



ARTICLES

Wolves outperform dogs in following human social cues

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(Received 6 June 2008; initial acceptance 23 July 2008;
final acceptance 24 July 2008; published online 21 September 2008; MS. number: A08-00385)

Domestic dogs, *Canis familiaris*, have been shown capable of finding hidden food by following pointing gestures made with different parts of the human body. However, previous studies have reported that hand-reared wolves, *C. lupus*, fail to locate hidden food in response to similar points in the absence of extensive training. The failure of wolves to perform this task has led to the proposal that the ability to understand others' intentions is a derived character in dogs, not present in the ancestral population (wolves). Here we show that wolves, given the right rearing environment and daily interaction with humans, can use momentary distal human pointing cues to find food without training, whereas dogs tested outdoors and dogs at an animal shelter do not follow the same human points. In line with past studies, pet dogs tested indoors were successful in following these points. We also show that the reported failure of wolves in some past studies may be due to differences in the testing environment. Our findings indicate that domestication is not a prerequisite for human-like social cognition in canids, and show the need for additional research on the role of rearing conditions and environmental factors in the development of higher-level cognitive abilities.

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Keywords: *Canis familiaris*; *Canis lupus*; dog; dog shelter; domestication; momentary distal point; object choice; social cognition; wolf

'Man's best friend' is also his most attentive witness. Domestic dogs, *Canis familiaris*, have been shown to find hidden food by following pointing gestures made with different parts of the human body (Miklósi et al. 1998), to beg for food preferentially from people who are able to see them (Gacsi et al. 2004) and are less likely to take forbidden food when an attending human is present than when the human is absent or looking away (Call et al. 2003). This has led researchers to propose that dogs possess a 'theory of mind' or an ability to understand the perspective of others (Hare & Tomasello 2005).

In recent years, studies investigating the use of human cues have also been conducted with the domestic dog's closest relative, the wolf, *Canis lupus*. Although earlier studies suggested that wolves could not follow even simple cues such as tapping or proximal pointing (pointing in which the human's hand is less than 50 cm from the baited object) to identify a target containing hidden food (Hare et al. 2002), later research indicated that highly

socialized hand-reared wolves could find food under easier conditions, such as when a container indicating the correct location was touched by a human. Two of four wolves also successfully used proximal pointing to solve the task (Miklósi et al. 2003). However, none of the wolves in this study were initially successful on a more difficult momentary distal point cue (where the human extremity is no closer than 50 cm from the target container): after hundreds of trials, only one wolf could perform significantly above chance (Miklósi et al. 2003).

A more recent study compared the ability of domestic dogs and socialized wolves as young as 4 months to follow points (Virányi et al. 2008). Similarly to the earlier reports, this study found that the dogs outperformed wolf pups in following a human momentary distal point. After months of training and many hundreds of trials of point-following, the wolves only attained the performance level of naïve dogs (Virányi et al. 2008).

The relative performance of dogs and wolves on point-following and other putative 'theory of mind' tasks has suggested to several authors that artificial selection during domestication may have led to human-like social cognitive skills in pet dogs. According to this domestication

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hypothesis, domestication would be a requirement for untrained sensitivity to human cues (Hare et al. 2002; Miklósi et al. 2003; Kubinyi et al. 2007; Virányi et al. 2008).

The presence of behavioural variation in the ability of pet dogs to follow points, even when the dogs are from the same litter (e.g. Virányi et al. 2008), suggests, however, that genetic endowment cannot be the sole source of behavioural variation on these tasks. Differences in the testing conditions used with pet dogs and socialized wolves are also relevant to the appropriate interpretation of the differential performance of these two species. In all cases, wolves have been tested outdoors (Hare et al. 2002; Miklósi et al. 2003; Virányi et al. 2008), whereas domestic dogs in these studies were tested indoors in an isolated room. In at least one case, wolves were tested from outside a fenced enclosure, creating a barrier between the experimenter and the wolf, where no such barrier existed for the domestic dogs tested indoors (Hare et al. 2002).

In the present study, we tested whether domestication is necessary for success in the use of human cues by canids and whether dogs and wolves may fail on these tasks for reasons other than their genetic predispositions.

