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Applied Animal Behaviour Science 83 (2003) 141–152

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# When dogs seem to lose their nose: an investigation on the use of visual and olfactory cues in communicative context between dog and owner

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Accepted 8 April 2003

## Abstract

In two experimental studies, we observed whether dogs rely on olfactory and/or visual information about the hiding place for food in a two-choice test. However, for some dogs direct olfactory (smelling the food) or visual (observing of the food being hidden) experience has been contradicted by human pointing (a well-known communicative gesture for the dog) to the ‘incorrect’ hiding place. We have found that dogs were able to use both olfactory and visual cues efficiently to choose above chance in a choice situation when there was no human cueing. However, in other experimental groups the dogs tended to choose the bowl pointed at by the human. This change in their behavior was more pronounced if they had only olfactory information about the location of the food. In contrast, if they had seen where the food was placed, dogs were more reluctant to follow the pointing gesture, but even so their performance worsened compared to the case in which they saw only the bowl baited.

These results give further support for the hypothesis that dogs regard the pointing gesture as being a communicative act about the placing of the food, but they do not rely on this gesture blindly and they can modify their behavior based on visual experience related directly to the hiding of the food. Further, contrary to general expectations dogs rely in this situation, only to some degree on olfactory cues.

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*Keywords:* Gestural communication; Dogs; Olfaction; Human–dog interaction; Learning; Food location

## 1. Introduction

It is well known that particular behavioral actions in any given species are bound to specific sensory inputs from the environment. In other words, although most animals are equipped with many basic sensory mechanisms (vision, hearing, olfaction, etc.) they rely

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usually only on one subset of sensory information depending on the particular behavioral context. For example, when looking for prey wolves, search for and follow odor trails that might indicate the direction of movement of their prey but upon seeing them, wolves 'switch to a visual mode' for executing attack and capture (Mech, 1970).

Being a descendant of the wolf, dogs are well known for their olfactory acuity. Historically, many breeds of dogs have been specially selected and maintained to assist humans during hunting in finding wounded prey or chasing out animals hidden under cover, etc. Rescue dogs searching for missing humans or humans trapped under ruins make a valuable contribution to human society. Not surprisingly there is a high awareness among researchers and laymen alike about the well-developed olfactory abilities of dogs.

The dog's superior sense of smell is also reflected in the large number of olfactory neurons in the olfactory epithelium that have been estimated between 220 million (Dröscher, 1967, cited in Schoon, 1997) and 2 billion (Moulton, 1977) in comparison to 2–5 million olfactory neurons in humans. Since some correlation has been found between receptor density and sensitivity to odorous (Apfelbach et al., 1991) anatomical observations also support extended olfactory function in dogs. Behavioral studies provided further evidence. In experiments focusing on detection of odorous (present or absent) it was found that dogs are generally 100 or 1000 times better at noticing the presence of an odor compared to humans. Given appropriate training experience dogs perform just as well in both discrimination learning and match to sample experiments with various odorous as stimuli (see Schoon, 1997 for a review).

The dog's sensitivity for odorous is also used for human scent identification as a forensic tool because there is still no technical device, which performs with comparable sensitivity (Brisbin and Austad, 1991, Settle et al., 1994, Sommerville et al., 1993). In spite of many experiments conducted so far it is still not clear to what extent dogs are able to discriminate human scent samples, for example whether they are able to detect the similarity of odorous originating from various parts of the human body. To overcome disagreements in the literature Schoon (1996, 1997) suggested, and has shown experimentally that the training experience of the dogs is crucial in this case. The dog has to be trained according to the task it has to perform later at work.

We should however make an often-overlooked distinction here. There is a major difference between having a particular ability (genetic or acquired) and using this ability in life, or more particularly in a given context. In the natural situation, one can suppose that wolves are continuously forced to use (and by this to 'train') their olfactory senses since this is the most important means for finding food. This contrasts strongly with the case of the domestic dog that is usually provided with food and lives in a very stable environment, and therefore despite having the potential ability of perceiving and discriminating odorous, dogs rarely experience situations where matching or discrimination of odorous is essential. It is not accidental that only highly trained dogs are able to perform odor discrimination work at levels required for hunting, or various forms of policing.

