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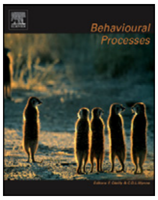

Review

Adapting to the human world: Dogs' responsiveness to our social cues

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ABSTRACT

Dogs are more skilful than a host of other species at tasks which require they respond to human communicative gestures in order to locate hidden food. Four basic interpretations for this proficiency surface from distilling the research findings. One possibility is that dogs simply have more opportunity than other species to learn to be responsive to human social cues. A different analysis suggests that the domestication process provided an opening for dogs to apply general cognitive problem-solving skills to a novel social niche. Some researchers go beyond this account and propose that dogs' co-evolution with humans equipped them with a theory of mind for social exchanges. Finally, a more prudent approach suggests that sensitivity to the behaviours of both humans and conspecifics would be particularly advantageous for a social scavenger like the dog. A predisposition to attend to human actions allows for rapid early learning of the association between gestures and the availability of food.

Contents

1. Introduction

Dogs and humans have shared essentially the same ecological niche for at least 14,000 (Clutton-Brock, 1995) and possibly as long as 135,000 years (Vilà et al., 1997). Some argue that dogs and humans are more than sympatric species, that this has been an association of mutual benefit (Coppinger and Coppinger, 2001). Humans provided early *canids* with a rich food source in the form of discarded food and fecal waste and the animals were tolerated, perhaps even encouraged, close to human settlements to fulfil their role as biological garbage disposal units. Admittedly, the symbiosis

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was lopsided; dogs became dependent on humans for their very survival, while for humans, dogs served primarily a hygienic function.

Distantly related species often show evidence of convergent evolution when they face similar ecological challenges. Recently the question has been posed whether dogs and humans may have converged in their evolution of social cognitive abilities (Miklósi et al., 2004; Hare and Tomasello, 2005a). Both species are characterized by complex social lives with rich communication systems but is it also possible that dogs, perhaps because of their reliance on humans for food, have evolved specialized skills for recognizing and interpreting human social-communicative signals?

The evidence that dogs are unusually responsive to human-given social cues is compelling. Dogs are experts at basing decisions about the location of hidden food on gestures provided by humans. One way this has been demonstrated is the *object choice task*. In a typical object choice task, the animal is presented with two, sometimes three, opaque containers. Food is hidden in one of the containers and the others are sham-baited. A human experimenter indicates to the animal the location of hidden food by using some type of communicative gesture, such as pointing or looking in the direction of the food. The animal is then permitted to make a selection and is rewarded with the food if it chooses correctly.

Nonhuman primates, including apes, are notoriously poor performers in the object choice task. They show little ability to read human social cues to calculate where food is hidden (Tomasello et al., 1997; Call et al., 1998; Hare et al., 2002). They can be taught to use human gestures to solve the object choice problem but the actions appear to function as discriminative stimuli – there is no indication that the animals comprehend the inherent attempt by the human experimenter to cooperate and communicate (Itakura and Anderson, 1996; Neiworth et al., 2002).

Contrast this with the discovery that the domestic dog far outperforms nonhuman primates in the object choice task. That dogs respond to human communicative cues, with no explicit training, opens the door for the possibility that they comprehend the intention of those cues. Does the dog understand that the person is attempting to communicate? Does the dog grasp that the person knows something the dog does not and is trying to assist him? The desire to answer these questions has produced a flurry of research activity exploring the scope and significance of dogs' social cognitive abilities.

Four basic hypotheses have been put forth to account for the findings. One assertion is that dogs, by way of their interactions with humans, learn to be responsive to human social cues through basic conditioning processes (Udell and Wynne, 2008). A second proposal is that by undergoing domestication, dogs not only reduced their fear of humans but also applied all-purpose problem-solving skills to their interactions with people. This largely innate gift for reading human social gestures was inadvertently selected for via domestication (Hare, 2007; Hare and Tomasello, 2005a). Still others favour the suggestion that dogs' co-evolution with humans equipped them with the cognitive machinery to not only respond to human social cues but to understand our mental states; a so-called theory of mind (Miklósi et al., 2000, 2004). Lastly, the more cautious explanation, which I favour, is that dogs are adaptively predisposed to learn about human communicative gestures. In essence they come with a built-in "head start" to learn the significance of people's gestures, in much the same way that white-crowned sparrows acquire their species-typical song (Marler, 1970) and ducklings imprint on their own kind (Lorenz, 1965).

In this review of the work on dogs' performance in the object choice task, I first summarize how dogs respond to a range of communicative gestures and examine specific observable cues they might use to solve this problem. I then outline the various accounts that have been proposed to explain this extraordinary proficiency and conclude with a cautious interpretation that begs further research.

2. Which human cues guide dogs to hidden food?

Human communication consists of a variety of gestures, including pointing, nodding, head turning, and gazing. Are dogs equally adept at responding to these different cues?