EXPERIMENT 1: FOLLOWING A MOMENTARY DISTAL POINT

Methods

Subjects

We tested five groups of eight adult canids each (Table 1). All pet domestic dogs were living in human homes as pets at the time of testing and were volunteered by their owners for participation in the study. Shelter dogs tested had been identified as strays (as opposed to pet surrenders or rescues), and were currently living in an animal shelter in individual indoor/outdoor runs. These dogs were selected for their readiness to approach the experimenters and accept food from them. All wolves in the study were from Wolf Park, Battle Ground, IN, U.S.A., and had been hand-reared by staff from 10–14 days of age. All wolves in this study were reared under the process described in Klinghammer & Goodmann (1987). At the time of testing, the wolves lived in large outdoor enclosures on the premises. Tristan, Kailani, Wotan, Renki, Ruedi were all living

Table 1. Name, sex, age, breed, group, testing location and relationship to experimenter for all subjects in experiment 1

| Name | Sex | Age (years) | Breed | Group | Testing location | Experimenter type |
|----------|-----|-------------|---------------------------|-------------|------------------|-------------------|
| Micki | F | 7 | Australian Shepherd | Pet dog | Outside | Unfamiliar |
| Taz | M | 15 | Mix | Pet dog | Outside | Unfamiliar |
| Kiera | F | 2 | Siberian Husky mix | Pet dog | Outside | Unfamiliar |
| Kodah | M | 3.5 | Boxer mix | Pet dog | Outside | Unfamiliar |
| Chloe | F | 3 | Boxer | Pet dog | Outside | Unfamiliar |
| Sasha | F | 9 | Chow Chow | Pet dog | Outside | Unfamiliar |
| Yuki | F | 0.5 | German Shepherd | Pet dog | Outside | Unfamiliar |
| Izzy | F | 4 | Boxer | Pet dog | Outside | Unfamiliar |
| Draco | M | 1.5 | Saluki | Pet dog | Outside | Familiar |
| Jack | M | 1.5 | Labrador Retriever mix | Pet dog | Outside | Familiar |
| Kahlua | F | 1.5 | Labrador Retriever | Pet dog | Outside | Familiar |
| Lena | F | 0.8 | Mix | Pet dog | Outside | Familiar |
| Ronin | M | 0.8 | Chihuahua/Pinscher mix | Pet dog | Outside | Familiar |
| Pearl | F | 0.7 | Collie mix | Pet dog | Outside | Familiar |
| Emma Lou | F | 1.5 | Australian Shepherd | Pet dog | Outside | Familiar |
| Nailah | F | 2 | Australian Shepherd | Pet dog | Outside | Familiar |
| Zoe | F | 4 | Australian Cattle Dog mix | Pet dog | Inside | Unfamiliar |
| Kaylee | F | 6 | Labrador Retriever mix | Pet dog | Inside | Unfamiliar |
| Gibson | M | 6 | Boxer | Pet dog | Inside | Unfamiliar |
| Paploo | M | 2 | Dachshund | Pet dog | Inside | Unfamiliar |
| Chewy | M | 1.3 | Dachshund | Pet dog | Inside | Unfamiliar |
| Skyler | M | 1 | Italian Greyhound | Pet dog | Inside | Unfamiliar |
| Raven | F | 0.5 | Pit Bull Terrier | Pet dog | Inside | Unfamiliar |
| Reesy | F | 2 | Dachshund | Pet dog | Inside | Unfamiliar |
| No. 11 | M | 0.75 | Chow Chow mix | Shelter dog | Inside | Unfamiliar |
| No. 60 | F | 1 | Bulldog | Shelter dog | Inside | Unfamiliar |
| No. 7 | F | 0.5 | Pit Bull Terrier mix | Shelter dog | Inside | Unfamiliar |
| No. 14 | F | Unknown | Beagle mix | Shelter dog | Inside | Unfamiliar |
| No. 15 | F | 3.5 | Akita mix | Shelter dog | Inside | Unfamiliar |
| No. 18 | M | 2 | Labrador Retriever | Shelter dog | Inside | Unfamiliar |
| No. 20 | F | 0.5 | Weimaraner | Shelter dog | Inside | Unfamiliar |
| No. 25 | F | 1 | Pit Bull Terrier mix | Shelter dog | Inside | Unfamiliar |
| Tristan | M | 9 | NA | Wolf | Outside | Familiar |
| Kailani | F | 3 | NA | Wolf | Outside | Familiar |
| Wotan | M | 2 | NA | Wolf | Outside | Familiar |
| Ayla | F | 3 | NA | Wolf | Outside | Familiar |
| Renki | M | 3 | NA | Wolf | Outside | Familiar |
| Ruedi | M | 3 | NA | Wolf | Outside | Familiar |
| Miska | M | 11 | NA | Wolf | Outside | Familiar |
| Marion | F | 9 | NA | Wolf | Outside | Familiar |

