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Reviews

Effects of shelter housing on dogs' sensitivity to human social cues

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ABSTRACT

Dogs are known to be skilled at using human social signals such as pointing at a target, gaze, visual direction of attention, and facial emotional cues. Two nonmutually exclusive hypotheses have been proposed to explain these abilities: the domestication hypothesis and the "Two-Stage" hypothesis. One way to test the Two-Stage hypothesis is to compare subpopulations of dogs with different histories with humans. For example, the abilities of pet dogs, who live in human homes and have developed strong affiliative bonds with humans, can be compared with those of shelter dogs, who live in social isolation and are deprived of extended contact with humans. Here, we review the extant literature on studies comparing these 2 subpopulations using identical protocols. Pet dogs perform better than shelter dogs at following human pointing and at estimating humans' attentional state or direction of visual attention. Shelter dogs seem to be more socially driven to gaze and interact with humans compared to pet dogs. Shelter dogs' impoverished contact with humans is the best candidate explanation for these results. We survey results highlighting the importance of life experience and learning in determining dogs' abilities to use human social cues and argue that shelter dogs may have learned not to respond to human cues that are not useful to them or have lost some previously acquired skills due to a lack of exposure to humans. Finally, we encourage further research that adds to both our theoretical and practical understanding of the impaired abilities of shelter dogs to use human social cues, and its link with the effect of life experiences.

With a history of domestication of somewhere between 15,000 and 33,000 years (Ardalan et al., 2011; Savolainen et al., 2002; Wang et al., 2016), the domestic dog (*Canis familiaris*) is widespread and well integrated in human society. Dogs are intensively studied in a variety of contexts, such as physical cognition (Bensky et al., 2013; Duranton et al., 2015; Pattinson et al., 2013), comparative psychology involving human infants (Bensky et al., 2013; Gaunet and El Massioui, 2014; Prato Previde et al., 2011; Topál et al., 2009), interspecific communication with humans (Kubinyi et al., 2009; Duranton and Gaunet, 2015: Udell and Wynne, 2010), and intraspecific sociality (Bonanni et al., 2010; Duranton and Gaunet, 2015; Horowitz et al., 2009).

The subjects in most of these studies are pet dogs, which are kept as companions and live in their owners' homes (Hart, 1995; Udell et al., 2010a; 2014). Pet dogs are known to be skilled at understanding and using human communicative signals (for reviews, see Bensky et al., 2013, and Duranton and Gaunet, 2015), moreso even than our closest genetic relatives the chimpanzees (Hare et al., 2002; Kirchhofer et al., 2012; Povinelli et al., 1999; Soproni et al., 2001). Different evolutionary (genetic) or developmental (ontogenic) nonmutually exclusive hypotheses have been proposed to explain these abilities. The domestication hypothesis holds that dogs are genetically predisposed to understand human signals with a genetical selection of communication skills (Hare et al., 2002, 2010; Vilá et al., 1997). A variant of this hypothesis has been offered by Topál et al. (2009a,b), proposing that several small genetic changes (linked to various aspects of dogs' behavior such as attachment, social attention, etc.) have led to dogs' communicative skills with human. The "Two-Stage" hypothesis holds that the sensitivity of an individual dog to human communicative cues depends on considering humans as social companions, and conditioning to follow human limbs (Udell et al., 2010a). This hypothesis

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proposed that it is individual dogs' ontogeny/life history that determines their abilities to understand human signals, as they develop and live in proximity with humans, learning through relevant stimuli and interactions (Wynne et al., 2008; Udell et al., 2010a; Udell and Wynne, 2010). Because environmental factors can influence genetic expression, it has recently been proposed integrative theories that combine both genetic and experiences-linked factors to explain dogs' unique skills to communicate with humans (Miklósi and Topál, 2013).

However, domestic dogs as a species are divided into different subpopulations, such as free-ranging dogs, pet dogs, working dogs (e.g., police dogs, guide dogs), and shelter dogs (Udell et al., 2014). Each has different degrees and types of interaction with/dependency on humans (Bonanni and Cafazzo, 2014; Udell et al., 2010b; Miklósi and Topál, 2013). Working dogs have recently become the focus of increased scientific attention. Other populations, such as free-ranging dogs and dogs living in shelters, are still underrepresented in research (Bensky et al., 2013; Udell et al., 2014). This lack of research is surprising because free-ranging dogs represent between 76% and 83% of the global dog population (Hughes and Macdonald, 2013; Bonanni and Cafazzo, 2014), while shelter dogs represent 10% of the dog population in the United States (Udell et al., 2010b). Studying and comparing these different populations of dogs is thus important, as it may provide information on the evolution of dogs' abilities to communicate and interact with humans (Bonanni and Cafazzo, 2014; Udell et al., 2014).

