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Do dogs get the point? A review of dog–human communication ability

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ABSTRACT

In recent years evidence has accumulated demonstrating that dogs are, to a degree, skilful in using human forms of communication, making them stand out in the animal kingdom. Neither man's closest relative, the chimpanzee, nor dog's closest living relative, the wolf, can use human communication as flexibly as the domestic dog. This has led to the hypothesis that dogs' skills in this domain may be a result of selection pressures during domestication, which have shaped dogs' skills tremendously. One hypothesis, the so-called by-product hypothesis, suggests that dogs have been selected against fear and aggression and as a by-product this paved the way for the evolution of generally more flexible social cognitive skills, which surpassed those of their ancestor, the wolf. Another hypothesis, the adaptation hypothesis, has claimed that dogs may have been specifically selected for certain tasks for which using human forms of communication was necessary. As of yet, the mechanism underlying dogs' understanding of human forms of communication is not fully understood. We argue here that understanding the mechanism involved will also shed light on possible evolutionary scenarios. We argue that the evidence to date suggests that dogs' understanding of human forms of communication may be more specialized than was predicted by some and may be best explained as the result of a special adaptation of dogs to the specific activities humans have used them for.

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Dogs' use of the human pointing gesture

More than a decade ago, initial studies revealed that dogs are capable of using various forms of human communication to a degree that many other non-human species cannot (e.g., Hare, Call, & Tomasello, 1998; Kaminski, Call, & Fischer, 2004; Miklósi, Polgárdi, Topál, & Csányi, 1998; Soproni, Miklosi, Topál, & Csányi, 2001). The vast majority of these studies used the so-called object choice paradigm (see Anderson, Sallaberry, & Barbier, 1995). In this task, a human experimenter hides food under one of several containers out of the dog's view and then indicates the target location by giving a social cue, most often pointing (for a review see Miklósi & Soproni, 2006). The results show that not only are dogs very skilful in using the pointing gesture to find a reward (e.g., Agnetta, Hare, & Tomasello, 2000; Miklósi et al., 1998; Soproni et al., 2001), but their behavior can also not be explained by possibly low-level mechanisms like, e.g., pure local enhancement. Hare et al. (1998) showed that when the human stands behind and therefore enhances the empty (hence incorrect) cup but from there points to the correct cup dogs still follow the pointing gesture. In another study, although the human actively moved away from the indicated location while pointing, dogs still followed the pointing gesture (McKinley & Sambrook, 2000).

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Dogs seem also to not just rely on odor cues to find the food. Various authors have used control conditions to exclude this possibility, with food hidden as in all the other conditions but with no social cue given before the dog was allowed to make a choice (e.g., Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Hare & Tomasello, 1999; Lakatos, Gácsi, Topál, & Miklósi, 2012; Miklósi et al., 1998). When no social cue was present, the dogs did not find the food above chance., thus indicating that odor alone was not sufficient.

Recent research has shown that other lower-level explanations can also not fully explain dogs' skills. It is unlikely for example, that dogs simply learn to follow human gestures during the course of an experiment. Different studies show that dogs' skills are present from the first trial onwards (Hare & Tomasello, 1999; Riedel, Buttelmann, Call, & Tomasello, 2006; Soproni et al., 2001) with no improvement over the course of multiple trials and therefore no evidence for any learning effect (e.g., Dorey, Udell, & Wynne, 2010; Gácsi, Kara, Belényi, Topál, & Miklósi, 2009; Wobber, Hare, Koler-Matznick, Wrangham, & Tomasello, 2009). Further, a mere associative account suggested by some, e.g., that dogs associate the humans' limbs with food (Bentosela, Barrera, Jakovcevic, Elgier, & Mustaca, 2008; Dorey et al., 2010; Elgier, Jakovcevic, Barrera, Mustaca, & Bentosela, 2009; Udell, Giglio, & Wynne, 2008; Wynne, Udell, & Lord, 2008) cannot explain dogs' behavior sufficiently. There is some evidence that dogs orient primarily to protruding body parts and generalize easily from the pointing cue to other gesture types (Lakatos, Soproni, Dóka, & Miklósi, 2009; Soproni, Miklosi, Topál, & Csányi, 2002). However, the part protruding from the body needs to be an actual part of the human's body as dogs ignore a pointing wooden stick or e.g., the "gesture" of a mechanical arm (Soproni et al., 2002; Udell, Giglio, et al., 2008).