Therefore, we should be aware that the ability of dogs (or other animals) to sense small amounts of chemical cues does not allow one to arrive at the conclusion (as is often done in popular texts) that dogs always and continuously rely on olfactory cues. It is more likely that, although dogs are able to use odorous as sensory input, at the same time (in parallel or instead of other cues) they also attend to acoustic and visual cues.

Recently several studies reported that dogs show an outstanding performance in responding to human gestural (visual) cues (Hare and Tomasello, 1999; Miklósi et al., 1998, 2000; Soproni et al., 2001, 2002). Although in these experiments researchers controlled for the presence of olfactory cues, the high level of correct responding in dogs lead some to suspect that odorous might also contribute to the dogs' success. In these experiments, an experimenter was standing between two small bowls and was pointing towards the one that hid some food. Then dogs were allowed to make their choice. In reality, both bowls contained some food that was hidden inside the bowl inaccessible for the dogs. Still one might argue that there was a difference in the scent gradient emerging from these bowls that might have guided the choice behavior of the dog.

Even if these criticisms do not apply to the set up used by others, and us there is a broader implication of these questions. As suggested earlier dogs can use various types of sensory input in this basically communicative situation. So one might ask what is the relative contribution of these different types of cues to the choice behavior of dogs. We can discriminate two types of information. The first type is directly related to the food (or objects), since olfactory or visual information, that is smelling or seeing food/objects, is a direct indication of their presence. Additionally, objects that have been seen to disappear at a particular location are not forgotten, as shown by many experiments on 'object permanence' (i.e. Gagnon and Dore, 1993), suggesting that dogs can remember the object even if they cannot perceive it directly any longer (see Doré and Goulet, 1998 for a review). Many assume (e.g. Gibson, 1990) that cooperative hunting (at least in chimpanzees, *Pan troglodytes*) is a determining factor in the evolution of sophisticated representational capacities of absent objects. However, a similar argument can be also made for the Canid species.

The second type of sensory information is confined to the visual mode (in the present situation) and is of a communicative nature bearing no direct relationship to the actual location of the hidden object. It has been shown that dogs can use human pointing gestures very flexibly to find the location of hidden food (Soproni et al., 2001, 2002). The main question of the present set of experiments is to find out about the relative importance of divergent types of information on the choice behavior of dogs. In both studies, dogs are provided with different types of cues or combinations in different experimental groups and we observed what kind of cues they regard as most appropriate for guiding their behavior in choosing between two possible food locations.

## 2. Study 1

With the evidence that dogs respond reliably to human pointing gestures we designed experimental groups to study the competing role of human gestural (communicative) cues versus physical (object-related) cues (visual and/or olfactory) for the dog in a two way food choice task (Fig. 1).

Two groups were designed to look for the effect of the odor cues only (food is present in only one of the bowls) either in the presence (Group 1) or absence (Group 2) of the experimenter. In Group 3, dogs received contradictory visual and olfactory cues about the location of the food (without human gesturing). In this case, the food seemingly was hidden in one of the bowls but the bait had been placed in the other one earlier.

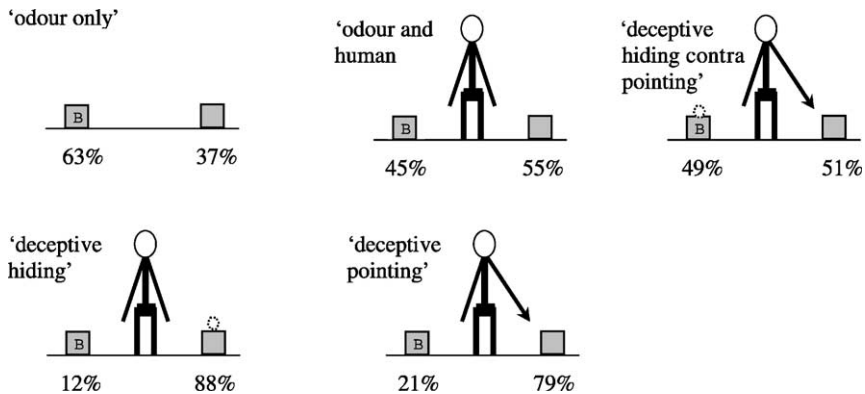


Fig. 1. Schematic illustration of the situation dogs were facing in different experimental groups in Study 1 (for details see also Sections 2 and 3). 'B' indicates the position of the baited bowl that was systematically changed within a dog, and between dogs. The percentages below the boxes ('bowls') indicate the mean distribution of choices of dogs (for details see also Fig. 2). The dogs never saw the baiting but in the 'Deceptive hiding' and 'Deceptive hiding contra pointing' conditions they were presented with a same-baiting action (indicated by the dotted circle).

