

Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*)

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Abstract Dogs have a remarkable skill to use human-given cues in object-choice tasks, but little is known to what extent their closest wild-living relative, the wolf can achieve this performance. In Study 1, we compared wolf and dog pups hand-reared individually and pet dogs of the same age in their readiness to form eye-contact with a human experimenter in an object-choice task and to follow her pointing gesture. The results showed that dogs already at 4 months of age use momentary distal pointing to find hidden food even without intensive early socialization. Wolf pups, on the contrary, do not attend to this subtle pointing. Accordingly in Studies 2 and 3, these wolves were tested longitudinally with this and four other (easier) human-given cues. This revealed that wolves socialized at a comparable level to dogs are able to use simple human-given cues spontaneously if the human's hand is close to the baited container (e.g. touching, proximal pointing). Study 4 showed that wolves can follow also momentary distal pointing similarly to dogs if they have received extensive formal training. Comparing the wolves to naïve pet dogs of the same age revealed that during several months of formal training wolves can reach the level of dogs in their success of following momentary distal pointing in parallel with improving their readiness to form eye-contact with a human experimenter. We assume that the high variability in the wolves' communicative behaviour

might have provided a basis for selection during the course of domestication of the dog.

Keywords Wolf · Dog · Object-choice task · Human pointing · Eye-contact · Socialization

Introduction

Recently, several studies have attempted to find the possible factors influencing the use of human pointing gestures in non-human animals, and three mechanisms have been proposed to facilitate the animals' success in locating hidden food based on human-given cues (Scheumann and Call 2004). In captive undomesticated species either extensive experiences with humans (Anderson et al. 1995; Call and Tomasello 1994) or formal training to use human-given communicative cues (Povinelli et al. 1997) may increase the animals performance in object-choice tasks. This is suggested by comparative studies on primates and by studies on other species like seals or dolphins that have regular and special interactions with humans (Shapiro et al. 2003; Pack and Herman 2004).

Thirdly, on an evolutionary scale, domestication appears to have a facilitating effect. The domestic dog's skill to use human-given cues, shown even by puppies reared with limited human contact, suggests that it might have been affected by direct (Hare et al. 2002) or indirect (Miklósi et al. 2003; Hare et al. 2005) selection processes during the course of domestication. Studying other domesticated species (horses—McKinley and Sambrook 2000; Maros et al. 2007, goats—Kaminski et al. 2005, domestic cats—Miklósi et al. 2005, foxes selected for “tameness”—Hare et al. 2005) can reveal the behavioural-level consequences of selection processes in the human environment. However,

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even when various domesticated species show behavioural similarities the underlying adaptational processes might have been different. This is initially because genetic adaptations of various species to the human environment include both convergent and divergent processes. Living in close contact with humans, and relying mostly on human provision domesticated animals might have been affected by similar selection pressures (e.g., reduction of neophobia or fear level; Price 1999). In addition, however diverse selective effects might have resulted from the differential relationship with humans, that depends both on the species involved and the part of the human environment to be inhabited by the animal (Zeder et al. 2006). It is also possible that changes in the process of human evolution had also consequences on domestication, which means that species that became associated with humans at different periods had to face different adaptive requirements. Second, even the convergent changes in domesticated species, which point to fundamental effects of the human selection process, may include a wide range of neural/behavioural mechanisms. For example, for a species to be in the vicinity of humans, domestication could increase preference for humans or alternatively decrease fear of humans. While the former process could take place via changes in the species-specific recognition-system, the latter effect can be achieved by the modification of the antipredator behaviour. Therefore, the ‘domestication’ process is not bound to a particular kind of selection process that acts invariably of the species and their human relationships.

For these reasons, hypotheses of the evolutionary processes of domestication can be tested only with limitations via comparisons of various species (for such a recent attempt, see Hare et al. 2005; Hare and Tomasello 2005). At the behavioural level, however, comparative studies can provide valuable information of which features are likely to be results of domestication. For instance, if a wide range of domesticated species representing several distantly related taxa perform a certain skill it is more feasible to assume this skill being a domestication-product than attributing it to the common ancestor. But even such conclusion can be reached only if the same studies provide negative evidence for the closest undomesticated relatives. If behaviour of the domesticated species is not such uniform, as in most cases, comparisons with the undomesticated relatives are even more essential.