In addition, dogs are able to use more subtle cues like head turning, bowing and nodding, with some individuals even able to use glancing towards the target location as a communicative cue (McKinley & Sambrook, 2000; Miklósi et al., 1998; Soproni et al., 2001; Udell, Giglio, et al., 2008). More importantly, recent research suggests that dogs seem to attend to the referential nature of the human's gaze during the communicative interactions (Kaminski, Schulz, & Tomasello, 2012; Soproni et al., 2001; Teglas, Gergely, Kupan, Miklosi, & Topal, 2012) and the communicative intent of the human (Kaminski et al., 2012). Kaminski et al. (2012) set up a situation during which the human either gestured intentionally or produced certain unintended movements, directed at the target location, which mirrored to some extent the communicative gesture (e.g., the human held her arm in an outstretched position to check the time on her watch and protruded her finger while doing so). While the dogs followed the intended gesture, they basically ignored the unintended movements even though they looked very similar. The key differences between both conditions was the eye contact between the human and the dog which, for the dogs, seemed to determine whether the gesture was intentional or not (Kaminski et al., 2012). In another study, Scheider, Grassmann, Kaminski, and Tomasello (2011) showed that dogs also take contextual information into account rather than blindly following a pointing gesture. In this study, dogs were led into an empty room and got the chance to investigate this room without the human interfering. During their search half of the dogs found a piece of food without the human having gestured towards it in any way while the other half did not find anything. After both left the room and then re-entered, the human pointed towards an empty spot within the room. The dogs which had previously found food followed the pointing gesture, while the dogs which had not found anything, did not. This indicates that certain contextual information was necessary for the dogs to take pointing as a relevant gesture.

Taken together these findings suggest that dogs are very skilful in using pointing as a communicative gesture to find food. Interestingly, research further suggests that selection pressures during domestication had an effect on dogs' skills in this domain.

The domestication hypothesis

The domestication hypothesis claims that dogs' ability to use human gesture (and other forms of communication) may be influenced by selection pressures during domestication (Hare, Brown, Williamson, & Tomasello, 2002; Hare & Tomasello, 2005; Miklósi et al., 2003). Support for this hypothesis comes from several facts. First, wolves, as dogs' closest living relatives, are not as skilful with human communication as are dogs (Hare et al., 2002; Miklósi et al., 2003). Even if raised under very similar conditions from birth on (in a human household) and tested at a young age, dogs outperform wolves (Gácsi, Gyoöri, et al., 2009; Miklósi et al., 2003; Virányi et al., 2008). Intensively socialized wolves can learn to use human gestures (Gácsi, Gyoöri, et al., 2009; Miklosi & Topal, 2011; Udell, Dorey, & Wynne, 2008) but they need to be more exposed to human social interactions than dogs to reach similar performance levels (Gácsi, Gyoöri, et al., 2009; Miklosi & Topal, 2011). Recently Udell, Dorey, et al. (2008) suggested that, if socialized intensively, adult wolves outperform dogs in how successfully they use human pointing. In their study this was especially true for dogs which had been housed in shelters and with little human contact, suggesting that ontogeny alone may account for dogs' skills in this domain (Udell, Dorey, et al., 2008). However, there are significant differences in methodology as well as in how data were analysed in comparison with most other studies using the object choice design, making it difficult to put these data in the context of the debate. Unlike all previous studies, Udell, Dorey, et al. (2008) used a procedure during which food was not hidden under the target cup but only dropped into the cup as a reward after the subject had walked towards the target location. In addition, subjects were presented with a 'clicker' sound-stimulus upon making the correct choice. Recently, Pongracz, Gacsi, Hegedus, Peter, and Miklosi (2013) showed that this difference in the method causes significant differences in the performance of pet dogs. The authors showed that subjects' performance increased significantly when a clicker was used, proving that a supposedly small modification in method can lead to a substantial difference in the results. A more substantial problem, however, results from the difference between the data analysis of Udell, Dorey, et al. (2008) and most other studies using the object choice paradigm. While most