Two additional groups of dogs could witness human pointing gesture before they made their choice, in both cases however, the pointing was an unreliable indicator of the hiding place (experimenter pointed always to the empty bowl). In one group (4), dogs witnessed human pointing gestures toward one bowl (the other containing the bait), in the other group (5) dogs saw food being hidden but the pointing that followed indicated the opposite container.

By comparing the performance of dogs in these various groups, we wanted to assess their preference in attending to different cues (communicative and versus object-related).

## 2.1. Method

### 2.1.1. Subjects

All together 55 adult dogs of various breeds (10 or 15 per experimental groups) participated in this study. Dogs and their owners (female/male: 38/17) were recruited on voluntary basis in dog camps and at dog training schools (for list of breeds in the experimental groups see Appendix A).

### 2.1.2. Procedure

The observations were carried out during the summer 2000 in partially closed enclosures (approximately 10 m<sup>2</sup> area that were enclosed by stone or concrete walls but had no roof) at a dog summer camp (Debrecen, Hungary) and at two further dog training schools near Budapest (Hungary). Only the experimenter, the owner, and the dog were present during the training and testing trials. Two identical bowls (brown plastic flower pots: 15 cm in diameter, 15 cm in height) were used to hide the bait. One bowl was always clean, and washed in hot water before each experiment (clean bowl), and only the other was used for

the baiting (baited bowl). Special care was taken that the baited bowl was picked up with one and the empty bowl by the other hand of the experimenter to prevent any food odor trace being transferred onto the empty bowl. We used odiferous (to the human nose) processed meat such as Hungarian salami or sausage as food rewards. For all trials, forceps were used to place food in the baited bowl.

*2.1.2.1. Pre-training.* The pre-training was necessary to make the dog familiar with the future testing situation in which the bowls would contain food. The experimenter (V.S.) placed the two bowls on either side of her position (one to the left and one to the right, approximately at a distance of 70 cm from her body), and tried to get the attention of the dog standing at a distance of 3 m (this topographical layout was applied in all subsequent experimental trials). When she achieved this, she showed the dog a food pellet and placed it into the baited bowl. Then the owner allowed the dog to approach the bowls and choose one of them. If the dog chose the baited bowl, it could eat the reward, and was also praised verbally by the owner. If the dog made an incorrect choice, the experimenter took the pellet from the other bowl and showed it to the dog. In this case, the dog did not get the food. This trial was repeated two times for both the left and the right side.

*2.1.2.2. Testing.* For each group, 10 testing trials were run by placing the baited bowl in a fixed and balanced order at equal number of trials to the left and the right, and to avoid the development of side preference, the bait was not placed for more than twice on the same side in two subsequent trials. Dogs were randomly assigned to one of the following experimental groups.

*Group 1: Odor only* ( $N = 15$ ). The dog was prevented from observing the baiting by the owners' covering its eyes and turning it away. The experimenter took both bowls, put a piece of meat in the baited bowl (by using forceps), and placed them back simultaneously on the ground. After the baiting, the experimenter went behind the dog, so the dog could not see a human standing between the bowls when he was making his choice. Then the dog was released (owners could say 'Go! It is yours!' (or something similar), but in most cases it was enough to release the leash of the dog), and it could choose freely between the two containers. Owners were instructed not to use any gestures or directional verbal commands. Owners (and their dog) that contradicted our instructions were excluded from the experiment. For this experiment, only the bowls were also covered with a lid to prevent visualization of the hidden food when the dog approached one. In this situation, a choice was noted if the dog touched the lid of the bowl with the intent to remove it.

*Group 2: Odor and human present* ( $N = 10$ ). Dogs in this group were tested in a similar way as described for the Group 1. In this case, however, when the dog faced the two bowls the experimenter stood motionless between them.