In this review, we survey the current state of knowledge on these issues as derived from studies comparing the abilities of pet dogs and shelter dogs to use human social cues when tested in the exact same conditions (thus ruling out any effect of protocol differences, as suggested by Udell et al., 2008a). Shelter dogs are stray dogs or former pet dogs which were relinquished due to behavioral problems or for various other reasons such as divorce, the birth of a baby, and so forth (Stafford, 2007; Van der Borg et al., 1991), so this type of comparison offers a way to investigate the role of life experience in the dogs' abilities to use human social cues. In addition, from a more practical point of view, this approach may also provide insights that help to increase the probability of shelter dogs' adoption and successful integration into new human families.

Living conditions

Pet dogs live in human homes (see Figure 1A), where they are surrounded by human beings, often including children, and typically encounter other humans (friends, other family members, strangers) and dogs (Marinelli et al., 2007; Pitteri et al., 2014) on a regular basis. Most pet dogs are walked every day, and many also practice skills with their owners, such agility or obedience (Gaunet et al., 2014; Marshall-Pescini et al., 2008). Pet dogs develop strong affiliative bonds with their owners (Horn et al., 2013; White et al., 2010) and consider them as a secure base (Horn et al., 2013; Prato-Previde and Valsecchi, 2014). Despite this strong relationship, many pet dogs spend at least part of the day alone in the home (Rooney and Bradshaw, 2014), and may be subject to stress and isolation, leading stress-related behavioral problems such as excessive barking, hole digging, and aggressive or destructive behavior (Dreschel 2010; Hsu and Sun, 2010; Odendaal, 1996; Overall, 1997; Parthasarathy and Crowell-Davis, 2006; Storengen et al., 2014; Takeuchi et al., 2001).

Shelter dogs usually live in small enclosures, often separated from other dogs, and suffer from chronic environmental stress (Barrera et al., 2010; Beerda et al., 1999; Hennessy et al., 1997; Tuber et al., 1999; see Figure 1B). Shelter dogs may also suffer from a lack of interaction/contact with humans (Kiddie and Collins, 2015; Taylor and Mills, 2007; Tuber et al., 1999). They are mostly alone, seeing the shelter employees briefly at feeding times or volunteers for occasional walks, and sometimes veterinarians. Some shelters try to reduce this deprivation as much as possible by offering other activities to the dogs, such as training (Luescher and Medlock, 2009; Protopopova et al., 2012) because regular interactions with humans reduce fear and stress in shelter dogs (Bergamasco et al., 2010; Hennessy et al., 2002). Despite these efforts, shelter dogs have different amounts and types of interactions with humans than pet dogs (Taylor and Mills, 2007; Udell and Wynne, 2010). Consequently, even if shelter dogs can form attachment bonds with handlers (Gácsi et al., 2001), they may not develop affiliative bonds as strong as pet dogs with their owners (Barrera et al., 2010; 2015; Buttner and Strasser, 2014; O'Hara and Reeve, 2011).

Following pointing gestures

As far as we know, only 1 study has compared the ability of adult shelter dogs and pet dogs to follow human pointing gestures using the exact same procedure. Udell et al. (2008a) tested the animals in a 2-way object-choice task, which investigates dogs' ability to use human cues to locate hidden food. This task has been extensively studied among pet dogs in the recent decades and is proposed to investigate dogs' ability to understand the perspective of others or if dogs have previously learn the association between a gesture and a reward (Hare and Tomasello, 2005; Udell et al., 2008a). An experimenter (human demonstrator) stood equidistant from 2 containers, 1 to the right and 1 to the left, in front of a dog. The experimenter then pointed toward 1 of the 2 containers for 4 seconds, before returning to a neutral position. The dog was then released to go to and "choose" 1 container. Trials using food were interspersed with control trials, where the demonstrator remained neutral, without pointing, and the dog was released to choose a container. The results were clear: the shelter dogs performed below

Figure 1. Example of living environments of (A) pet dogs (credit: Nastasia Froloff) and (B) shelter dogs (credit: Louise François).