2.1. Pointing

The research overwhelmingly confirms that dogs are able to use the information provided by a variety of pointing gestures to identify the location of hidden food. In most studies, the experimenter positions himself between the two containers, facing the dog, and uses his arm, sometimes the ipsilateral and other times the contralateral, to point at the container with food in it. It appears to make little difference whether pointing is combined with looking at the dog or at the container (e.g., Hare and Tomasello, 1999; Hare et al., 2002; Soproni et al., 2001); dogs find the food at levels often exceeding 90% correct (Miklósi et al., 1998; Soproni et al., 2002; Udell et al., 2008b).

Bräuer et al. (2006) demonstrated that dogs perform more accurately when the experimenter continues to point at the container while the dog makes its choice (sustained) than if the experimenter points and then assumes a neutral position prior to the dog making its choice (momentary). While dogs are more accurate when the pointing hand extends close to the correct container – a proximal point (10–20 cm), they still perform well above chance when the pointing hand is farther away – a distal point (70–80 cm) (Soproni et al., 2002; Miklósi et al., 2005). Movement is a helpful component. Hare et al. (1998) demonstrated that dogs could interpret a static point, although performance was poorer than with a dynamic point.

What dogs do not respond to is a gesture that has been termed the "belly point" or the cross elbow point and its various modifications (Hare et al., 1998; Soproni et al., 2002; Udell et al., 2008b). To perform this gesture, the human uses the arm opposite to the correct container to point but does not extend the hand past the torso. Hare et al. (1998) also determined that dogs were unable to discern the correct container when the experimenter pointed toward the middle of three choices. With this configuration, the pointing arm also does not extend to the side of the person's torso. Pointing with the elbow is slightly more informative – a few dogs perform above chance when presented with this presumably unfamiliar cue (Soproni et al., 2002; Udell et al., 2008b). However, pointing with a leg is decidedly more informative (Udell et al., 2008b). It seems that dogs rely on gestures that protrude from the person's body toward the container.

Udell et al. (2008b) presented dogs with inanimate objects, such as a mechanical arm and a doll's arm, extended toward the correct choice. For the most part, the dogs performed at chance levels. A few dogs in the Soproni et al. (2002) study scored above chance when the experimenter used a stick to point to the food, however, this cue does not preclude movement of the arm.

Clearly, the majority of dogs respond to pointing gestures to locate hidden food. Not surprisingly, dogs respond best to salient cues so they are more accurate when the point is held in position while they make their choice and when the pointing hand extends closer to the container. Although movement is particularly attractive to dogs, they still perform well with a static point.

2.2. Head turning

People often turn and look toward something of significance when communicating with each other and dogs also respond to this cue with some degree of accuracy. Overall they are not as proficient with head turning cues as they are with pointing (McKinley and Sambrook, 2000; Udell et al., 2008b); however, some individuals perform well from the outset and others learn to respond to them (Miklósi et al., 1998). Combining the head turn with looking at the correct container generally improves accuracy (Hare et al., 1998). Nodding, which entails more movement than head turning, also leads to more accurate choices (Miklósi et al., 1998). Tilting the head, a gesture that would be unlikely in dog–human interactions, was not very informative (Udell et al., 2008b).

2.3. *Bowing*

Bowing is a cue not commonly used by people to communicate the location of something yet dogs are able to select a container with food at greater than chance levels on the basis of a bowing cue (Miklósi et al., 1998), particularly if the person looks at the dog while bowing (Udell et al., 2008b). It's been well established in other experimental setups that dogs respond differentially when people attend to them (Call et al., 2003; Gácsi et al., 2004; Schwab and Huber, 2006; Virányi et al., 2004).

2.4. *Eye gazing*

Several studies have tested dogs for their ability to find the location of food when the experimenter merely looks at the correct container while keeping his head oriented toward the dog. In some cases, the experimenter moves his eyes back and forth between the dog and the container while in others, the experimenter stares continuously at the container until the dog makes its choice. Overall, the findings suggest that most dogs are not proficient with interpreting human eye gaze without accompanying body movement (Hare et al., 1998; see Agnetta et al., 2000 for an exception). Dogs performed better with a sustained gaze than a momentary glance (Bräuer et al., 2006; McKinley and Sambrook, 2000). Some individuals learn to use the gaze cue over the course of trials (Miklósi et al., 1998; Udell et al., 2008b). Interestingly, McKinley and Sambrook (2000) report that several of their dogs whined and barked at the experimenter giving the eye gaze cue whereas they did not behave this way on control trials. Did the dogs recognize the person's attempt to convey information, yet they were unable to interpret it? This is similar to the trained dog that vocalizes when presented with a discriminative stimulus that has yet to gain adequate control over the dog's behaviour.

2.5. *Arbitrary markers*

Several studies have investigated whether dogs can select the correct container in an object choice task when the only information provided about the location of food is the placement of an arbitrary marker. The marker, which may be a sponge, a wooden block, or a round disk, is placed on top of, in front of, or next to the correct container. In some experiments, the object remains in place while the dog makes its choice while, in others, the experimenter removes the object before the dog chooses.