When comparing domesticated species with either other domesticated or wild-living species, it is very important to avoid at least three fallacies in order to draw valid inferences (see also Kamil 1998). First, one has to ensure that there are no a priori reasons why one species is not able to perform the task. Species-specific preferences or phobias often counteract the performance in experimental tasks, and the species-difference obtained in such comparisons is not the result of the behaviour actually investigated (perfor-

mance bias). Second, species to be compared must have the same environmental experiences both in terms of their entire development (Mignon-Grasteau et al. 2005) and the testing situation (experience bias). For example, differences in sensitivity to novelty or in speed of habituation can lead to false interpretations (Lefebvre 1995). In order to exclude these influences one should modify the experiment so that the ‘inferior’ species is also able to improve its performance (‘positive control’).

In behavioural research, the dog and the wolf represent the most intensively investigated pair of a domesticated species and its closest wild relative, but even in this case, controlled experimental evidence targeting special aspects of cognition is rare and restricted to a small number of animals. For example, Fentress (1967) hand-reared one wolf and reported differences compared to pet dogs in its social behaviour toward humans. Frank and Frank (1982) socialized four wolves and four dog puppies (malamutes) in parallel both to humans and wolves/dogs, and in a replication study hand-reared seven wolf pups with higher exposure to people and contact with only littermates. These animals have been tested in various tasks involving visual discrimination learning (Frank et al. 1989), problem solving (Frank and Frank 1982) and training tasks (Frank and Frank 1987). More recently, there have been two studies comparing dogs’ and wolves’ use of human-given cues to find hidden food in object-choice tasks. In a pilot study (Agnetta et al. 2000), the simultaneous reaction of two wolves to the pointing and gazing cues of an experimenter standing in front of their cage was tested in a zoo. Hare et al. (2002) compared the success of seven family dogs and seven sanctuary-kept wolves in using human-given tapping and proximal pointing cues. None of these studies found the wolves to rely on any human gestures. In these two studies, however, the validity of comparing the success of the wolves to that of dogs is highly questionable on a methodological basis, since experiences of these wolves are hardly comparable to those of dogs (see also Miklósi et al. 2003). This aspect may have a special importance, since in a visual discrimination task the wolves’ performance was found to depend on their rearing history: the ones socialized thoroughly to humans outperformed the dogs, whereas others reared both by humans and a wolf were slower than the dogs in reversal learning (Frank et al. 1989).

In the present series of experiments a bigger number of young wolves and dogs that were socialized to humans in a comparable level was tested in the same way in order to compare their performance to follow human-given cues to find hidden food. Further on, instead of reporting only their success, two behavioural aspects were examined that had already been documented to be important in dog–human communication. These are the dogs’ sensitivity to human gestural cues when locating hidden food (Soproni et al.

2001), and their tendency to look at humans in problem situations (Topál et al. 1997; Miklósi et al. 2000; Pongrácz et al. 2001; Miklósi et al. 2003; Gácsi et al. 2005). Accordingly, dogs and wolves were compared in both of these aspects. 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 domestication of the dog began.

Further on, our second aim was to see which aspects of wolf–human communication can be influenced either by hand-raising and extensive experiences with humans or formal training in object-choice tasks. Third, the wolves were tested thoroughly with various human pointing gestures ranging from simple cues with strong local enhancement effect (e.g. touching) to more subtle ones (e.g. momentary distal pointing).

Study 1: comparing wolf and dog puppies in a two-way choice task with human distal pointing

Studies of Klinghammer and Goodmann (1987) and Frank et al. (1989) show that the duration and management of early socialization in wolves is critical for later behaviour toward humans. They have found that wolves who were exposed to conspecifics for extended periods before the age of 8–10 weeks, later developed wariness and avoidance in presence of humans. To prevent the development of this avoidance reaction in wolves very early, individual and intensive socialization (extensive hand-rearing) is necessary. However, pet dogs are usually not raised individually in constant contact with humans during their first few weeks. In order to compare the behaviour of wolves socialized intensively we had to apply the same socialization procedure to a group of dogs. This also offered the possibility to investigate whether early intensive socialization, compared to the usual upbringing of dog puppies in human families from week 6–9 on, improves the dogs' performance in using human distal pointing in a two-way choice task. Up to now only pet dogs and litter-reared puppies have been compared in their usage of proximal pointing (Hare et al. 2002).

Methods

Subjects

Three groups of 4-month-old animals were observed in this test: hand-raised wolves, hand-reared dogs and pet dogs. All dogs and wolves had attended a puppy class at the dog school (Top Mancs Dog School, Budaörs, Hungary) where the tests were carried out.