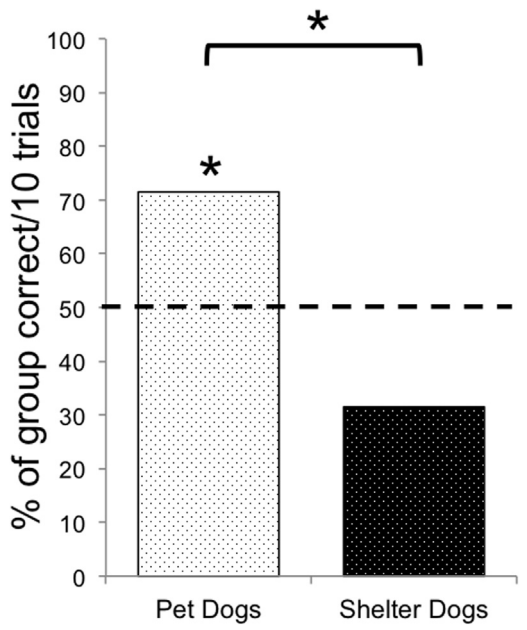

Figure 2. Percentage of correct choices on the 10 experimental pointing response trials for pet dogs and shelter dogs. The 50% line represents chance level. *Indicates a significant difference from chance level or a significant difference between the 2 groups ($P < 0.05$). Adapted from Udell et al., 2008a.

chance, and they were less successful at the task than were the pet dogs (Udell et al., 2008a; Figure 2). The authors concluded that although the shelter dogs showed themselves to be very willing to interact with humans, they failed to follow the demonstrator's momentary distal pointing. However, these studies involved no control for the stress level of the tested dogs, as it is known that shelter dogs have a higher cortisol level than pet dogs (Hennessy et al., 1997). In addition, dogs were considered to make the wrong choice when they chose no container (Udell et al., 2008a), a behavior driven by various mechanisms. Hare et al. (2010) proposed that the inclusion of dogs who did not choose biased the results and proposed a reanalysis excluding individuals that did not choose any containers. Regardless, even with this correction, shelter dogs did not perform above chance. The authors proposed that for various reasons such as temperament or rearing history, shelter dogs were less skilled in using human communicative cues than were pet dogs (Hare et al., 2010). Hare et al. (2010) tested other shelter dogs in slightly different conditions (e.g., in Udell et al. 2008a, food was put above the containers during the warmup session, whereas in Hare et al. 2010, food was put inside the containers during the warmup session) and found that even naive shelter dogs were able to use human communicative cues within this experimental design. However, as they did not conduct the same experiments in the exact protocol with pet dogs, it is possible that with these more classical methods, pet dogs would also have improved their abilities, still performing at higher rates that shelter dogs.

Another study (Udell et al., 2010b, experiment 1) tested whether shelter dogs would fail to use other types of human pointing as well. The authors compared shelter dogs' performance in an object-choice task in 2 pointing conditions: a momentary distal point condition (the experimenter stood and pointed at a container for 2 seconds) and a dynamic proximal point condition (the experimenter kneeled, pointed at a container and kept his arm in this position until the end of the test). The shelter dogs failed to follow the momentary distal point but succeeded in following the dynamic proximal point. In addition, the authors investigated whether further experience with the momentary distal point would allow shelter dogs to improve their performance (Udell et al., 2010b, experiment 2). They found that most shelter dogs that initially failed to use the momentary distal point learned to do so after additional exposure to this cue. The results of these 2 experiments thus emphasize the importance of life history and learning experience in determining shelter dogs' abilities to use human cues.

These results are in line with a recent finding in research dogs, another subpopulation of dogs that live in conditions similar to shelter dogs and that are also deprived of contact with humans. Lazarowski and Dorman (2015) compared the performance of adult research dogs and pet dogs in an object-choice task using the exact same protocol. The dogs were again tested in dynamic proximal point and momentary distal point conditions. The research dogs succeeded at the task in the dynamic proximal point condition, although pet dogs outperformed them. In the momentary distal point condition, the research dogs performed at the level of chance, in contrast to pet dogs. The authors thus concluded that exposure and experience influences dogs' abilities to use human communicative gestures.