While dogs perform equally well whether the marker is removed or remains in place, they choose the correct container above chance only if they have seen some movement on the part of the person placing the marker (Udell et al., 2008b). Riedel et al. (2006) systematically varied the amount of human movement associated with marker placement. Overall, dogs performed best when they saw the person's hand placing the marker, although they were almost as proficient when they saw the person reaching to remove the marker. They selected at random when a marker was already positioned by the container. Most of the dogs tested by Agnetta et al. (2000) were successful even though they were unable to see the person's hand placing the marker, as long as they saw the accompanying eye gaze and shoulder movement.

These results suggest that dogs are attentive to the movement of the experimenter, with the marker itself being irrelevant. However, Riedel et al. (2006) showed that dogs respond best to a combination of movement and marker placement. Regardless of which container was touched first with the marker, most dogs chose the container touched last. However, if the experimenter first placed the marker by the correct container and then touched the incorrect container with her hand, most dogs selected the container with the marker (Riedel et al., 2006).

Dogs are clearly more likely to find hidden food when the person places something next to the correct container. Reaching to place a marker and pointing to a container are very similar movements, yet the dogs are also drawn to the actual object. This is hardly surprising – the actions people make when feeding dogs consist primarily of reaching toward and manipulating objects of interest to dogs.

3. A simple solution for a sophisticated behaviour?

How are dogs able to solve the object choice task? Are they truly capable of interpreting communicative gestures or are they simply responding to some observable aspect of the testing procedure? For instance, sensitivity to odour could help dogs choose the correct container whilst paying no attention to human gestures. Alternatively, dogs' experiences with people may render them highly likely to respond in ways that increase the likelihood of success, such as "always approach the closest extension of the person" or "always approach the person's movement." By following either of these rules of thumb, a dog would most often end up closest to the correct container and subsequently investigate it. Before broaching the tantalizing idea that dogs are sensitive to the communicative intentions of people, it is essential to rule out these less sophisticated strategies that dogs might use to solve the problem.

3.1. *Odour cues*

Numerous studies have demonstrated that dogs are unable to solve the object choice task by smelling the hidden food. Even when particularly pungent smelling food is used, dogs are unable to choose correctly unless they are first given the opportunity to sniff both containers (Szetei et al., 2003). Remarkably, if dogs are permitted to sniff the containers and then they observe a human pointing to the incorrect container, they tend to choose the incorrect one (Szetei et al., 2003). Apparently dogs believe what they see, not necessarily what they smell.

3.2. *A tendency to approach people*

It is possible that dogs perform well on object choice tasks simply by approaching the nearest part of the human – a local enhancement cue. Many of the pointing study results can be explained by suggesting that the dog approaches the person's extended hand, which then places the dog in closer proximity to the correct container. Indeed, when tested from behind a chain-link fence that prevented the dogs from approaching the experimenter, they performed significantly poorer than dogs not behind a fence (Udell et al.,2008a).

Nonetheless, there is more to dogs' excellent performance in the object choice task than the mere inclination to approach humans' limbs or faces. The person presenting the cue can stand next to or behind the incorrect container and dogs are still able to find the food with a pointing gesture or a head turn toward the other container (Hare et al., 1998). Dogs are also able to find the food when the experimenter moves closer to the incorrect container while pointing to the correct one (McKinley and Sambrook, 2000). Riedel et al.

(2008) excluded from their analysis those trials in which puppies first sniffed the experimenter's pointing finger before selecting a container and still, the puppies found the food more often than by chance. Nearness of the human to one of the containers only biases dogs to that container when the person provides no additional information (Hare and Tomasello, 1999).

3.3. *A tendency to approach movement*

It is plausible that dogs perform reasonably well on the object choice task simply by being attracted to the direction of human movement. Several studies substantiate that movement toward a container biases dogs to select that container (Bräuer et al., 2006; Soproni et al., 2002). However, dogs still perform competently with static cues, in which the experimenter positions himself before being viewed by the dog (Hare et al., 1998). And dogs are able to select the correct container on the basis of a point even when the experimenter is simultaneously stepping closer to the incorrect container – which, arguably, is a larger movement that should bias the dog to choose the incorrect one (McKinley and Sambrook, 2000). Furthermore, the movement of shoulders and elbows are insufficient cues for dogs in most situations (Udell et al., 2008b). Evidently, movement is attractive to dogs but this attraction alone cannot account for all the findings.

Bräuer et al. (2006) showed that when the experimenter looked at the dog while shaking one of the containers, dogs primarily selected that one, whether correct or incorrect. However, when the experimenter looked directly at the container and manipulated it as though trying but failing to open it, dogs performed no better than chance. So perhaps movement with a social component trumps movement in isolation?

Researchers have shown due diligence in ruling out simple rule-of-thumb strategies that dogs might use to solve the object choice task. Clearly, dogs are sensitive to the communicative efforts of people when they search for hidden food. But how does this happen? One reasonable suggestion is that dogs learn this skill – that dogs respond to human gestures as they do to any of a variety of learned discriminative stimuli.