together as part of the main pack. Ayla, who was a previous member of the main pack was being housed alone in a separate enclosure at the time of testing. Miska and Marion were housed together in a third enclosure. All wolves interacted with humans daily and regularly received food treats directly from humans. As such they were thoroughly habituated to the presence of humans and would readily eat from human hands.

Human-reared wolves were individually tested by a familiar experimenter in an outdoor arena where fences and vegetation separated the animal under test from conspecifics. Auditory, olfactory and some visual contact with the other wolves was maintained. A group of pet dogs of varying breeds was tested under conditions as close to those of the wolves as possible (outdoors, physical isolation, auditory, olfactory and some visual contact with conspecifics, familiar experimenter); eight more pet dogs were tested under identical conditions except the experimenter was unfamiliar. Another eight pet dogs were tested in their homes. Finally, eight domestic dogs from a county dog pound, shelter dogs, were tested indoors under similar conditions. Only dogs and wolves that would approach the experimenter and eat from her hand before testing were used.

Materials

Two metal unmarked paint cans (15 cm diameter, 22 cm tall), filled with gravel and with lids tightly fastened, served as the response choice objects. No food was present in or on the containers until and unless the subject indicated a choice of the correct can by touching or coming within 10 cm of it with its snout. This method was adopted because preliminary studies with wolves indicated that they could detect even small pieces of prehidden food in a container by smell alone. When a correct choice was made, the experimenter clicked a standard dog-training clicker and dropped a piece of food on the lid of the chosen container. Clickers were used for all individuals, dogs and wolves, to mark a correct choice and to bridge any delay between a correct choice and the presentation of a reinforcer. Clicks were always followed by the earned food reward, maintaining the association between the primary and secondary reinforcer. Incorrect choices had no direct consequences and the subject was called back to the starting position to begin the next trial.

We determined the correct container pseudorandomly before sessions began with the constraints that no one location was designated correct more than twice in a row and each location was correct for 50% of the trials. Food rewards included 2 cm cubes of Spam Hormel Foods, LLC, Austin, MN, U.S.A., Bil-Jac Liver Treats Kelly Foods Corporation, Berlin, MD, U.S.A., and Pet Botanics dog food rolls Cardinal Laboratories Inc., Azusa, CA, U.S.A.

Pretraining

The animal was separated from conspecifics and brought into the testing area. It was then called by the assistant who stood at a distance of 2.5 m from the mid-line between the cups. The assistant distracted the subject with treats or social reinforcement until the experimenter

was ready to proceed. The experimenter then called the subject, waited until it oriented towards her, and held up a piece of food in the subject's view and placed it on top of one of the containers. The subject was allowed to eat the food from the container, and the experimenter then placed another piece of food on top of the other container. Each approach to a container was also marked by a standard animal-training clicker. This continued until the subject was no longer showing signs of neophobia to the apparatus and was reliably eating off the containers. A minimum of four trials was completed. In no case did pretraining last longer than 10 min or eight trials.

Testing

During experimental trials the experimenter stood between two empty paint cans on the ground and pointed to one of them for 4 s when the animal was approximately 2.5 m away (Fig. 1). The point was given from a standing position with the can at least 0.5 m from the experimenter's finger, qualifying as a momentary distal point. The experimenter returned to a neutral position before the subject reached the containers. When a subject indicated a correct choice, the experimenter clicked and then dropped a piece of food on the chosen container. For an incorrect choice the experimenter remained in a neutral position and no food was presented. The assistant then called the subject back to the starting location. Ten experimental trials were presented to each subject. If any individual made three incorrect responses in a row, two pretraining trials were given (one to each side) to ensure that the subject was still motivated to obtain the food if it saw the placement of the food directly. No individual ever failed a test of motivation.