Finally, in a recent study on dog puppies, Zaine et al. (2015) compared the performance of pet dog puppies and shelter dog puppies aged from 20 to 24 weeks old in an object-choice task. There was no age difference between the 2 groups: they were distinguished only by the difference in their experience of living in human homes. The puppies experienced 3 different types of pointing: a dynamic proximal point, a momentary proximal point, and a momentary distal point. All puppies succeeded in following the dynamic proximal point, with no difference between groups, but pet puppies outperformed shelter puppies in both more complex momentary pointing conditions. The puppies' ability to follow pointing gestures was positively correlated with their experience with humans.

To conclude, these different studies highlight that the domestication of *Canis familiaris*, alone, does not explain dogs' great sensitivity to human cues. Domestic dogs with different life histories, such as pet dogs and shelter dogs, differ in their ability to use human pointing.

Gazing toward humans

Dogs spontaneously gaze at human faces when confronted with a novel situation or stimulus (Duranton et al., 2016; Miklósi et al., 2003). They do so for several nonmutually exclusive reasons: to gain information from the human on how to react (Duranton et al., 2016), to search reassurance from the human (Duranton et al., 2016), or to ask the human for help (Gaunet, 2008, 2009; Miklosi et al., 2000, 2003).

To examine the effect of experience with humans on dogs' gazing behavior, Udell (2015) compared the performance of adult pet dogs and shelter dogs in a solvable task (i.e., dogs can solve the task without any help of the human). In the task, the dogs had to open an unfamiliar puzzle box to obtain food with a human present in the room, either maintaining a neutral attitude or vocally encouraging the dogs. No difference was found between pet dogs and shelter dogs in the total time the dogs spent gazing at the human in either condition. Udell proposed that this equivalent tendency to gaze toward humans may reflect a generalized social inhibition of independent problem-solving behavior in dogs that is independent of housing condition.

Barrera and colleagues performed studies directly comparing the gazing behavior of pet dogs and shelter dogs when confronted with an unsolvable problem (i.e., one that needs human help to be solved) in 2 complementary settings. In Barrera et al. (2011), pet dogs and shelter dogs were observed in a situation with food in sight but out of reach (see Figure 3A). Dogs were first tested in an

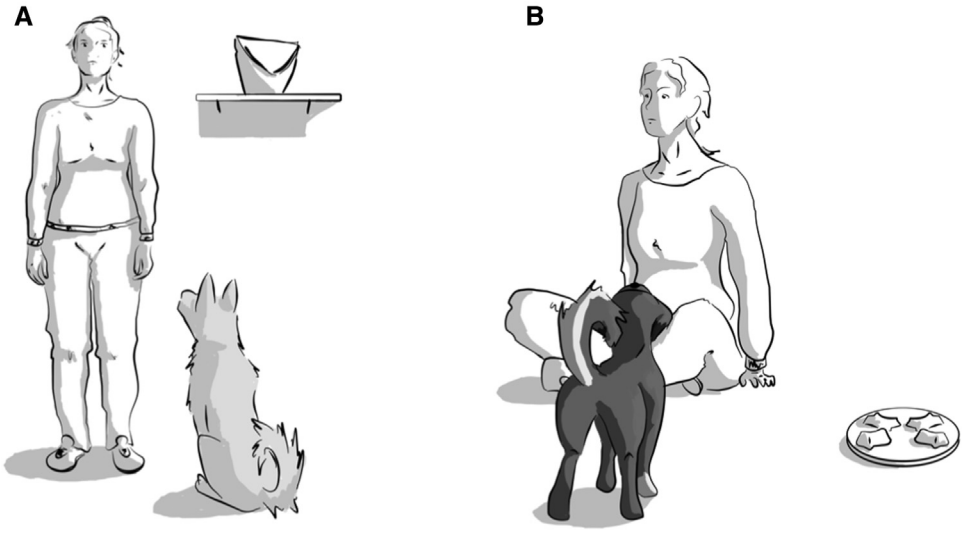

Figure 3. When confronted with a puzzling situation [(A) food out of reach and (B) unsolvable problem), both shelter dogs and pet dogs gazed at humans. Adapted from Barrera et al. 2011, 2015.

acquisition phase, where they had to gaze at the experimenter to receive a piece of food, and then in an extinction phase, where even if they gazed at the experimenter, they no longer received food. The results indicated that pet dogs and shelter dogs showed similar gazing behavior during the acquisition phase, with no difference in latency before the first gaze at the experimenter or in the total duration of gazing at the experimenter. During the extinction phase, both pet dogs and shelter dogs presented the same latency before their first gaze at the experimenter; however, the 2 groups differed on total gaze duration, with shelter dogs looking at the human experimenter for less time than pet dogs, showing a faster extinction in this group of dogs.