4. The role of general process behavioural conditioning

The simplest explanation for dogs' responsiveness to human social cues is that dogs are frequently exposed to these stimuli, and they learn their significance in precisely the same fashion that they learn a host of other meaningful stimuli. Trained dogs can acquire an astonishing set of auditory, visual, and olfactory cues through respondent and operant conditioning procedures. (Rico, the border collie that possesses a vocabulary of over 200 words for specific toys is a noteworthy example (Kaminski et al., 2004).) Even without explicit training, pet dogs learn a vast array of stimuli signifying such important events as feeding, walks, and the dreaded bath time. There is no question that we humans attempt to communicate with dogs in much the same way as we do with each other, so it is certainly in dogs' best interest to learn to respond in accordance with our communicative gestures. From the evidence we have, can we ascertain the role of general process behavioural conditioning in dogs' responsiveness to human-given cues?

4.1. *Learning during the experiment*

The objective of the studies on dogs' receptivity to human social cues is to assess their existing capabilities in the absence of learning during the testing. Therefore, most studies consist of no more than 20 or so trials per condition to minimize the opportunity for the dog to learn the significance of the gestures. In many studies, a comparison of performance between early and later trials provides little evidence to suggest that dogs get better with experience (e.g., Hare et al., 2002; Riedel et al., 2008; Soproni et al., 2001). Sometimes this is because of a ceiling effect: from the outset dogs do extremely well, particularly with pointing gestures and markers, so they cannot improve. Other studies show clear signs of dogs learning the significance of the cues (McKinley and Sambrook, 2000; Udell et al., 2008b; see Wynne et al., 2008 for a re-analysis of the Riedel et al., 2008 data which suggests the younger puppies became more proficient during testing). On the basis of the findings thus far, it is safe to conclude that dogs may learn to refine their responses to cues presented during the experiment but the majority enter the studies already displaying a tendency to respond to at least the pointing gestures.

4.2. *Formalized training*

Hare et al. (1998) tested a gundog trained for hunting duties, and it consistently out-performed an untrained pet dog on pointing and head turning. McKinley and Sambrook (2000) went on to specifically compare trained and untrained gundogs to untrained non-gundog breeds in an attempt to ascertain if the superiority of the gundog in the Hare et al. (1998) study was due to genetic selection or formalized training. They found that the trained gundogs performed significantly better than the pet dogs when presented with the pointing gesture but not with the head turn or eye gaze cues. The trained gundogs also seemed quicker to learn than the pet dogs – they learned to interpret the head turn and the eye gaze during the testing phase. McKinley and Sambrook (2000) found no difference in the performance of the untrained gundog and the untrained non-gundog breeds. Evidently formalized training in obedience and hunting teaches dogs to be more responsive to human pointing gestures and may prepare them to recognize the significance of novel cues. But even when dogs lack such training, they still perform overwhelmingly better than chance, so are they learning the significance of these cues through their everyday interactions with people?

4.3. *Enculturation*

It is conceivable that dogs learn to respond to human social cues because of their thorough familiarity with people. Most dogs rely on humans for their very existence. Everything of significance – food, water, touch, and social interaction – is provided by humans. And much of this is delivered to the dog by means of our hands, often in conjunction with our attention. Hence one could argue that any organism being cared for intensively by people would become highly attuned to our body movements, particularly our arms and hands, as well as our attentional state. Indeed, there is evidence that apes raised with humans perform better on object choice tasks than conspecifics raised without extensive human contact (Call and Tomasello, 1996).

Hare et al. (2002) compared the performance of pet dogs with seven adult wolves that had lived with humans from 10 days to 5 weeks of age. As a group, the dogs performed above chance with both a point and a point-plus-gaze cue, while the wolves chose at random. Miklósi et al. (2003) tested four highly socialized wolves and found that though they were able to find the hidden food when the experimenter touched the correct container, only two succeeded with a pointing gesture.

A study conducted by Virányi et al. (2008) on enculturated wolves also lends support to the argument that dogs' superiority at reading human cues is due to more than simply exposure to them. These extensively socialized wolves were hand-reared by people from the third day to the third month of life. When tested at four months of age and again several months later, the wolf pups still performed more poorly than dog puppies reared in comparable conditions. While the wolves, as a group, performed above chance on some gestures, there was tremendous individual variation in their abilities. A major drawback of this study was that after three months of age, the hand-reared wolves were integrated into an existing pack. Even though the human caretakers visited them frequently, the wolves may have lost much of their attentiveness to human cues once living in a conspecific social group.

Virányi et al. (2008) argue that wolves' inability to interpret human gestures results from their unwillingness to make eye contact with humans, making them less attentive to all forms of cuing. Studies substantiate that wolves are less likely than dogs to initiate eye contact with humans (Virányi et al., 2008) and are unlikely to look at humans when faced with a difficult or insoluble task (Miklósi et al., 2003). The question remains whether this is an inherent species distinction that speaks to the crux of the issue – that dogs have been selected for their attentiveness to human social cues – or whether wolves simply experience a less rich history of reinforcement linked to human attentional states.