Control

Every two experimental trials were followed by a control trial. On control trials, a to-be-rewarded container was still determined, but the experimenter remained in a neutral position throughout the subject's approach and indication of choice. A click and a piece of food still followed a choice of the container nominated as correct (Fig. 2).

Statistical analysis

A one-way ANOVA was used to determine whether there was a significant difference between the performances of

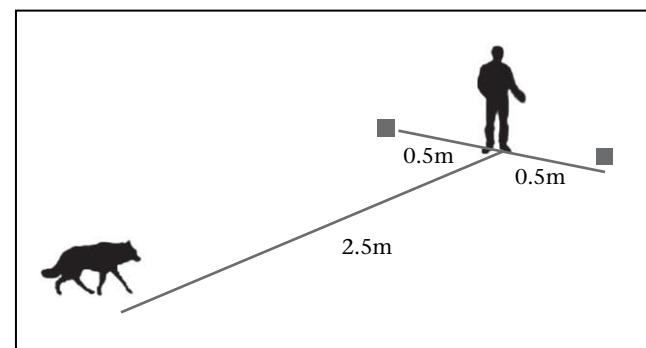


Figure 1. Sketch of testing layout.



Figure 2. Images of the testing procedure: (a) control trials; (b) experimental trials; (c) rewarding a correct choice.

the five groups of canids. A homogeneity of variances test was used to test the key assumption of the ANOVA and there were no grounds to reject its use ($P = 0.60$). Bonferroni tests were used to determine whether significant differences in average performance existed between groups. One sample t tests were used to determine whether each group of canids performed significantly above chance. An alpha level of 0.05 was adopted for all statistical tests. Performance of individual subjects was assessed with a binomial test. Scores of eight or more correct choices out of 10 trials were considered mastery of the task by an individual animal ($P = 0.05$).

Results

Five groups of canids were tested on an object choice paradigm requiring the use of a human momentary distal

point with the experimenter's hand more than 50 cm from the target bucket when extended. These groups were (1) wolves tested outside by a familiar experimenter; (2) pet dogs tested outside by a familiar experimenter; (3) pet dogs tested outside by an unfamiliar experimenter; (4) pet dogs tested inside by an unfamiliar experimenter and (5) shelter dogs tested inside by an unfamiliar experimenter. The performance levels of the five groups of canids differed significantly from each other ($F_{4,35} = 4.40$, $P = 0.006$). Wolves tested outdoors and pet dogs tested indoors were the only subjects that followed a momentary distal point at above chance levels (one sample t test: $t_7 = 2.69$, $P = 0.03$ and 4.12 , $P = 0.004$, respectively; Fig. 3). Average performance levels of these two groups were similar, but more individual wolves (six of eight subjects) followed the point on eight or more of 10 trials (binomial, test: $P = 0.05$) more often than did domestic dogs (three of eight subjects). Both groups of pet dogs tested outdoors did not successfully use the human pointing cue, but two individuals in each group followed the point at above chance levels (8 of 10 or better). None of the shelter dogs followed a point, and a Bonferroni test indicated that as a group, shelter dogs were significantly less successful at using a point than were wolves ($P = 0.012$) and dogs tested indoors ($P = 0.012$). No canid could identify the can to be rewarded on control trials, in which no point was made.

EXPERIMENT 2: PRESENCE OF A PARTIAL VISUAL BARRIER

In this experiment we investigated the effects on performance of a chain-link fence barrier between the subject and the experimenter on an object choice task. We chose simpler task than the momentary distal pointing of experiment 1, because in that experiment dogs were unable to follow the experimenter's point at above chance levels in an outdoor testing environment. Thus, in this

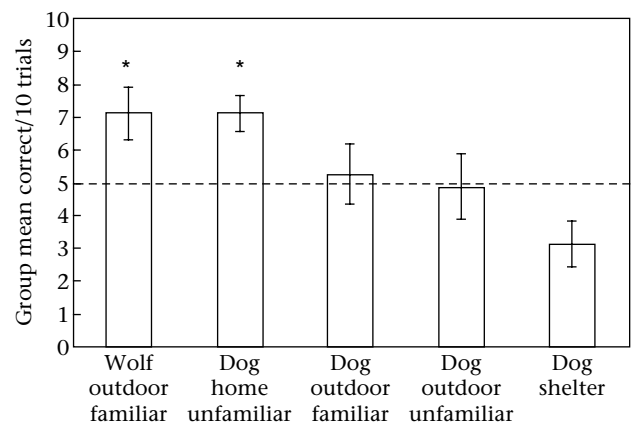


Figure 3. Performance of the wolves and dogs tested for their ability to follow a momentary distal point to receive a food reward. Bars show mean number of trials correct out of 10. Error bars show standard error. Dashed line shows chance level (5/10). *Indicates significant above-chance performance (single sample t test: $P < 0.05$).

experiment, the dogs were exposed to an experimenter tapping directly on the correct container.

