deserved more discussion. Many personal and environmental factors underlie individual differences in human emotional processes (e.g., Tomarken et al. 1992, Canli et al. 2002, de Rosnay & Harris 2002, Gross & John 2003), and similar variation also occurs in dogs (see e.g., Gosling et al. 2003, Fratkin et al. 2013, Cook et al. 2014). Dominance relations may affect canine emotions through cerebral neurochemical concentrations (for review, Chichinadze et al. 2014). Skull shape in dogs can also affect brain formation and hence cognition and emotion (McGreevy et al. 2004, Helton 2009, Roberts et al. 2010, McGreevy et al. 2013). There is also no reason dogs could not have unique emotional states that humans do not have, for example, states related to their olfactory world and the function of the piriform cortex. These topics will certainly receive more attention in the future. We need

more studies of the emotional world of dogs along with sensible caution in interpreting and generalizing the results.

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