Udell et al. (2008a) compared the performance of highly socialized wolves with pet dogs on their responsiveness to a pointing gesture. In contrast to the previous work, their wolves, tested outdoors, performed as well as pet dogs tested in their homes. And the wolves' accuracy was superior to the dogs when the dogs were tested in a comparable outdoor setting. However, this may not be a fair comparison. When outdoors, individuals of both species were separated from conspecifices but had olfactory, auditory, and visual contact with them. While the wolves were familiar with the other wolves that were present, it is unlikely the dogs were as familiar with the other dogs present during their testing because it was a private dog park. Still, even if the outdoor testing presented distractions that hampered the dogs' performance, the wolves performed just as well as the dogs when the dogs were tested in their homes. While it is not readily apparent why these wolves performed better than wolves in the previous studies, one potential explanation is that they interacted with humans on a daily basis and this maintained their responsiveness to human gestures.

If enculturation in human society is the reason why dogs show a knack for responding to our communicative cues, then dogs lacking extensive experience with people might be expected to perform less well than dogs living as pets. While studies aimed directly at comparing the proficiency of dogs as a function of the amount of exposure to people have yet to be conducted, puppies living in kennels and puppies yet to leave breeders' homes have proved to be just as competent as their cohorts residing with human families (Hare et al., 2002; Riedel et al., 2008). However, Udell et al. (2008a) found shelter dogs with unknown histories were unable to follow a pointing gesture to locate hidden food. Clearly more research is needed on the effect of experience. It is hard to imagine that dogs would not pick up on the import of our gestural communication system while sharing their lives with us, but is enculturation the sole explanation for their proficiency?

4.4. *Age effects*

If dogs learn to respond to human social cues through their interactions with people, then it stands to reason that puppies might not perform as well as mature dogs that have had more time to learn the significance of human-given gestures. Surprisingly, this is not what researchers report. Agnetta et al. (2000) observed the performance of dogs on marker placement and eye gaze and found four-month-old puppies performed as well as adults. Hare et al. (2002) compared puppies ranging in age from 9 to 26 weeks and reported no age effects. Riedel et al. (2008) tested puppies of various breeds between 6 and 24 weeks of age and found they performed well above chance levels with two types of pointing gestures and a marker cue. The only age difference they detected was that the 24-week-old pups were better at interpreting the marker cue than six-week-old pups. However, Wynne et al. (2008) re-analyzed these data in a way that increased statistical power and argued that performance of the puppies did improve with age from 6 to 24 weeks.

The fundamental question of whether dogs learn to respond to human social cues in the same fashion that they learn about arbitrary discriminative stimuli cannot be answered definitively. Adult dogs are capable of rapidly learning the significance of human gestures and formalized training further enhances this ability (McKinley and Sambrook, 2000; Wynne et al., 2008). If the skill is purely learned, however, one would expect other species that live with humans to be similarly accomplished. Yet dogs' closest relative, the wolf, generally fails to perform as well as the dog, even after extensive socialization (Kubinyi et al., 2007). And there is some suggestion that puppies are quite adept at responding to human pointing cues even as young as six weeks of age (Riedel et al., 2008), although further research is needed to flush out the role of early experience (Wynne et al., 2008). On the basis of these and related findings, some researchers propose that dogs' sensitivity to human social cues exists as an innate ability, largely independent of experience (Hare, 2007; Hare and Tomasello, 2005a).

5. A by-product of domestication

Domestic dogs differ from wolves and nonhuman primates in that they have been subjected to artificial selection for domestic traits. Dogs have undergone two phases of domestication. First, they evolved as a species distinct from their wild ancestral form. Second, they diverged into the various breeds with their characteristic behavioural and morphological traits. Hare and Tomasello (2005a,b) have offered the hypothesis that dogs outperform other species in their ability to respond to human social cues as a result of traits selected for during domestication. They do not propose that humans selected directly for dogs' abilities to read human communicative gestures. Rather, the selection pressures placed on the species for tameness and other desirable domestic traits, such as dogs' willingness to eat in the presence of humans and perhaps even dogs' acceptance of restraint by humans, may have provided the driving force for a specialized set of social skills. Thus, dogs emerge as expert readers of human social cues as a by-product of their domestic status. Would this have taken place during the first wave of domestication for basic tameness or during the second wave when the breeds diverged?

5.1. *A tameness spin-off*

During the first phase of domestication, dogs were presumably selected for their tameness – the tendency to approach and affiliate with people without exhibiting high levels of fear or aggression. This may have been an intentional process on the part of humans (Clutton-Brock, 1995), or it may have been via natural selection as dogs moved into the new niche provided by human settlements (Coppinger and Coppinger, 2001). Belyaev and co-workers (1979; Trut, 1999) experimentally domesticated silver foxes on a fur farm in Russia and revealed that the process of selective breeding for tame behaviour produced unanticipated changes in physiology, morphology, and behaviour. Successive generations of foxes began behaving more like dogs: they approached people instead of running away and they barked and wagged their tails. The sensitive period for socialization with humans lengthened (Belyaev et al., 1985). These tame foxes also started to look a bit like dogs: many were born with floppy ears, curly tails, shortened tails, spotted and speckled coats, or lighter bone structure. Like dogs, female foxes came into estrus biannually. Importantly, none of these changes were purposefully selected for but rather, came part and parcel with specific selection for low levels of fear and aggression.