Methods

Subjects

We randomly assigned 14 domestic pet dogs to one of two testing groups (Table 2). All dogs were living in human homes as pets at the time of testing and were volunteered by their owners for participation in the study. The Fence group was tested from outside a fenced outdoor enclosure so that a barrier was present between the experimenter and the dog being tested. The No-fence group was tested with the experimenter inside the same outdoor enclosure with no barriers present between the dog and experimenter during testing. The testing containers used for the object choice test were always located on the same side of the fence as the experimenter. However, dogs from both groups were physically able to bring their paw and snout within the required 10 cm of the containers as determined in pretesting, and therefore the requirements for indicating a choice remained the same as in experiment 1 for both groups. If the correct container was indicated, food was placed on top of the container for the dog to consume. In some cases dogs in the Fence group could not get the food off the container on their own because of the fence. When this occurred the experimenter promptly pushed the food from the container through the fence so the dog could consume it.

Materials and procedure

The materials and procedure were identical to those in experiment 1, except that instead of giving a momentary distal point to indicate the correct container, the experimenter tapped on the lid of the correct container with the index finger of her cross-lateral hand on experimental trials.

Statistical analysis

A two way *t* test was used to determine whether there was a significant difference between the performance of dogs in the Fence versus No-fence groups. Binomial tests were used to determine whether if an individual dog

Table 2. Name, sex, age, breed, and group for all subjects in experiment 2

| Name | Sex | Age (years) | Breed | Condition |
|--------|-----|-------------|------------------------|-----------|
| Arlo | M | 5 | Cattle Dog mix | No fence |
| Nicki | F | 1 | Shepherd mix | No fence |
| Luna | F | 3 | Sheltie | No fence |
| Pepsi | F | 1 | Italian Greyhound | No fence |
| Chase | M | 7.5 | Greyhound/Ridgeback | No fence |
| Maria | F | 4 | Border Collie | No fence |
| Audrey | F | 8 | Beagle mix | No fence |
| Zoe | F | 4 | Australian Cattle Dog | Fence |
| Lina | F | 1.5 | Shepherd mix | Fence |
| Nali | F | 0.75 | Fox Terrier | Fence |
| Mateo | M | 2 | Basset Hound | Fence |
| Pinki | F | 1 | Labrador Retriever mix | Fence |
| Baily | M | 4 | Boston Terrier | Fence |
| Bently | M | 2 | Dachshund | Fence |

performed significantly above chance on the object choice task. One sample *t* tests were used to determine whether either group of dogs performed better than would be expected by chance. An alpha level of 0.05 was adopted for all statistical tests.

Results

The mean performance of a group of dogs tested from within the fenced enclosure (i.e. with no barrier between them and the experimenter) was significantly better than the performance of the dogs tested with a chain-link fence separating them from the experimenter (two-tailed *t* test: $t_{12} = 2.18, P = 0.04$). All seven dogs tested from inside the enclosure (No fence) were able to use a human tapping cue to identify the target can at above chance levels (binomial test: $P = 0.05$). However, only three of the seven dogs tested from outside the fence were able to perform above chance using the same cue. As a group, the dogs tested without a fence were successful in using the cue more often than would be expected by chance (one sample *t* test: $t_6 = 25.62, P < 0.001$), whereas the group tested behind a fence barrier were not (one sample *t* test: $t_6 = 1.17, P = 0.28$).