Barrera et al. (2011) proposed 3 hypotheses to explain the lack of difference between the 2 groups during the acquisition phase. The first was that the gaze response is independent of housing conditions; the second was a ceiling effect, due to the task being easy for the dogs; and the third was that the dogs had to stop gazing at the experimenter to eat the treat, and the protocol thus did not capture what their gazing behavior would have been had this not been the case. The authors argued that the difference in gaze duration during the extinction phase can be understood in light of the intermittent reinforcement of gazing behavior that pet dogs experience when interacting with their owners in daily life, unlike shelter dogs. Intermittent reinforcement is known to be linked with increased extinction resistance in nonhuman animals (Amsel, 1962).

To test whether these findings were actually linked to extinction properties *per se* and not to the dogs' communicative ability, Barrera et al. (2015) investigated the gazing responses of pet dogs and shelter dogs in a nonsocial problem-solving task. The task required the dogs to open a toy to obtain food (see Figure 3B). There were presented with the toy first baited (acquisition phase) and then empty (extinction phase). The experimenter sat close to the apparatus, and the time the dogs spent gazing at her was analyzed (experiment 1). During the acquisition phase, no difference was found between the 2 groups in the total time spent gazing at the experimenter. This is in line with the results of the study of Udell (2015) presented previously, in which the dogs were presented with a new apparatus for the first time and had to find a solution to open it. It is also comparable to Barrera et al. (2011) results from the acquisition phase. However, Barrera et al. (2015) found that during the extinction phase, shelter dogs looked significantly longer at the experimenter than pet dogs. This result is linked to the finding that during the extinction phase, the pet dogs interacted longer with the apparatus than the shelter dogs and thus spent less time looking at the human experimenter (see Barrera et al., 2015 for statistical data on variables other than gaze duration). The authors offered 2 mutually nonexclusive explanations for these findings. The first was that, as mentioned previously, pet dogs are more exposed to intermittent reinforcement in daily life, increasing their resistance to extinction, consistent with the findings of the previous study (see Barrera et al., 2011). The second hypothesis they proposed is that the unfamiliar human experimenter was of greater interest to the shelter dogs, who are deprived of human contact. On this hypothesis, the shelter dogs thus stopped interacting with the box earlier and gazed longer at the human during the extinction phase because their level of social motivation was higher than that of pets. Barrera et al. (2015) also discussed the possibility that the chronic stress experienced by shelter dogs (Hennessy et al., 1997) played some role in these results. Could stress be responsible for the faster extinction of learned responses in shelter dogs? They argued that this is unlikely, as the literature on other animals (e.g., rats) has shown that chronic stress leads to impaired extinction (i.e., to more persistent learned responses).

To conclude, Barrera and colleagues found that when confronted with a puzzling situation (i.e., extinction phases, where a previously effective action no longer works), pet dogs are more resistant to extinction than shelter dogs (Barrera et al., 2015). They also argued that shelter dogs are more socially motivated than are pet dogs (*sensu* Gácsi et al., 2001), influencing their gazing reactions. It appears that domestication alone does not explain dogs' communicative responses: their life history also influences their gazing behavior towards humans.

Attentional state

To our knowledge, only 1 study has compared pet dogs and shelter dogs' sensitivity to the human attentional state or direction of visual attention. Udell et al. (2011) tested dogs in a begging task: the dogs were faced with 2 humans, and had to approach one of them to beg for food. One of the 2 humans was attentive to the dog, whereas the other was unattentive, or prevented from seeing the dog in some way. The correct response was for the dog to beg for