Nine *hand-raised grey wolf* pups (three males and six females, from five different litters; four born in May 2001

and five in May 2002; mean age 4.0 ± 0.6 months) were tested: four of them in August 2001, the other five 1 year later at the same time. All wolf pups were individually hand-raised by humans after being separated from their native mothers and littermates on days 4–7 after birth. They were bottle-fed and later hand-fed by humans, and they spent the first 2–4 months of their life in 24-h close human contact, participating in every activity of their owner. The wolf pups were exposed to other humans frequently (visiting novel places like other families or the university, walking on the street), experienced novel objects and situations on regular basis, and got used to travel in cars and with public transport, etc. At 2–4 months of age, the pups were homed at a private “wolf farm” where they lived around the owner's house with his dogs and could interact with humans and other wolves daily. The hand-rearers visited the pups two times a week for half a day, took them for a walk and played with them. There were many regular and occasional visitors at the wolf farm most of whom made short contacts with the wolves. As a result of this socialisation regime, the wolves displayed no sign of wariness or avoidance in the presence of humans (even strangers), in contrast, they were keen to interact with unfamiliar persons (Topál et al. 2005; Gácsi et al. 2005; Virányi et al. 2002). They also showed no fear of the testing apparatus at any time and adapted very skilfully to the rules of the testing situation.

Eight *hand-reared dog* puppies (five males and three females, all mongrels, from four different litters; mean age 3.5 ± 0.3 months) were also tested. The puppies were taken from litters born in a dog shelter, and were individually hand-raised by humans after being separated from their native mothers and littermates on days 4–10 after birth and have been raised in the same way as the wolves. Five of the puppies were raised by persons who had reared also wolves 1 and 2 years earlier. All puppies spent daily 20–24 h in close contact with humans and participated in every activity of their owner. At the age of 2 months they were rehomed to volunteers or stayed at their hand-rearers' home and lived as pet dogs.

Nine *pet dogs* (four males and five females, one Golden Retriever, Rottweiler, Airedale Terrier, German Shepherd, Rhodesian Ridgeback, Pumi, Border Collie, Groenendael and a mongrel; mean age: 3.6 ± 0.8 months) were tested in the same procedure. They all were reared by their natural mothers together with their littermates at dog breeders and adopted by a human family at the age of 6–9 weeks.

Procedures

Pretraining

For all puppies the observations were carried out in an unfamiliar room at a dog-training centre that the animals

attended regularly. In a corner, a cameraman was standing who recorded the entire procedure. The subjects entered the room together with their owner/foster parent and were allowed to explore the room for a few minutes before the test.

Two bowls (brown plastic flower-pots; 15–20 cm in diameter, 15–20 cm height) were used for hiding the bait. We used small pieces of raw meat or cold cut as bait depending on the feeding habits of the puppy. There were no strict restrictions on the feeding regime of the animals, however they had not eaten at least 1 h prior to the training session.

The two bowls were placed 1.5 m apart and the female experimenter kneeled 30 cm behind on the middle line between the pots. The subject and the owner stood facing the experimenter at a distance of 2.5 m from her. The experimenter showed a piece of food to the subject and placed it into one of the bowls slowly to make sure that the animal could see the baiting. Then the owner dropped the leash, so the animal was free to approach the bowl and eat the meat. This procedure was repeated two times for each bowl prior to both ten-trial test sessions. Subjects that did not eat the food from the bowls during the pretraining trials were excluded from the test (two pet dogs).

Testing

Two test sessions, each including ten trials, were carried out for each subject. Baiting the bowls was randomized and counterbalanced between the two sides with the restrictions that one side could be rewarded for only two times in a row and this did not happen at the very beginning of the trial.

The arrangement of the bowls, the experimenter, the subject and the owner was the same as in the pretraining (see also Miklósi et al. 1998; Soproni et al. 2001). During the trials the experimenter was kneeling to facilitate the puppies to establish eye contact with her and to observe the gestures.

Before the testing trials the experimenter held both bowls in front of her body and put a small food pellet into one of them. Then she kept exchanging the bowls in her hands for two times, and placed them at the same time on the floor. Next, she kneeled with hands bent in front of her chest and tried to establish eye contact with the subject prior to signalling. If the subject did not look at the face of the experimenter she called it by its name or produced some sounds (i.e. hand clapping) to direct the pup's attention. As soon as the eye contact was achieved the experimenter pointed to the baited bowl (momentary distal pointing—see below). If the animal looked or turned away during the pointing, the experimenter tried to redirect the pup's attention to herself and repeated the gesture. If the subject did not leave the starting point within 5 s after being released

by the owner the cueing was repeated. The experimenter looked always at the subject while pointing.