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researchers decide to discard or repeat trials during which subjects did not make any choice, Udell, Dorey, et al. (2008) rated these trials as incorrect (resulting for example in the inclusion of a subject which *never* made any choice). This is especially problematic given that the statistical analysis relies on using 50% as random choice. Therefore, by coding no-choices as incorrect, incorrect choices have a greater expected probability than correct choices (Hare et al., 2010). Hare et al. (2010) re-analysed Udell et al.'s data, discarding trials during which subjects did not make any choice; with this more conventional analysis the effect that wolves outperform dogs vanished (but see Udell & Wynne, 2010 for further discussion) therefore not challenging the domestication hypothesis (Hare et al., 2010).

The second piece of evidence for the domestication hypothesis comes from the fact that dogs' skills in this domain cannot be explained by major learning taking place during ontogeny. Studies show that even young dog puppies are skilful in using human gestures (Agnetta et al., 2000; Hare et al., 2002; Kaminski et al., 2012; Miklósi et al., 2003; Riedel, Schumann, Kaminski, Call, & Tomasello, 2008; Virányi et al., 2008). Riedel et al. (2008) showed that dog puppies at the age of 6 weeks already use the pointing gesture directed at an object *behind* them. This can therefore not be explained by simple local or stimulus enhancement or by a general preference for approaching the human's hand. The puppies in the Riedel et al. study had to actively move *away* from the hand in order to be successful. This study also showed that puppies of different ages (from 6 weeks of age to 24 weeks of age) do not improve their skills, as there was no improvement in puppies' success rate with the two pointing gestures used (see also Agnetta et al., 2000; Hare et al., 2002, 2010; Riedel et al., 2008). In addition Gácsi, Kara, et al. (2009) found that dogs' performance is not influenced by dogs' age, keeping conditions (inside vs. outside the house), time subjects spent interacting with their owner or dogs' training background (dogs participate in agility activities, an activity which involves a lot of communicative interaction between dog and owner, or not). These results were confirmed by a very recent study of Pongracz et al. (2013) looking at a different group of dogs. There is also evidence that these skills do not depend on the dogs' breed (e.g., Dorey, Udell, & Wynne, 2009; Gácsi, Kara, et al., 2009). Some studies revealed differences in the dogs' performance when comparing groups of two particular phenotypes, suggesting that rather than ontogeny, breed differences may affect dogs' ability in using human pointing. Dogs from cooperative working breeds seem more skilful than independent workers and mongrels; and brachycephalic (broad skulled) breeds outperform dolichocephalic (long skulled) ones (Gácsi, McGreevy, Kara, & Miklósi, 2009; see Helton & Helton, 2010 for a re-analyses of the data according to dogs' size). Similar results were found by Wobber et al. (2009), who showed that working breeds (e.g., huskies and shepherds) outperformed non-working breeds (e.g., basenji and toy poodle). However, it is important to note that all groups in both studies used human gestures significantly above chance level, indicating that dogs as a population are skilful with human gestures.

Another way to look at ontogenetic effects on dog behavior is by studying dogs which grew up with as little human contact as possible, e.g. street dogs or dogs which have lived in a shelter for a long time. Studies focusing on shelter dogs (some of which were former street dogs) found mixed results. Udell, Dorey, et al. (2008) and Udell, Dorey, and Wynne (2010) did not find positive results when testing shelter dogs. To the contrary, Hare et al. (2010) showed that shelter dogs, which were former street dogs, were able to use a human's pointing gesture equally as well as dogs which had lived with a family their entire lives. Some may argue that the only way to test if learning during ontogeny alone may account for dogs' skills would be by raising puppies in complete isolation from human contact (Udell et al., 2010). However, dogs deprived of human social contact may not be suitable subjects for socio-cognitive tests (Miklosi & Topal, 2011) as the deprivation may possibly cause deficits in dogs' cognitive development (analogous to human children, see Rutter et al., 2007).