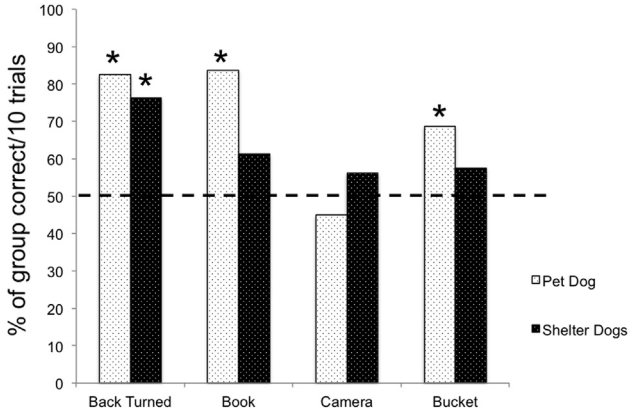

Figure 4. Mean percentage of correct choices (of the attentive human) out of 10 experimental trials for pet dogs and shelter dogs. The 50% line represents chance level. *Indicates a significant difference from chance level ($P < 0.05$). Adapted from Udell et al., 2011.

food from the attentive human. This task can be used to investigate which cues dogs use to evaluate a human's attentional state.

Udell et al. (2011) compared pet dogs and shelter dogs to test the effect of life experience on the dog's ability to discriminate and respond to human attentional states. Dogs had to beg for food from either an attentive human who was in the same situation in all conditions, facing them, or an unattentive human in different conditions: with her back turned, facing the dog but with a book occluding her view of the dog, facing the dog but with a bucket over her head, or facing the dog while holding a camera over her eyes. The results revealed that in the back-turned condition, both pet dogs and shelter dogs chose the attentive human significantly above chance level. In the book and bucket conditions, only pet dogs chose the attentive human significantly above chance level. Finally, in the camera condition, neither pet dogs nor shelter dogs' differed from chance (see Figure 4).

Udell et al. (2011) argued that the explanation for this performance difference is that dogs are more sensitive to human cues that are common in their living environments (see also Savalli et al., submitted). The dogs chose which human to beg from based on their past reinforcement histories. Thus, both pet dogs and shelter dogs often see a human with their back turned when leaving, when stopping interaction or ceasing giving food. This explains that for this condition, both groups were able to differentiate the attentional states of the 2 humans and begged for food from the attentive person. The performance difference in the book condition is similarly explained. It is common for pet dogs to see their owners reading a book or other documents, while not paying attention to them. Shelter dogs have restricted interactions with humans and presumably do not commonly see humans reading in their presence and so may have forgotten that this behavior is associated with reduced attention. The same class of explanation can be used for the decreased performance of pet dogs in the bucket condition. Finally, the authors proposed 2 hypotheses concerning the camera condition, where neither pet dogs neither shelter dogs performed above chance level. First, it is possible that the camera was too small for the dogs to interpret that it could occlude the human's view (Udell et al., 2011). But a more plausible possibility is that both pet dogs and shelter dogs are used to seeing humans with cameras in front of their faces as they take photos (recording family memories, promoting adoption) and have thereby learned that a human can see through a camera. Furthermore, when humans are taking a picture of a dog, they often reinforce the dog for looking or orienting at them. Thus, it is plausible that the dogs considered both humans facing them with eyes unoccluded and humans looking toward them through a camera to be attentive and chose both correspondingly.

Udell et al. (2011) also mentioned the possibility that stress may influence the performance of shelter dogs and acknowledged that further research is needed to better understand the role of this factor in dogs' performance in this task.

To conclude, this study demonstrated that different populations of dogs respond differently to stimuli predicting human attentional state, with shelter dogs being less responsive than pet dogs (Udell et al., 2011). It appears that dogs' life experiences are linked to different levels of responsiveness to human social cues to attentional state.

Emotional contagion

An emergent field of research on dog social cognition is emotional contagion from humans to dogs, or dogs' sensitivity to emotionally driven human behaviors. Can dogs share humans' emotional states? More generally, are they sensitive to behaviors driven by human emotions? If so, what mechanisms underlie this sensitivity? One way to answer these questions is to study yawning contagion. In humans, contagious yawning is considered an empathetic response. This idea has recently been extended to dogs (Joly-Mascheroni et al., 2008; O'Hara and Reeve, 2011). Dogs may have the ability to empathize with humans (Silva and de Sousa, 2011) and/or they may be sensitive to human behavioral emotional cues (Duranton and Gaunet, 2015), as they adjust their behavior in response to that of humans. Interspecific yawning contagion between dogs and humans has been reported (Joly-Mascheroni et al., 2008; Madsen and Persson, 2012; Romero et al., 2013), but there is some inconsistency in the findings of different studies (e.g., Harr et al., 2009), which may be due to differences in arousal and context (Buttner and Strasser, 2014).