*Group 3: Deceptive hiding* ( $N = 10$ ). The actions by the experimenter and the owner followed the same sequence as described above but now the dog could witness the baiting of the empty bowl after the experimenter placed the two bowls on the ground. Importantly however, as the experimenter showed the hiding process as clearly as possible, she removed the bait (hiding it in the hollow of her hand) before removing her hand from the empty bowl. An effort was made to prevent the food odor remaining in the empty bowl. This was achieved by putting on disposable plastic gloves on the hand hiding (sham baiting) the food.

Note that as in the case of the control groups, unknown to the dog food had been hidden in the baited container. So from the point of view of the dog, the bait was seen to be placed into the ‘empty’ bowl, but actually food was present in the baited bowl when it made the choice. Importantly, the experimenter stood motionless between the containers without pointing by folding her arms and hands at the mid-line of her back.

*Group 4: Deceptive pointing* ( $N = 10$ ). In general, the experimenter and the owner acted as described in the Group 1 but in this case the experimenter also pointed to the empty bowl before the dog was released. Here again, the baited bowl contained the hidden food. Before the pointing gesture, the experimenter made eye contact with the dog to get its attention, and she continued to look at the dog during pointing. The experimenter pointed briefly toward the baited bowl with extended arm and index finger and then lowered her arm back to the downward position beside her body. As soon as the experimenter resumed her resting position the dog was released. It was allowed to eat the food only if it approached the correct bowl.

*Group 5: Deceptive pointing contra hiding* ( $N = 10$ ). Dogs in this group were exposed to the combination of manipulations observed by other dogs in Groups 3 and 4. First, they could observe the hiding of the bait (but now the food was left in the baited bowl), the experimenter pointed to the other (empty) bowl.

*2.1.2.3. Data analysis.* Only the first choice of the dog was taken into account, that is, the bowl he touched first or approached to within few centimeters. Choices of the baited bowl were taken as being ‘correct’ and were analyzed statistically and are displayed on the figures. The difference of choice behavior was compared using non-parametric Kruskal–Wallis ANOVA, and between-group differences were analyzed by post-hoc Dunn’s test ( $P < 0.05$ ). The bias from the expected random choice (5 in 10 trials) was calculated for each individual group by the means of one-sample Wilcoxon signed-rank tests.

*2.1.2.4. Results and discussion.* In most cases, dogs displayed a clear choice approaching one of the bowls in a straight line without the obvious signs that they were attending the potential olfactory cues by sniffing. We have found a significant difference among the different experimental groups ( $H = 27.913$ , d.f. = 4,  $P < 0.01$ ). Dogs seem to be able to find the location of the food if the experimenter was not present (‘Odor only’) group ( $N = 15$ ,  $T = 20$ ,  $P = 0.04$ ) although their performance was relatively poor (Fig. 2). Compared to the expected chance level the ‘Odor and human present’ group showed no difference from the chance level ( $N = 10$ ,  $T = 3$ ,  $P = 0.096$ ) (we should note that according to the Dunn’s post-hoc test there was no difference between these two groups). Nevertheless, it is interesting that dogs performed somewhat better if the human was not present, suggesting, that the human who was withholding communicative gestures (and by doing so behaved unnaturally in the present situation) might have had a disturbing effect.

Dogs showed clear choice in the ‘Deceptive hiding’ group (without pointing) by going to the place where they have seen the bait disappear ( $N = 10$ ,  $T = 0$ ,  $P < 0.01$ ), and not to the place where the bait and therefore the odor cue actually was. This supports the observation that the location of the bait (and so the odor source) during choice plays only a relatively minor role (see also Gagnon and Dore, 1992). This is further supported by dogs that were following human pointing to an empty bowl (Group 4: Deceptive pointing) in spite of the