When tested on the object choice task, Belyaev's domesticated foxes performed comparably to pet dogs (Hare et al., 2005). Domestic fox kits ranging in age from two to four months did just as well as age-matched dog puppies with pointing and gazing cues. Further, in a comparison of domestic and non-domesticated fox kits, the domestic kits out-performed their non-domesticated counterparts.

While it is tempting to conclude that domestication is key, it is not possible to ascertain from these results whether the superiority of the domestic kits is due to genetics or experience. Admittedly both groups were housed and maintained identically and received the same amounts of handling. However, the domesticated kits would have been more inclined to approach people and more attentive to people delivering their food each day so these foxes had more opportunity to learn an association between human actions and reinforcement. Furthermore, the domestic kits would have been less reactive during handling and, therefore, would have had more opportunity to learn to approach human hands. The non-domesticated kits, by contrast, would have been fearful during handling. Indeed, Hare et al. (2005) report that the latency to approach and touch an object handled by a person was dramatically longer for the non-domesticated animals (37.6 s for non-domesticated, 7.2 s for domesticated). Certainly a lack of neophobic tendencies gives the domesticated foxes a decided advantage, whether the vehicle is genetics or learning.

5.2. *An off-shoot of breed-specific traits*

An alternative possibility is that dogs have evolved to respond to human communicative gestures through artificial selection for cooperative traits. Purposeful selection for specific morphological and behavioural traits has resulted in the myriad of dog breeds we see today. It is conceivable that the ability to respond to human social cues piggy-backed along with the traits of tractability and trainability that were selected for in many present-day breeds. If so, we might expect to see breed differences in responsiveness to human-given cues.

The New Guinea Singing Dog (NGSD), a dingo-like *canid*, is unique among domestic dogs because although it underwent the first phase of domestication it is thought that since then, there has been no further selection for specific behavioural or morphological specialization (Koler-Matznick et al., 2003). Physiologically and behaviourally, the NGSD is intermediate between dogs and wolves. Thus, the NGSD may shed light on whether the ability to respond to human social cues arose during the first or the second phase of domestication. Wobber et al. (in press) compared NGSDs, well socialized with people, with pet dogs in a standard two object choice task. The NGSDs performed worse than the pet dogs on the point-plus-eye-gaze cue, although they were still above chance. That the NGSD can respond to human social gestures indicates that this ability likely arose during the first phase of domestication.

Wobber et al. (in press) reasoned that further analysis of the origin of dogs' socio-cognitive abilities may derive from evaluating domestic breeds classified according to their wolf-like traits. They tested individuals of various breeds categorized into wolf-like and non-wolf-like in accord with the genetic testing of Parker et al. (2004). They also included working and non-working breeds to produce four groups: (1) wolf-like working dogs (Siberian huskies), (2) non-wolf-like working breeds (retrievers, spaniels and herders), (3) wolf-like non-working dogs (Basenjis), and (4) non-wolf-like non-working dogs (toy and hound breeds). Dogs from all four groups found the hidden food on the basis of the pointing cue, with the working dogs slightly out-performing the non-working dogs. In contrast, only the Basenjis found the food with the head-turn-plus-eye-gaze cue. As these breed differences in performance do not map onto their genetic distance from the ancestral wolf, it is probably safe to assume that sensitivity to human social cues was not selected for while dogs' behavioural traits and functional capabilities were being refined into breeds. Rather, it is likely that traits selected for during the first phase of domestication led to the dog's receptivity to human communicative gestures. This begs the question: are other domesticated species similarly endowed?

5.3. *Other domesticated species*

If dogs' responsiveness to human social cues represents a capability inadvertently brought to the fore during the domestication process, then it stands to reason that other domesticated species might also prove adept in the object choice task. In support, Miklósi et al. (2005) report that cats, a species that underwent domestication some 6000–10,000 years ago (Serpell, 2000; Driscoll et al., 2007), perform with a pointing cue almost as well as dogs. Thus, even though cats have never been selected for trainability and cats are certainly less reliant on humans for food than dogs, this preliminary result suggests that domestication may have bequeathed cats with a similar talent for reading human gestures.

Like cats, herbivorous species are also less dependent on humans for food than dogs yet they have a lengthy history of domestication. Goats, a species that has been domesticated for some 10,000 years (Luikart et al., 2001), possess the ability to find hidden food on the basis of pointing gestures in an object choice task (Kaminski et al., 2005). The jury is out on the adeptness of horses, however. McKinley and Sambrook (2000) found only one of 10 horses was able to locate hidden food when the person pointed to it. In contrast, Maros et al. (2008) found their horses selected the correct bucket at levels above chance when given sustained points and a momentary proximal point. They were only unable to respond to the most difficult gesture: a momentary distal point. The Maros et al. (2008) horses were held and encouraged by their owners which may have prompted the horses to feel more comfortable with the experimental procedures or may have resulted in a "Clever Hans" effect. Further investigation is warranted to ferret out the reason for the contradictory results.