O'Hara and Reeve (2011) tried to replicate earlier findings of yawning contagion between humans and dogs and tested the hypothesis that yawning contagion reflects emotional connectedness. For this purpose, they compared pet dogs and shelter dogs in the same setting, with the working hypothesis that pet dogs (which are involved in strong human-bonded relationships with owners) would more likely show yawning contagion than shelter dogs (which are contact deprived and/or involved in weakly bonded relationships with caregivers; O'Hara and Reeve, 2011). Each dog was tested in 4 different conditions: human yawn, mouth movement, audio only, and conspecific yawns. In their first analysis, they combined the data from the human and conspecific yawn conditions to form a single "yawning presentation" condition, and the audio-only and mouth movement conditions as a single control condition. In this analysis, they found an effect of condition in shelter dogs (who yawned more in the yawning presentation condition than in the control condition) but not in pet dogs.

In the human demonstration condition, a human demonstrator sat on the floor of the room and yawned continuously for 3 minutes. The dogs were tested in 2 sessions of 4 trials each (the first with a familiar human demonstrator, and the second with an unfamiliar human demonstrator). In all conditions combined, no difference was found between pet dogs and shelter dogs' rate of yawning. In trials with human demonstrators, however, a group effect was found, with shelter dogs yawning more than pet dogs. Although they detected some yawning contagion effect in shelter dogs at the descriptive level (see Figure 5), the results did not reveal any significant evidence for contagion either at the individual level or in the overall sample. The authors concluded that if dogs yawn contagiously, then they do so at a low level, and that familiarity or bonding to humans failed to predict yawning contagion between

Figure 5. Some shelter dogs seemed to show yawning contagion with humans, but no significant effect was found at either the individual or group levels. Adapted from O'Hara and Reeve, 2011.

dogs and humans. According to O'Hara and Reeve (2011), there is little support for yawning contagion from humans to dogs based on emotional connectedness, or the view that dogs are sensitive to human yawning as a social cue (but see Duranton and Gaunet, 2015).

The authors discussed the interesting fact that they nonetheless found a low level of yawning contagion, at least between shelter dogs and humans. Given that the failure to find this effect in pet dogs suggests that it is not empathy related, they proposed a low-level explanation as suggested by Yoon and Tennie (2010): nonconscious mimicry (or behavioral synchronization). It is well established that in humans, the desire to create affiliative interaction with others is linked with behavioral synchronization (Chartrand and Bargh, 1999; Duranton and Gaunet, 2015; O'Hara and Reeve, 2011). Dogs are also thought to synchronize their behavior with humans (see Duranton and Gaunet, 2015). O'Hara and Reeve (2011) suggested that nonconscious behavioral synchronization might explain their finding that shelter dogs yawned more than pet dogs and that they did so mostly with the unfamiliar human demonstrator. Contact-deprived dogs faced with an unfamiliar human may see an opportunity for new social affiliation and respond by unconsciously mimicking the human's actions.

Caution is required, as it is also possible that O'Hara and Reeve (2011) failed to perfectly control for stress-related yawning and that shelter dogs experienced more stress when confronted with an unfamiliar human or situation. Buttner and Strasser (2014) presented relevant evidence in another investigation of yawning contagion in shelter dogs. They tested 60 shelter dogs and found apparent evidence of yawning contagion in only 12 shelter dogs. These dogs differed from the other dogs in having persistently elevated cortisol levels following exposure to human yawning. These results are apparently not due to these dogs being inherently more nervous/stressed, leading them to yawn more in general, as the authors found no relationship between baseline cortisol levels and yawning rates. The shelter environment is a situation of uncertainty for dogs, and their arousal levels are persistently high (Buttner and Strasser, 2014: Hennessy et al., 1997). Buttner and Strasser proposed that in the high-arousal shelter situation, dogs may perceive human yawns as a stress signal. Dogs could mimic human yawns, or human yawns could elicit tension yawns in dogs. In both cases, dogs would perceive human yawns at least partly as communicative, conveying emotional state. This hypothesis could also apply to the findings of O'Hara and Reeve (2011) and explain why shelter dogs were more subject to yawning contagion than pet dogs.