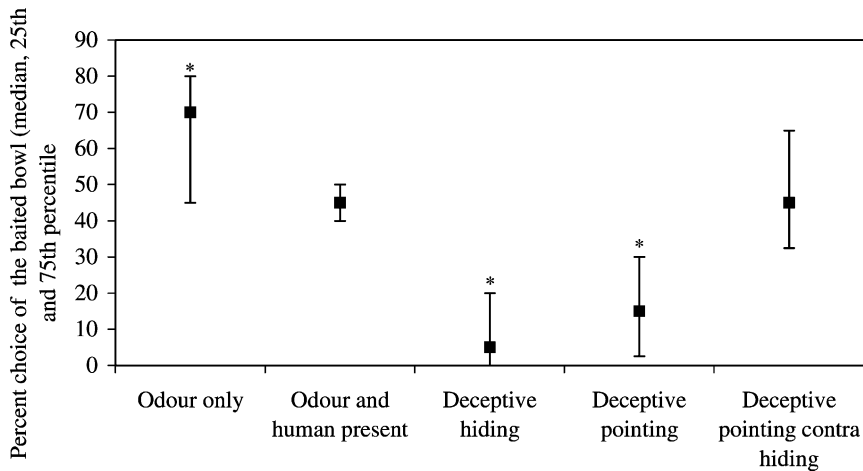


Fig. 2. Median percentage of choice of the baited bowl (25th and 75th percentiles) in Study 1. Dunn's post-hoc test ( $P < 0.05$ ) showed that dogs choose the baited bowl significantly fewer times in the 'Deceptive hiding' test than in 'Odor only' or 'Odor and human present'. \* indicate significant difference from chance level.

fact that there was food (odor cues only) in the other bowl ( $N = 10$ ,  $T = 1$ ,  $P < 0.01$ ). Interestingly, dogs that had witnessed hiding of the bait (visual and odor cues) were more reluctant to choose the empty bowl on the basis of human pointing. On the group level, this meant that they performed at chance level (Group 5:  $N = 10$ ,  $T = 16.5$ ,  $P = 0.831$ ) but six dogs seemed to have some preference of choice (dogs were categorized as having a preference if they based their choice on the same cue in at least 7 out of 10 trials). Three dogs preferred to choose the (empty) bowl that was indicated by the experimenter, and another three went mostly for the bowl where they had seen food disappear. Individual variability could be explained by the differential rearing history and experience of the dogs but it also could be attributed partially to their relationship with the owner (Topál et al., 1997, 1998; Gácsi et al., 2001).

### 3. Study 2

The aim of this study was to replicate the findings of the previous study with a new set of dogs but we were also interested in whether more extended experience with the odor cues would lead to different results. In Study 1, dogs might have had problems in sensing odor cues from the baited bowl because they might have been less attentive to the situation (distracted by environmental stimuli during the tests) or due to the openness of the experimental area the odor concentration reaching the dog's nose might have been too low. This study was conducted in the owners' home to provide a quieter environment. We increased the dogs' chances to rely on odor cues by allowing them to investigate (by sniffing only) both bowls (this time covered with a lid) before making their choice (Fig. 3).

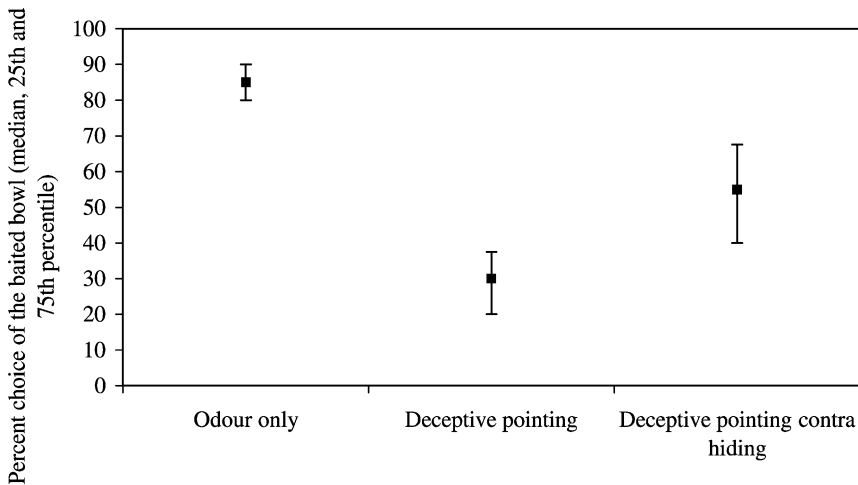


Fig. 3. Median percentage of choice of the baited bowl (25th and 75th percentiles) in Study 2.