Dogs compared to other species

The third piece of evidence, which supports the hypothesis that dogs evolved specialized skills in reading human communicative gestures, comes from comparisons of dogs with other species outside the Canidae. Not only do dogs seem to outperform their closest living relative, the wolf, but dogs also seem to outperform man's closest living relative, the chimpanzee, when it comes to using human gestures successfully while searching for a reward. When dogs and chimpanzees are compared directly, dogs outperform chimpanzees in how successfully they use human given communicative cues (Bräuer et al., 2006; Hare et al., 2002; Kirchhofer, Zimmermann, Kaminski, & Tomasello, 2012). In a recent study, Kirchhofer et al. (2012) compared twenty chimpanzees and sixteen dogs in their ability to use an imperative pointing gesture indicating which of two objects to fetch. All individuals in this study had been pre-selected for their general motivation to fetch objects and then hand them over to the human. The general setting for both species was as similar as possible. Chimpanzees and dogs were allowed to move freely in a room in which two objects were presented to them on a wooden board. The human then pointed to one of the two objects, indicating her desire to obtain the object and in return for the correct object, the subjects were rewarded. While the dogs had no problem using the human's pointing gesture to select the correct object, the chimpanzees ignored it while making their decision (Kirchhofer et al., 2012). Dogs' success in this study is remarkable for several reasons. First, while observing the human point to one of the objects, the dogs could not see the objects, as the objects were located behind them. Vice versa, while facing the objects and making their decision, the dogs could not see the pointing gesture anymore, as then the human was located behind them. This suggests that dogs can follow pointing to a referent out of their view, making it unlikely that a sheer association between the human's hand and the target can explain dogs' success. The fact that chimpanzees fail this task even though they have an otherwise sophisticated understanding of others' psychological states (see for a review Call & Tomasello, 2008), shows that being successful in this task is not trivial. The other great ape species and also several monkey species seem also not very skilful in using human gestures to find

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hidden food (for a review see Call & Tomasello, 2005; but see Lyn, Russell, & Hopkins, 2010, for a current debate on this issue). There is evidence that animals, with a particular training background (e.g., training for public shows) have some skills in reading human given gestures (see Scheumann & Call, 2004 for seals; Tschudin, Call, Dunbar, Harris, & van der Elst, 2001 for dolphins) but those are most likely the result of positive reinforcement (e.g., to go where the hand is) during the training.

Even among other domesticated mammals, dogs' skills stand out. Though there is evidence that other, domesticated species use pointing (see Hernádi, Kis, Turcsán, & Topál, 2012 for ferrets; Kaminski, Riedel, Call, & Tomasello, 2005 for goats; McKinley & Sambrook, 2000; and Maros, Gácsi, & Miklósi, 2008 for horses; Miklósi, Pongrácz, Lakatos, Topál, & Csányi, 2005 for cats) those animals' skills were not as flexible as the dogs'. The horses as well as the goats tested only used more salient cues like dynamic pointing or tapping but unlike dogs had problems with less salient cues like e.g., static pointing (Kaminski et al., 2005; Maros et al., 2008). Or subjects (e.g., cats) had to be strongly pre-selected during a pre-test period to find individuals, which would follow human given gestures (Miklósi et al., 2005). This suggests that when compared to mammalian species outside the Canidae, dogs' skills with human gestures stand out. Taken together, all this evidence suggests that particular selection pressures during domestication shaped dogs' skills in this domain. The question is how.

How did selection during domestication influence dogs' skills?