The exceptional social talents of the dog may not be so curious after all. This small body of evidence suggests that other domesticated species exhibit some skill in responding to human communicative gestures, albeit not as expertly as the dog. However, no other domesticated species has had such a lengthy dependence on humans as the dog, nor has any species been subjected to such intensive artificial selection for their behavioural traits. Hare and Tomasello (2005a) argue that all domesticated species exhibit lower levels of fear and aggression, which aids them in their ability to solve the object choice task. However, they propose that dogs also possessed specialized social problem-solving skills and, once the systems mediating fear and aggression were dampened, these skills could then be applied to new situations, such as social exchanges with humans. Hare and Tomasello's (2005b) "emotional reactivity" hypothesis proposes that by selecting for tame behaviour, dogs became as comfortable interacting with humans as they were with conspecifics – if not more so because of the climate of cooperation characterizing dog–human relations (Hare and Wrangham, 2002). In this new "adaptive space," dogs further benefited from the generalized ability to respond to the idiosyncracies of our social-communicative system. While the theory is certainly plausible, evidence to directly support the notion of dogs' spontaneous use of human social cues, emerging independent of experience, is still lacking. Wynne et al. (2008) rightly assert that we need to conduct research on dogs that differ in their experiences with human hands delivering food and other notable stimuli. Until we have additional studies that carefully control dogs' ontogenetic experiences, we cannot confirm or deny the domestication by-product explanation.

6. Theory of mind

Miklósi and Topál (2005) reject the emotional reactivity hypothesis on the grounds that they believe domestication alone is insufficient to account for the highly developed social skills of dogs. They make the case that dogs and humans have evolved together to such an extent that human-like social skills have materialized in the dog. Miklósi et al. (2004) claim that certain findings – such as dogs responding spontaneously to various forms of human gestural cues and dogs easily generalizing to novel forms of visual communication (elbow pointing and the like) – imply that they actually possess some level of referential understanding of the cues. They go on to suggest that dogs make excellent models for the study of human social evolution because their ability to comprehend social cues is an example of convergent evolution. Therefore, according to Miklósi et al. (2004), dogs serve as functional analogues of their human counterparts. This perspective prompts a host of titillating questions. Are dogs merely responding to human social cues, or do they actually comprehend the meaning of these cues? Do dogs understand that the person knows the location of food and is trying to convey this information to them? What do dogs grasp about the unobservable mental states of humans?

Some of the research cited as supporting the notion that non-dog species possess "theory of mind" – that they are able to impute mental states to others and to reason about the relationship between these mental states and subsequent behaviour – involves animals' ability to take the perspective of others and to respond to others' attentional states (Penn et al., 2008). Chimpanzees, for instance, are able to assess a feeding situation and recognize which food items their competitor can and cannot see (Hare et al., 2000, 2001). They take circuitous routes to food in order to obscure their approach from a human competitor (Hare et al., 2006), and they conceal visual and auditory cues that would notify the person of the location of a contested food source (Melis et al., 2006). Corvids are more likely to re-cache food in the presence of a conspecific but only if they have had previous experience stealing another bird's caches. It seems as though they extrapolate what they need to do in order to avoid being pilfered themselves (Emery and Clayton, 2001). Dogs' mastery of the object choice test cannot hold a candle to these apparent feats of socio-cognitive dexterity yet even these can be explained without recourse to theory of mind capabilities (Penn and Povinelli, 2007; Shettleworth, 2008).

At best, dogs probably enjoy a precursory theory of mind – they are sensitive to the attentional states of people. When faced with a piece of forbidden food, dogs are quicker to take it if the experimenter's eyes are closed, his back is turned, or he is distracted than they do if the experimenter is looking at them (Call et al., 2003). Gácsi et al. (2004) showed that dogs are less likely to beg from a person wearing a blindfold or from a person facing away from them. Dogs that know where food is hidden vocalize and gaze back and forth between the food and their owner, even if the owner was not present when the food was hidden (Hare et al., 1998; Miklósi et al., 2000). And dogs faced with an insoluble problem are inclined to look back at the experimenter, as though soliciting assistance (Miklósi et al., 2003, 2000).

While intriguing, these observations do not require anything remotely as sophisticated as theory of mind – they simply require that dogs be sensitive to the contextual and discriminative cues associated with reward and non-reward (Emery, 2000; Udell and Wynne, 2008). People are unlikely to provide dogs with food or other types of rewards without also looking at them. Dogs seldom succeed in appropriating prohibited food if a person is watching them. That dogs modify their behaviour in accord with stimuli in the environment requires no awareness of others' mental states. Dogs employing gaze alternation to "show" the location of inaccessible food need not be intentionally communicating information to an unknowing participant. Orienting toward a desired object is a normal behaviour in dogs and looking back and forth between a human and a reward has very likely been reinforced in the animal's past.