### 3.1. Method

#### 3.1.1. Subjects

Thirty adult dogs of different breeds were divided equally among the three experimental groups (see [Appendix A](#)).

#### 3.1.2. Procedure

The observations were carried out during autumn 2000 in the owners' flats in the living room of the family. Pre-training and the general procedure for testing was done in the same way as described for Study 1.

*Group 6:* Odor only ( $N = 10$ ). The dog was prevented from observing the baiting by the owner covering his eyes and turning him away. The experimenter took both bowls, put a piece of meat in the baited bowl, and placed a lid over both the empty and the baited bowl, and put them back simultaneously on the ground. Next the dog was made to face the two bowls, and then the owner approached one of the bowls with the dog on leash (in half of the trials, the left bowl was visited first, and the bowl on the right second, in the other half the visits went in the reverse order). The dog was allowed to have a sniff of the bowl, and then he was led gently to the other bowl. Finally, they both went back to the starting place, and at the same time the experimenter moved behind the dog. Having sniffed the bait it took approximately 10 s for the dog and owner to walk over to the empty bowl and get back to the starting place. Then the dog was released (owners could say 'Go! It is yours!') but in most cases it was enough to release the leash of the dog, and they could choose freely between the two containers.

*Group 7:* Deceptive pointing. The procedure was the same as for Group 6 but here the experimenter was standing between the bowls and was pointing toward the empty container before the dog was released. Therefore, the dogs were provided with (direct) olfactory cue



about the location of the bait, but they perceived a ‘contradictory’ pointing signal before they were allowed to make their choice.

*Group 8: Deceptive pointing contra hiding* ( $N = 10$ ). The procedure for this group was basically the same as for dogs in Group 5 in Study 1 but after witnessing the bait being hidden in the baited bowl (visual cue) dogs were also allowed to sniff at both bowls (direct olfactory cue). Here again, the experimenter had been pointing to the empty bowl just before the dog was released.

#### 4. Results and discussion

There was significant difference among the different experimental groups ( $H = 20.18$ , d.f. = 2,  $P < 0.01$ ). In this study, dogs seemed to have no problems in choosing the correct bowl if they had the opportunity of getting a (direct) olfactory cue about the location of the food, as this time dogs in Group 6 (‘Odor only’) performed well above chance ( $N = 10$ ,  $T = 0$ ,  $P < 0.01$ ). As indicated earlier there could have been several reasons why dogs were less successful in the previous study when the only possibility to make this discrimination was to perceive the odor of the bait from a distance of approximately 2 m. It could be that odor concentration reaching the dog was just too low to allow for a correct choice. However, even when given the opportunity to sniff at the baited bowl, this olfactory cue about the location of food seems not to be enough to overcome their tendency to respond to the pointing signal, and as a consequence dogs choose the empty bowl pointed at by the experimenter and not the place which they had experienced the presence of the food a few seconds earlier ( $N = 10$ ,  $T = 2$ ,  $P < 0.01$ ). Finally, the situation changes however, if the dog can also witness the process of hiding (Group 8). In this case, dogs became more reluctant to follow ‘blindly’ in the direction indicated (wrongly) by the human, resulting at group level to a random choice ( $N = 10$ ,  $T = 19.5$ ,  $P = 0.72$ ). The results of this group are basically identical to those obtained for the similar group in the previous study (Group 5: Deceptive pointing contra hiding) with a similar procedure but outside the home environment. The individual differences seem to surface in this group of dogs again, with half of the dogs showing preference to ‘believe’ either the human pointing ( $n = 2$ ) or their visual experience ( $n = 3$ ) (dogs were categorized as having a preference if they based their choice on the same cue in least 7 out of 10 trials).

#### 5. General discussion

In this series of experiments, we wanted to establish the relative effect of various sensory experience (visual and/or olfactory) on the behavior of dogs in a choice situation. It seems to be clear that given appropriate circumstances dogs can base their choice both on olfactory and visual information. In other words, if dogs witness an object being hidden, or have the opportunity to sniff the hiding place, they are able to make a correct choice a few seconds later.