There are two main hypotheses about how selection during domestication affected dogs' social skills, the by-product hypothesis (Hare & Tomasello, 2005; Hare et al., 2005) and the adaptation-hypothesis (Miklósi et al., 2003). The by-product hypothesis states that dogs' selection on one trait e.g., tameness, paved the way for further social cognitive evolution and therefore as a by-product of the initial selection for tameness, dogs' evolved outstanding social cognitive skills one of which is dogs' ability to read human given communicative cues (Hare & Tomasello, 2005). Support for this scenario comes from a study conducted with Siberian Foxes in Russia. In this study Hare et al. (2005) tested two groups of silver fox puppies for their ability to read human given gestures. Over several generations, one group of this fox population had been selected for tameness (Trut, Plyusnina, & Oskina, 2004). The selection procedure involved the human reaching into the fox's cage with her hand, after which the fox's reaction was recorded. If a fox approached the hand in a friendly way and remained calm, it was selected for the tame group. If a fox reacted aggressively or was aversive towards the approaching hand, it was not selected for the tame group. After only six generations, the foxes from the group selected for tameness showed dog-like behaviors and anatomical features, like e.g., floppy ears, tail-wagging behavior etc. (Trut et al., 2004). When tested for their ability to use human-given pointing gestures, the fox puppies from the group selected for tameness outperformed the puppies from the unselected foxes. Hare et al. (2005) take these findings as evidence that selection for tameness alone can lead to flexible social cognitive skills, one of which is dogs' ability to read human gestures. Unfortunately the fox puppies were only tested with relatively simple cues, e.g., cues where the human extended her arm towards the correct cup while the human's hand was close to the target location. It is therefore possible that a quite simple mechanism, like local enhancement, may explain the results. It is also possible that the gesture basically resembled the initial selection procedure during which puppies were selected for their motivation to approach a human's hand without aggression and fear. It would be interesting to further explore to what extent the fox puppies' use of the pointing gesture is comparable to dog puppies' use of pointing. In a recent study, Hernádi et al. (2012) showed that domestic ferrets (*Mustela furo*) show similar skills to dogs in using a human pointing gesture, whereas their (highly socialized) wild counterparts (*Mustela putorius*) were not able to use these communicative signals (Hernádi et al., 2012). Though the selection process during the domestication of ferrets is not well documented, selection against aggression and fear (like in dogs) was most likely part of it, as domesticated ferrets were used for hunting (Price, 2002). Though the selection process within this group is therefore not as well controlled as the selection of the silver foxes, this study might be further support of the by-product hypothesis.

The by-product hypothesis would predict generally more sophisticated social cognitive skills in dogs. We should expect dogs to be also more skilful compared to other mammals in social cognitive domains other than reading human gestures. Further, we would also predict dogs' understanding of human gestures (and other forms of communication) to be quite flexible, meaning that we would not expect it to be restricted to certain contexts or based on a rather restricted mechanism.

The adaptation-hypothesis on the other hand states that humans have actively selected dogs for their ability to use human communicative signals. In this scenario, humans selectively bred dogs for certain purposes (e.g., hunting and herding) and therefore specifically selected dogs which were particularly good at reading human cues (which is important for hunting and herding activities involving communication over distance). The adaptation-hypothesis predicts that dogs' skills in reading human gestures are a specialization, which may not necessarily reflect a truly flexible understanding of the communicative interaction but is rather restricted. Also we would not expect dogs' outstanding social cognitive skills to extend to other domains but would expect it to be restricted to the communicative context only. One way to explore this further is by taking a closer look at dogs' social cognitive skills in domains other than communication and also at the underlying mechanisms involved in how dogs actually use human communication.

General outstanding social cognitive skills in dogs?

Dogs are known to be sensitive to a human's attentional state. Call, Bräuer, Kaminski, and Tomasello (2003) set up a situation during which a dog was forbidden to take a piece of food lying on the ground. Then the human's attentional state was varied. In one condition, she remained attentive with her eyes open and directed at the food while in the other

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conditions she either had her eyes closed, was distracted by a computer game or had her back turned to the food. Dogs clearly differentiated those situations and stole significantly less food when the human was attentive compared to all other situations. In a similar study, Schwab and Huber (2006) set up a situation in which the dog's owner commanded the dog to lie down. Afterwards, she looked at the dog, left the room, read a book, watched TV or turned her back to the dog for one minute. In the condition during which the dogs were observed directly, they obeyed the command longer than in all other conditions. Furthermore, dogs obey a "down" command faster, if the owner faces them during instruction compared to a situation in which the owner is oriented towards another person or out of dog's sight (Virányi, Topál, Gácsi, Miklosi, & Csányi, 2004). Dogs are also able to differentiate between an attentive and an inattentive person in a begging task. They preferentially begged from the facing person than from a person who was not oriented towards them (Gácsi, Miklósi, Varga, Topál, & Csányi, 2004; Virányi et al., 2004). Therefore the initial findings by Call et al. (2003) have been replicated several times, showing that dogs are highly sensitive to the human's attentional state (Call et al., 2003; Gácsi et al., 2004; Schwab & Huber, 2006; Virányi et al., 2004).