Likewise, dogs finding food on the basis of human gestures demands no sophisticated cognitive arsenal. Clearly, they are responsive to the cues but there is no evidence to suggest that they understand their meaning or that they recognize the person knows information they do not. A variety of social behaviours, ostensibly complex, can be accounted for by means of straightforward associative learning (for an elegant example of gouramis displaying social flexibility in response to a classically conditioned stimulus, see Hollis et al., 2004). Shettleworth (2008) wisely cautions that when we attempt to infer cognitive processes we must not lose sight of causal mechanisms of behaviour. We are still a long way off being able to make the claim that dogs possess theory of mind.

7. An adaptive specialization of learning

The upshot of all this research on dog social cognition is that we really have no idea why they are so good at responding to human communicative gestures. It may be a reflection of general process learning that results from an extensive exposure to reinforcement contingencies during the lifetime of the individual. It may be that dogs' superiority arises as a by-product of domestication and is now an innate skill that emerges spontaneously. Alternatively, dogs, through the selective pressures placed on them during their co-evolution with humans, may have evolved specialized cognitive abilities for interpreting the meaning of human communicative gestures and engaging in intentional exchanges of information with people. None of these explanations is wholly satisfying. Dogs are too skilled for it to be pure trial-and-error learning. Yet it is improbable that a versatile behaviour like this would be largely innate. And support for dogs having theory of mind is nonexistent (Penn and Povinelli, 2007).

I contend that dogs' proficiency with human social cues represents an adaptive specialization of learning (Shettleworth, 1972), the genetic variability for which rests with the dogs' complex social system combined with an opportunistic foraging strategy. The dog is unique amongst domesticated species in its role as scavenger. Could this feature, which typically results in animals being acutely aware of other individuals in their social group for opportunities to scrounge (Giraldeau and Caraco, 2000), have impacted on their behavioural flexibility during our co-evolution?

It is completely sound to maintain that the dog has experienced profound selective pressures as a result of its affiliation with people. Whether by their design or ours, dogs have adapted to our world with resounding success, and it is likely that this is due, in large part, to their capacity to respond appropriately in their interactions with us. Dogs that learned to approach us when we gestured to nearby food sources and to avoid us when we motioned for them to go away were at a decided advantage over dogs that could not respond to these signals. A systematic study of dogs' foraging and communicative behaviour could provide us with valuable insight into the question of whether their social savoir-faire originated in part from feeding tactics favouring sensitivity to others' actions.

From a very young age, dogs seem to be especially sensitive to actions performed by humans. I wager this is due to a genetically programmed selectivity in the dog's perception. Once dogs evolved a biological predisposition to attend to the actions of others, their everyday lives provide innumerable opportunities to learn the significance of specific human gestures. With an in-born propensity to learn firmly ensconced, even extremely subtle human behaviours can serve as discriminative stimuli. This melding of predisposition and selective learning can account for the existing body of evidence without recourse to innate skills or human-like social comprehension.

Very young puppies demonstrate some competence at responding to certain human communicative gestures. Yet just because a skill appears early in development does not preclude learning. It does, however, demand that puppies be highly attentive to the actions of humans, a tendency that has been confirmed in studies of dog–human attachment (Frank and Frank, 1982; Gácsi et al., 2005). And the rapidity with which puppies learn novel arbitrary responses on the basis of reinforcement contingencies certainly lends credence to the argument that dogs can learn to respond to human gestural cues with limited exposure. McConnell (1990) provides an excellent example of such prepared learning with her analysis of dog–human communication. She first demonstrated that dogs are especially responsive to sounds that resemble human verbal cues commonly used to train dogs. She then showed that puppies learned to come running in response to stimuli that replicated the acoustic features of sounds eliciting motor activity more readily than they did for sounds that inhibited motor activity. Like puppies learning the relevance of human verbal cues, dogs may learn very early in their development the significance of human communicative actions.

Is it possible to test whether dogs' responsiveness to human social cues is an example of adaptive early learning? A thorough analysis of the ontogenesis of this ability in puppies is a necessary first step because we need to know if experience with human hands is necessary (Wynne et al., 2008). Such a demonstration calls for isolating the factors of interest during development. For instance, some puppies would need to be well socialized with people yet deprived of the experience of human hands delivering significant things, such as food or tactile stimulation. Comparing the responsiveness to human social cues of these puppies with normally-raised puppies would tell us if the ability develops free of experience. Next, we need to know if dogs are biologically prepared to learn human gestures. For this, a set of naïve puppies could be taught a set of arbitrary communicative signals and their performance compared with other naïve puppies learning our species-typical cues. If responsiveness to human social cues is truly a functional adaptation in dogs, then we expect them to be more adept at learning genuine gestures than mock ones.

We would also benefit from an understanding of individual differences in skill level. Does a dog that responds to a variety of human gestural cues also perform well in other social problem-solving tasks? Is this proficiency restricted to interactions with humans or are these dogs equally skilled in their exchanges with conspecifics? And how did the individuals that do not excel differ during development from those that do?

As Shettleworth (1998) suggests, once the important issues are defined, a coherent research program often falls into place. There are many fascinating questions that can be asked about the mind of the dog. It is left to us to hone the questions, to devise clever ways to address them, and to be prudent in our interpretation of the answers.

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