In the case of contradictory cues, dogs prefer to rely on the human communicative signaling (pointing) when they have only olfactory information about the hiding place. Their willingness to do this decreases, however, if they themselves are in the position to obtain

visual information about the ‘state of the world’. This means that if a dog sees where the food is placed, it is more reluctant to go in the opposite direction pointed at by the human, even if they had some ever-day experience (with their owner for example) that pointing strongly correlates with the presence of food. This suggests that dogs do not follow human pointing blindly; they seem to have some control over their response to the pointing gesture. However, it is interesting to note that in both studies about half of dogs in these experimental groups seem to fall in either the two following categories. Some dogs mostly ‘believed’ their own eyes, whilst others would go to the empty bowl indicated by the pointing. This also suggests that, possibly due to social experience for some dogs, human pointing becomes one of the most reliable sources of information in the environment. A similar trend was to some extent observed in young children who seem to depend to a great degree on information provided by pointing (J. Call, personal communication). The argument in this case, as it can be also applied to the dogs, could be that although the children have the mental capacity of discriminating between situations, they do not do so because of the constraints of this social context. Children at this age (and dogs in general) depend to a great extent on information provided by the parents (owners), and they have only limited control over it, so it is somehow natural for them to respond preferentially to communicative gestures even if sometimes those gestures might contradict their own perception of an event.

However, another alternative explanation is also possible. One could argue that in human–dog (or adult–child) relationship the pointing gesture has also acquired a commanding character, that is, the subject is allowed to visit only the signaled bowl. Accordingly, dogs show some preference for the bowl pointed at independently of the fact that they have unequivocal information about the content of both bowls (empty or baited). The ambiguous choice of dogs that have actually witnessed the hiding could be explained by postulating that putting food in a bowl (for the dog) could have some kind of permissive character in dog–human communication, therefore having a facilitative effect on choosing the baited bowl.

We should also note that there is little competition between dog and owner (or an adult and a child), so dogs might be better at understanding the communicative aspect of the present situation (see also Hare et al., 2000). It is clear that with age children gain more control over their response under such conditions, and, in the case of dogs, their behavior depends probably also greatly on to their relationship with their owner.

In summary, our results indicate that dogs seem to ‘lose their nose’ in some social situations, and communicative gestures can not only provide ‘information’ relative to location of objects but are also be part of a broader social interactive situation where dogs (and presumably also children) depend socially on the provider (owner/parent) of the signal.

## **Acknowledgements**

This work has been supported by OTKA (T029705) and grants of the Hungarian Academy of Sciences (F226/98) and the Ministry of Education (FKFP-0127/2001). We are also grateful to Márta Gácsi for discussion concerning the experimental design, Krisztina Soproni and Peter Pongrácz for comments on an earlier version of this manuscript.

## Appendix A

The list of dogs participated in Studies 1 and 2 (the numbers in brackets indicate the number of animals participated). All dogs are older than 2 years, five males and five bitches.

Group 1: German Shepherd, Airedale Terrier, Belgian Tervueren (2), Hungarian Vizsla, Boxer, Basenji, Pumi, Mongrel (2).

Group 2: Border Collie, Weimaraner, Husky (3), Belgian Tervueren, Samoyed, Mongrel (3).

Group 3: Belgian Tervueren (4), Bobtail, Irish Wolfhound, German Shepherd (2), Hungarian Vizsla, Rottweiler.

Group 4: Mudi, Tibet Spaniel, Bearded Collie, Belgian Tervueren, Rough Collie, Groenendale, Boxer, Husky (2), German Shepherd.

Group 5: Yorkshire Terrier, German Shepherd, Rough Collie, Mongrel (2), Pumi, Golden Retriever, German Pointer, Belgian Tervueren (2).

Group 6: Kerry-blue Terrier (2), Irish Wolfhound (3), Bedlington Terrier, Pug, Hungarian Vizsla, Belgian Tervueren (2).

Group 7: Husky, Hannoveraner Hund, Bull Terrier, Puli, Mongrel (2), Bavarian Hund, Irish Wolfhound (2), Mudi.

Group 8: Whippet, Irish Wolfhound (2), Boxer, Mongrel (2), Staffordshire Terrier, Puli, West Highland White Terrier, Flandrian Bouvier.