Dogs seem to also understand something about a human's visual perspective. Bräuer, Call, and Tomasello (2004) confronted dogs with a situation during which the dogs were again forbidden to take a piece of food from the ground but now the food was hidden from the human's view by one of three different types of barrier. The barrier was either large such that the dog was hidden by it completely while eating the food, or it was small, such that the dog was not hidden during the approach but merely while eating the food. A crucial control condition was a condition in which the barrier hiding the food was large but had a small window cut out exactly where the food was lying. Dogs stole significantly more food in the large-barrier condition compared to the other two, showing that to some extent dogs seemed to be sensitive to the human's visual perspective. (Bräuer et al., 2004; Kaminski, Bräuer, Call, & Tomasello, 2009).

However, dogs' abilities in this domain seem to be limited. Kaminski et al. (2009) showed that dogs did not differentiate between two toys based on the human's knowledge about them. In this paradigm two toys were hidden from a human's view by small opaque barriers while they were in full view of a dog, which was located opposite the human. The human then watched the placement of one toy but not the other and was therefore knowledgeable about the location of one toy but not the other. Upon the human's request to fetch a toy dogs did not distinguish between the two toys, contradicting the hypothesis that they can distinguish between knowledge and ignorance in other individuals (Kaminski et al., 2009; see also Virányi, Topál, Miklósi, & Csányi, 2006). So while dogs seem to show some understanding of a human's attention and maybe even the ability to take a human's perspective, dogs' understanding of seeing in humans is limited. In addition, if compared to other species, there is no evidence that dogs stand out in any way in how they understand others' psychological states. There is now evidence that many mammalian species are able to understand when other individuals are or are not attentive (see for reviews Call & Tomasello, 2008; Emery, 2000; Rosati & Hare, 2009). While most research has been done with primates, there is also evidence for attention reading and perspective taking in species outside the primate order (for pigs, see Held, Mendl, Devereux, & Byrne, 2001; Nawroth, Ebersbach, & von Borell, in press; for goats, see Kaminski, Call, & Tomasello, 2006; for dolphins, see Xitco, Gory, & Kuczaj, 2004; for wolves, see Udell, Dorey, & Wynne, 2011; (though see Virányi & Range, 2011, for a discussion of these findings)). Therefore, the hypothesis that dogs' social cognitive skills stand out in any other domain but reading human gestures is not supported by the current evidence; rather, some of these skills seem to be widespread in the animal kingdom and may have had an urgent evolutionary function for social living mammals (Emery, 2000).

To further explore how restricted dogs' social cognitive skills are, we need to take a closer look at the mechanisms underlying dogs' use of pointing. If dogs' use of human gestures is a specialization, we would expect it to be fairly restricted to a certain set of cues and signals and not reflecting a general understanding of human communication in a "human-like" way.

Do dogs get the point?

Humans from an early age produce and understand gestures as a means to share information (e.g., Liszkowski, Carpenter, Striano, & Tomasello, 2006; Liszkowski, Carpenter, & Tomasello, 2008; Tomasello, 2008; Tomasello, Carpenter, Call, Behne, & Moll, 2005). There are certain cognitive as well as motivational prerequisites for an individual to be able to recognize communication as informative. A cognitive prerequisite is the ability to determine when others are ignorant about certain aspects in the environment and informing them is actually necessary. Children from an early age seem to have the cognitive capacity to determine when others have not witnessed certain events in the past (e.g., Moll & Tomasello, 2007; Onishi & Baillargeon, 2005) and they seem to take others' knowledge states into account during communicative interactions with them (Liszkowski et al., 2006, 2008). The second prerequisite for communicating informatively is having the motivation to provide information when necessary. From early age, humans seem uniquely motivated to share information with others (Tomasello et al., 2005). Children from early age provide others with information they need, even if doing so has no direct benefit for them (e.g., Bullinger, Zimmermann, Kaminski, & Tomasello, 2011; Liszkowski et al., 2008). Dogs have been shown to indicate the location of a target object by producing typical "showing-behaviors" like e.g., gaze alternation towards the target location (Miklósi, Polgárdi, Topál, & Csányi, 2000). These types of signals are produced with persistence, which means that dogs will only stop producing them once they have acquired the target (Gaunet, 2010). This shows that these signals are communicative and referential signals produced in order to indicate the location to the human. However, Kaminski, Neumann, Bräuer, Call, and Tomasello (2011) show that dogs produce these signals mainly when the target was interesting