DISCUSSION

Prior to this study, the domestic dog's sensitivity to humans has been attributed to human-like social cognitive abilities that evolved during domestication (Hare et al. 2002; Miklósi et al. 2003; Hare et al. 2005). It has been argued that dogs' wild progenitors, wolves, do not share this sensitivity (Hare et al. 2002; Miklósi et al. 2003; Virányi et al. 2008). Our results clearly show that wolves, given proper socialization and daily experience with humans, are not only capable of following a human cue, but in some cases outperform domestic dogs. Unlike the wolves studied by Miklósi et al. (2003) and Virányi et al. (2008), which were only mildly successful after hundreds of trials, the wolves in our study succeeded in using a momentary distal point with no prior exposure to the task and were presented with only a minimal number of trials during testing, suggesting that their performance is truly comparable to that of domestic dogs tested in this and previous studies. This finding shows that domestication alone cannot be responsible for an individual's untrained sensitivity to human cues. Virányi et al. (2008, page 375) stated: 'If we find dogs and wolves to be different even after comparable upbringing, then (and only then) their special characteristics can be attributed to genetic changes developed since the domestication of the dog began'. We not only show that wolves exposed to intensive human socialization and daily interaction perform as well as the best performing group of pet dogs; but that pet dogs reared in comparable conditions can perform differently from each other in different testing environments (indoors versus outdoors and fence versus no fence). Furthermore, domestic dogs with different life histories (pets versus shelter dogs) also show differences in performance on human-guided tasks when compared to other groups of domestic

dogs, showing that, for shelter dogs, domestication was not a predictor of sensitivity to human cues, despite the willingness of the dogs to interact with the experimenter.

It is unlikely that breed differences are responsible for the success of wolves tested here in comparison to those tested in (Hare et al. 2002) because the two facilities used exchange animals for breeding purposes. Of greater likely relevance is the fact that wolves in the study by Hare et al. (2002) and in the studies by Virányi et al. (2008) were tested under different conditions from their own domestic dog comparison groups and thus interfering or distracting aspects of the wolves' testing environment may not have been accounted for. For example, in Hare et al. (2002), wolves were tested outdoors and from outside a fenced enclosure, whereas the domestic dogs were tested indoors in a presumably quieter environment and with no barrier between the experimenter and subject.

In experiment 2, we found that domestic dogs tested from outside a fenced enclosure performed at significantly reduced levels compared with dogs tested without a fence barrier. In fact, the difference in performance between the two domestic dog groups in our study differs little from the difference in performance between the dogs and wolves tested in Hare et al. (2002). In our comparison of dogs tested with and without a fence barrier, the presence of a fence led to a decrement of 31% in performance. This is similar to the difference between dogs (no fence) and wolves (behind a fence) in Hare's (2002) study (35%), suggesting that the inferior performance of socialized wolves in past studies may have been influenced by the testing environment and other methodological inconsistencies between the testing groups.

These findings shed light on the origin of human-like social cognition and have implications for the understanding of the role of domestication in the behaviour and cognition of social animals. Although the shelter dogs in our study interacted with the experimenters without hesitation and readily ate food from our hands and off the testing cans, every dog in this group failed to follow a momentary distal point. This shows that domestication alone cannot account for canids' sensitivity to human social cues involved in following a point.

This is not say that domesticated dogs do not differ in important developmental milestones from nondomesticated wolves, or that these differences are unimportant in the ability of dogs and wolves to develop a responsiveness to human cues. Domestic dogs, for example, can begin socialization with humans as late as 16 weeks and still successfully accept humans as social companions, whereas wolves must begin socialization before 10–14 days to form a successful bond with humans (Coppinger & Coppinger 2001). Clearly, the relative ease with which a dog accepts humans as social companions is relevant to how readily a dog may come to follow a human gesture.

Several other domesticated animals have been found to be capable of following human points to uncover hidden food (Miklósi & Soproni 2006). Their success does not, however, provide strong support for the domestication hypothesis. These domesticated species also have high levels of proximity to humans. For example, they may be fed by humans or spend time with humans in other

activities on a daily basis. These experiences may be responsible for the ability to follow human hands to find food, rather than any genetic potentialities bred into the species during domestication. It is also possible that variation between domesticated species or even breeds may occur based on their predisposed tendencies for social behaviour in general. A strong test of the domestication hypothesis requires comparison of domesticated and non-domesticated species with controls for the life histories of tested individuals of each species.