Discussion

This review surveyed evidence that even in a single species, the domestic dog, different populations with different life histories have different abilities to understand and use human social cues. In this context, comparing the skills of pet dogs and shelter dogs is valuable, as it allows us to better understand the effect of life history. Both of these dog populations interact with humans, but the amount and type of contact and opportunities for affiliative bonding substantially differ. Pet dogs perform better than shelter dogs at following human pointing and assessing human attentional state (Udell et al., 2008a, 2011). In addition, pet dogs are more resistant to extinction in a social task compared to shelter dogs (Barrera et al., 2011). However, shelter dogs appear to be more socially driven to gaze at and interact with humans than pet dogs, likely due to their generally limited and poor-quality contact with humans (Barrera et al., 2015; O'Hara and Reeve, 2011).

It is important to note that these differences in ability are likely due to differences between the 2 populations not in cognitive function, but in learning history. Shelter dogs may have learned not to respond to human cues that are of little use to them in their daily environment or they may have forgotten due to a lack of exposure to human social cues and positive or negative behavioral reinforcements. Importantly, shelter dogs are able to improve their abilities after additional exposure to humans and training. For example, although shelter dogs initially exposed to a human pointing to a container in an object-choice task failed to choose the correct container, after additional training, they learned to respond to the pointing and succeed at the task (Udell et al., 2010b, Experiment 2). Evidence that dogs' ability to use human social gestures changes with life experience has been found not only in shelter dogs, but also in pet dogs. For example, pet dogs are able to learn to follow novel human gestures such as elbow pointing or leg pointing (Udell et al., 2008b), and they can learn to change or stop using human communicative signals (Bentosela, et al., 2008; Elgier et al., 2009). In addition, a recent study showed that pet dogs' ability to follow human gaze direction is modulated by training (Wallis et al., 2015). These findings emphasize the role of ontogeny in dogs' ability to use human social cues, which does not contradict the existence of adequate genetic substrates (Wynne et al., 2008) due to the species' history of domestication (see Miklósi and Topál, 2011 for more details on integrative theories). Recent studies show that other canids, such as foxes (Barrera et al., 2012), coyotes (Udell et al., 2012), and wolves (Udell et al., 2008a, 2012; Virányi et al., 2008), can learn to follow human gestures if the canids are actively socialized with humans. We encourage further research in this direction.

Shelter dogs may have been traumatized due to mistreatment, neglect, or abandonment. It is essential to keep in mind that this population is variable and routinely includes dogs whose history is unknown. They may be stressed by the protocols of the studies themselves, and future studies should use more careful controls for the dogs' stress levels.

Finally, from a more practical point of view, the results reviewed here help us understand the effect of life in a shelter on dogs. Shelter dogs suffer from limited and impoverished opportunities to interact with humans, which affects their skills in dealing with human communicative signals. These impaired abilities may in turn

influence shelter dogs' behavior toward both shelter staff and potential adopters. This point is reinforced by results from another area that we did not directly review here: research on bonds between human and dogs. Various studies investigating social attachment between dogs and their owners using the Strange Situation Test have shown that pet dogs treat their owners as a secure base (for a review, see Prato-Previde and Valsecchi, 2014). Shelter dogs that suffer from social bond disruption are nonetheless still able to form bonds with new humans such as their caregivers (Gácsi et al., 2001; Prato-Previde and Valsecchi, 2014). Shelters should increase the amount and quality of human interactions they offer to their dogs as much as possible. An extended pattern of interactions with a specific person is one promising option. Another possibility is to have shelter dogs work with a dog trainer who can interact regularly with the dogs and train them to understand and respond to human communicative signals, such as pointing. This type of training can be very helpful to shelter employees, making it easier to manage the dogs during walks, medical cares, and feeding (Arhant and Troxler, 2014; Kiddie and Collins, 2015). Moreover, and importantly, if a dog does not respond to potential adopters' communicative signals (e.g., to come closer, to play), it is less likely to be adopted (Protopopova and Wynne, 2014). If a professional trains shelter dogs to look at potential adopters, move close to them, interact with them in a similar way to pet dogs, this should increase their chances of being adopted (Protopopova and Wynne, 2014; Weiss et al., 2012).

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Ethical considerations

Approval was not required for this review article.

Conflict of interest

The authors declare that there is no conflict of interest.

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