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and relevant to them but not when the target was only interesting for the human. In this paradigm the human was in the room with a dog and interacted with a target object in one of four possible ways. Either dog and human were both interested in the object and interacted with it jointly, or the dog was interested in the object but the human ignored it completely, or it was an object the human was interested in and needed it for a certain activity (e.g., scissors for cutting a piece of paper) or neither the dog nor the human were interested in the object. After a certain amount of time elapsed, the human left the room and a second person entered and hid the target object in one of four possible locations, witnessed by the dog. Upon the first person's return, the dog now indicated the location by producing showing-behavior but only in those conditions in which it had an interest in the object. If the object was relevant to the human (e.g., the scissors), the dogs as a group indicated very little, showing that dogs may either lack the motivation to be helpful in this situations or simply, as described above, lack the cognitive prerequisites necessary to understand the human's lack of knowledge and need for information.

To understand communicative signals as informative, an individual should also utilize any gesture meant as helpful and informative, regardless of the intended recipient of that cue. Children at 14 months have been shown to use gestures given to a third party. Thus, they were able to utilize the information conveyed by a signal via "eavesdropping," paying attention to the informative value of the cue even though it was not directed at them (Gräfenhain, Behne, Carpenter, & Tomasello, 2009). Kaminski et al. (2012) confronted dogs with a situation during which the experimenter was sitting opposite the dog with another person seated next to her. Then the experimenter indicated the location of the food by either looking at the dog directly while doing so or by looking at the person next to her. Dogs were found not to use the gestures when making their choice if they were not directed at them but at the third person (Kaminski et al., 2012; see also Virányi et al., 2004). A simple association with the human's eyes alone may not explain the results, as dogs readily followed communicative gestures when her back was turned to them (Kaminski et al., 2012). Also, it is not that dogs seem to learn to ignore communicative gestures not directed at them over time, as puppies show the same strategy and there does not seem to be major age effects (Kaminski et al., 2012). Dogs' behavior therefore suggests that the informational value of the gesture is not as valuable for dogs as it is for children. If dogs attend to the informational value of the gesture we would expect them to follow the gesture no matter whom it is directed at, as the informational value of the gesture never changes. Dogs' behavior therefore suggests that a fundamentally different mechanism may underlie their understanding of communicative gestures. Rather than interpreting human given gestures as carrying information, which the human is intending to share, dogs may instead interpret human gestures as imperative directives ordering them where to go (Kaminski et al., 2012; Topál, Gergely, Erdőhegyi, Csibra, & Miklósi, 2009; Wobber & Kaminski, 2011). Evidence supporting this hypothesis comes from several additional facts. Different studies have shown that dogs prefer following a human's gesture even if it is against their better knowledge that the food is in fact in a different location (Scheider, Kaminski, Call, & Tomasello, 2012; Szetei, Miklósi, Topál, & Csányi, 2003). Szetei et al. (2003) found that dogs follow an experimenter's pointing gesture to the incorrect location in 79% of the cases, although they could sniff both containers before their choice and therefore know where the food was hidden. Also, Elgier, Jakovcevic, Mustaca, and Bentosela (2009) found that dogs were more likely to follow certain cues from their owner than from a stranger, suggesting that the owner's increased authority may cause dogs to interpret these signals as stronger imperatives. Taken together these results therefore argue against generally more sophisticated social cognition in dogs but seem to point in the direction of a very specialized set of skills rather restricted to receiving human given directives.