Our study suggests that environment and development affect a social animal's ability to react in situation-appropriate ways to the social cues of other individuals. Instead of treating social cognition or 'theory of mind' as a unitary psychological faculty, present or absent in all members of a species at birth, we propose that animals genetically capable of responding to social cues will still differ in their ability to use specific forms of cue depending on their individual histories and environments during critical developmental periods. This view is compatible with theories of human social cognition that not only emphasize the physiological development of pre-existing species-specific traits, but also the effects of the environment and early experiences to which a child is exposed (Baldwin & Moses 1996; Hughes et al. 2005). One study looking specifically at individual differences in the theory of mind abilities of children found that the majority of individual differences were linked to nonshared environmental factors. Genetic differences only accounted for 7% of the variance in theory of mind (Hughes et al. 2005).

Canids are an excellent model for better understanding the phylogeny and ontogeny of complex social cognition. Many diverse niches already exist for domestic dogs, as do genetically distinct lines with stud books going back more than 100 generations. Pet dogs are also found in environments similar to those of human children, thus providing ample opportunity to explore the factors that influence the development of various aspects of social cognition.

Future studies should focus on developmental and environmental factors that lead to or hinder the development of human-like social cognition in canids. Such knowledge could provide information about aspects of the environment that affect our own social cognitive development and prove useful in assessing environments that are likely to stunt sensitivity to social cues across species.

Acknowledgments

We thank Patricia Goodmann, Holly Jaycox, Erich Klinghammer, Ken McCort, Gale Motter and Tom O'Dowd for their warm welcome and expert help at Wolf Park, Battle Ground, IN. We also thank Janet Hobson for letting us use the facilities at Dogwood Park, the staff and director of the Alachua County Animal Services for their cooperation and the many dog owners who made their animals available to us. This research adhered to the Association for the Study of Animal Behaviour/Animal Behavior Society Guidelines for the Use of Animals in Research, the legal requirements of the country in which the work was carried out and all institutional guidelines.

References

- Baldwin, D. A. & Moses, L. J. 1996. The ontogeny of social information gathering. *Child Development*, **67**, 1915–1939.
- Call, J., Brauer, J., Kaminski, J. & Tomasello, M. 2003. Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans. *Journal of Comparative Psychology*, **117**, 257–263.
- Coppinger, R. & Coppinger, L. 2001. *Dogs: A Startling New Understanding of Canine Origin, Behavior and Evolution*. New York: Scribner.
- Gacsi, M., Miklósi, A., Varga, O., Topal, J. & Csanyi, V. 2004. Are readers of our face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent recognition of human's attention. *Animal Cognition*, **7**, 144–153.
- Hare, B. & Tomasello, M. 2005. Human-like social skills in dogs? *Trends in Cognitive Science*, **9**, 439–444.
- Hare, B., Brown, M., Williamson, C. & Tomasello, M. 2002. The domestication of social cognition in dogs. *Science*, **298**, 1634–1636.
- Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R. & Trut, L. 2005. Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology*, **15**, 226–230.
- Hughes, C., Jaffee, S. R., Happé, F., Taylor, A., Caspi, A. & Moffitt, T. E. 2005. Origins of individual differences in theory of mind: from nature to nurture? *Child Development*, **76**, 356–370.
- Klinghammer, E. & Goodmann, P. A. 1987. Socialization and management of wolves in captivity. In: *Man and Wolf: Advances, Issues, and Problems in Captive Wolf Research* (Ed. by H. Frank), pp. 31–61. Dordrecht: W. Junk.
- Kubinyi, E., Virányi, Z. & Miklósi, A. 2007. Comparative social cognition: from wolf and dog to humans. *Comparative Cognition & Behavior Reviews*, **2**, 26–46.
- Miklósi, A. & Soporoni, K. 2006. A comparative analysis of animals' understanding of the human pointing gesture. *Animal Cognition*, **9**, 81–93.
- Miklósi, A., Polgárdi, R., Topal, J. & Csanyi, V. 1998. Use of experimenter-given cues in dogs. *Animal Cognition*, **1**, 113–121.
- Miklósi, A., Kubinyi, E., Topal, J., Gacsi, M., Virányi, Z. & Csanyi, V. 2003. A simple reason for a big difference: wolves do not look back at humans, but dogs do. *Current Biology*, **13**, 763–766.
- Virányi, Z., Gacsi, M., Kubinyi, E., Topal, J., Belenyi, B., Ujfalussy, D. & Miklósi, A. 2008. Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Animal Cognition*, **11**, 373–387.