## References

- Apfelbach, R., Russ, D., Slotnick, B., 1991. Ontogenetic changes in odor sensitivity, olfactory receptor area and olfactory receptor density in the rat. *Chem. Senses* 16, 209–218.
- Brisbin Jr., I.L., Austad, S.N., 1991. Testing the individual odor theory of canine olfaction. *Anim. Behav.* 42, 63–69.
- Doré, Y.F., Goulet, S., 1998. The comparative analysis of object knowledge. In: Langer, J., Killen, M. (Eds.), *Piaget, Evolution and Development*. Lawrence Erlbaum, Mahwah, NJ, pp. 55–72.
- Gácsi, M., Topál, J., Miklósi, A., Dóka, A., Csányi, V., 2001. Attachment behavior of adult dogs (*Canis familiaris*) living at rescue centres: forming new bonds. *J. Comp. Psychol.* 115, 423–431.
- Gagnon, S., Dore, F.Y., 1992. Search behavior in various breeds of adult dogs (*Canis familiaris*): object permanence and olfactory cues. *J. Comp. Psychol.* 106, 58–68.
- Gagnon, S., Dore, F.Y., 1993. Search behavior in dogs (*Canis familiaris*) in invisible displacement problems. *Anim. Learn. Behav.* 21, 246–254.
- Gibson, K.R., 1990. New perspectives on instincts and intelligence: brain size and the emergence of hierarchical mental constructional skills. In: Parker, S.T., Gibson, K.R. (Eds.), *'Language' and Intelligence in Monkeys and Apes*. Cambridge University Press, Cambridge, pp. 97–128.
- Hare, B., Tomasello, M., 1999. Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *J. Comp. Psychol.* 113, 1–5.
- Hare, B., Call, J., Agnetta, B., Tomasello, M., 2000. Chimpanzees know what conspecifics do and do not see. *Anim. Behav.* 59, 771–785.
- Mech, L.D., 1970. *The Wolf: Ecology and Behavior of an Endangered Species*. Natural History Press, New York.
- Miklósi, Á., Polgárdi, R., Topál, J., Csányi, V., 1998. Use of experimenter-given cues in dogs. *Anim. Cogn.* 1, 113–121.
- Miklósi, Á., Polgárdi, R., Topál, J., Csányi, V., 2000. Intentional behavior in dog–human communication: an experimental analysis of 'showing' behavior in the dog. *Anim. Cogn.* 3, 159–166.

- Moulton, D.G., 1977. Minimum odorant concentrations detectable by the dog and their implications for olfactory receptor sensitivity. In: Muller-Schwarz, D., Mozell, M.M. (Eds.), *Chemical Signals in Vertebrates*, Plenum Press, New York, pp. 455–464.
- Schoon, A., 1996. Scent identification line-ups by dogs (*Canis familiaris*): experimental design and forensic application. *Appl. Anim. Behav. Sci.* 49, 257–267.
- Schoon, A., 1997. *The Performance of Dogs in Identifying Humans by Scent*. Ph.D. Dissertation, Rijksuniversiteit, Leiden.
- Settle, R.H., Sommerville, B.A., McCormick, J., Broom, D.M., 1994. Human scent matching using specially trained dogs. *Anim. Behav.* 48, 1443–1448.
- Sommerville, B.A., Settle, R.H., Darling, F.M.C., Broom, D.M., 1993. The use of trained dogs to discriminate human scent. *Anim. Behav.* 46, 189–190.
- Soproni, K., Miklósi, Á., Topál, J., Csányi, V., 2001. Comprehension of human communicative signs in pet dogs (*Canis familiaris*). *J. Comp. Psychol.* 115, 122–126.
- Soproni, K., Miklósi, Á., Topál, J., Csányi, V., 2002. Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. *J. Comp. Psychol.* 116, 27–34.
- Topál, J., Miklósi, Á., Csányi, V., 1997. Dog–human relationship affects problem solving behavior in the dog. *Anthrozoös* 10, 214–224.
- Topál, J., Dóka, A., Csányi, V., 1998. Attachment behavior in the dogs: a new application of the Ainsworth's (1969) Strange Situation Test. *J. Comp. Psychol.* 112, 219–229.