The adaptation-hypothesis states that humans have actively selected dogs for their ability to use human communicative signals. This hypothesis states that in this scenario humans have specifically selected dogs for certain purposes (e.g., hunting and herding). For all of these activities dogs had to be good in reading human given communicative signals over a certain distance. It is conceivable that humans used familiar teaching and communicative patterns to instruct dogs during these activities and then selected dogs for their ability to follow these patterns.

While humans understand other individuals' communicative intent based on some understanding of them as mental agents (Tomasello, 2001; Tomasello & Kruger, 1992; Tomasello et al., 2005), evidence to date suggests that dogs' interpretation of referential behaviors is based on a fairly restricted set of cues (Kaminski et al., 2012; Wobber & Kaminski, 2011). In their model for knowledge transfer in humans, Csibra and Gergely (2006) propose a set of skills they summarize as the pedagogical stance. They propose an innate sensitivity to so-called ostensive cues (e.g., eye contact, tone of voice etc), which function to signal relevance in a learning situation. This sensitivity is accompanied by an innate understanding of indexical reference. This understanding of reference is thought to be object related (Gergely, Egyed, & Király, 2007), therefore not mentalistic, and to be the precursor for symbolic and iconic reference. This theoretical framework may very well apply to dogs, as specific ostensive cues seem to be important during dogs' use of human gestures. If dogs were selected for their ability to follow instructional patterns, telling them what to do and where to go, we could speculate that maybe dogs were selected for some kind of "instructional stance" (Tempelmann, personal communication), which included following communicative gestures as 'orders' to move in a certain direction.

In this context, it is also interesting that while dogs do not seem to stand out compared to other animals in how they understand others psychological states, they do seem to stand out in how sensitive they are to others' eyes and eye contact in general (Call et al., 2003; Miklósi et al., 2003). While different mammalian species (though the list of species tested is unfortunately far from extensive) do not seem to attend to the status of the eyes specifically when making the decision if others are or are not attentive (e.g., Kaminski, Call, & Tomasello, 2004; Tomasello, Hare, Lehmann, & Call, 2007), dogs seem to attend to the eyes specifically (e.g., Call et al., 2003; Gácsi et al., 2004; Miklósi et al., 2003; Schwab & Huber, 2006).

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A non-mentalistic model like the 'instructional stance' would be sufficient to explain dogs' skills with human communication and enough for guiding dogs' movements within space, which is why it is most likely that this is what dogs had been specifically selected for (Wobber & Kaminski, 2011).

Conclusion

Dogs' ability to use human-given gestures is remarkable and outstanding compared to other animal species. Evidence further suggests that selection processes during domestication had an influence in shaping dogs' abilities in this domain. There are two main hypotheses about the possible ways this may have happened. The by-product hypothesis states that dogs' selection on one trait, e.g., tameness, paved the way for further evolution of outstanding social cognitive skills, one of which is dogs' ability to read human-given communicative cues. The alternative hypothesis, the adaptation hypothesis, states that humans actively selected dogs for their ability to use human communicative signals. We argue that one way to address this question is to study the mechanism underlying dogs' understanding of human gestures and other aspects of dog social cognition. If dogs' ability to use human gesture is part of generally outstanding social cognitive skills as a by-product of dogs' selection for tameness, we would expect dogs to show outstanding skills in other social cognitive domains. Evidence to date, however, suggests that this is not the case. Rather, dogs' ability to use human gestures and other forms of communication outstandingly well seems to be a specialized set of skills rather restricted to receiving human-given directives, which would therefore rather support the so-called adaptation hypothesis. It is conceivable that dogs, during the course of domestication, were selected for a special set of skills, especially a high sensitivity to humans' ostensive cues like eye contact, communicative gestures etc. A non-mentalistic model similar to the one proposed for humans by Csibra and Gergely (2006) would be sufficient to explain dogs skills with human communication and enough for guiding dogs' movements within space, which was what was needed to use dogs during certain activities like hunting and herding.

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