For the momentary distal pointing gesture the experimenter enacted a short, definite pointing toward the baited bowl after which her hands were placed back to her chest. The distance between the tip of the pointing finger and the bowl was approximately 50 cm. When the experimenter's hand returned to the starting position at her chest, the subject was released and allowed to make a choice. The bowl first approached by the subject within 5 cm was considered as chosen. After choosing the baited bowl the subject was allowed to eat the food, and praised verbally. If the subject visited the empty bowl first, it failed to get the food.

Behavioural and statistical analysis

The following two variables were measured from the videotapes:

Number of correct choices: We calculated the number of correct choices from the 20 trials for each individual and used Wilcoxon signed rank test to compare the groups' performance against chance performance (50%). The individual performances were also analyzed statistically with binomial test (according to the binomial distribution five errors out of 20 results in a P value of 0.041, so a subject was reported as relying on the pointing gesture over chance if it achieved 15 or more correct choices).

For this variable inter-observer reliability was not assessed because the subjects' choices could be determined without ambiguity.

Latency of attending to the experimenter: This parameter was obtained by measuring the time elapsed from the moment when the experimenter stood up after placing the bowls on the ground and was ready to produce the pointing gesture till the moment of finishing the gesture to which the animal attended continuously (and after which it was released—see testing procedure). This variable was measured in order to provide information on the subjects' willingness for establishing eye contact with the experimenter and maintaining it during the production of the signal.

To assess inter-observer reliability this variable in all trials of four individuals (44 or 50% of all subjects) from each group was measured by two independent coders. Solidity of using the above procedural definition instead of assessing eye-contact from the videotapes is reflected in the high reliability. For seven of the eight double-coded dogs in no trial and for the eighth dog in one single trial was the difference bigger than 1 s between the two values measured by two coders. For the four double-coded wolves in 0, 1, 1 and 3 trials out of 20 the two values differed more than 1 s.

Due to significantly different standard deviations, we used Kruskal–Wallis ANOVA when comparing both the choices and the latencies among the three groups, and

Mann–Whitney U tests for the planned pair-wise comparisons (Miliken and Johnson 1992) between the hand-reared subjects (dogs vs. wolves) and between the differently raised (hand-reared vs. pet) dogs.

Results and discussion

We found significant differences among the performance of the three groups ($\chi^2 = 8.672$, $df = 2$, $P = 0.013$). The performance of pet dogs and hand-reared dogs was not different ($U = 33$, $N_1 = 9$, $N_2 = 8$, $P = 0.770$), showing that early intensive socialization is not necessary for 4-month-old dogs' following human distal pointing. The performance of the wolves and dogs reared in the same way proved to be different ($U = 16$, $N_1 = 9$, $N_2 = 8$, $P = 0.050$; Fig. 1a). This finding was supported also by Wilcoxon signed rank tests that showed significantly different performance from chance level in dogs ($T(-) = 0$, $df = 8$, $P = 0.004$ for pet dogs; $T(-) = 0$, $df = 7$, $P = 0.031$ for hand-reared dogs) but not in wolves ($T(-) = 5.5$, $df = 8$, $P = 0.313$). Analyses of the individual performances showed similar results: none of the wolves were successful above significance level whereas four pet dogs (44%) and three hand-reared dogs (38%) performed above chance level.

We found similar differences among the groups in the latencies of eye-contact and maintaining attention ($\chi^2 = 9.158$, $df = 2$, $P = 0.010$): pet dogs and hand-reared dogs established eye-contact with the experimenter and watched the gesture similarly soon ($U = 29$, $N_1 = 9$, $N_2 = 8$, $P = 0.500$), while this latency was significantly longer in hand-reared wolves than in hand-raised dogs ($U = 11$, $N_1 = 9$, $N_2 = 8$, $P = 0.009$; Fig. 1b).

These results indicate that already at the age of 4 months dogs and hand-reared wolves respond differently to distal pointing gestures of humans, and only the dogs use these cues to locate the food. In the present experiment, this species difference cannot be attributed to environmental effects or to differences in experience since the wolves and the dogs were hand-raised identically.

Study 2: use of different human pointing gestures in young wolves

Various species in object-choice tasks have been found (e.g. Povinelli et al. 1997; Anderson et al. 1995; Maros et al. 2007) to be less successful in using momentary distal pointing compared to other human-given gestures, e.g. when the pointing hand is closer to the pointed object or the gesture can still be seen when the choice is made. This suggests that the actual form (both spatial and temporal) of the pointing gesture is critical in using the gestural cue provided by the experimenter in a two-choice test (see Miklósi

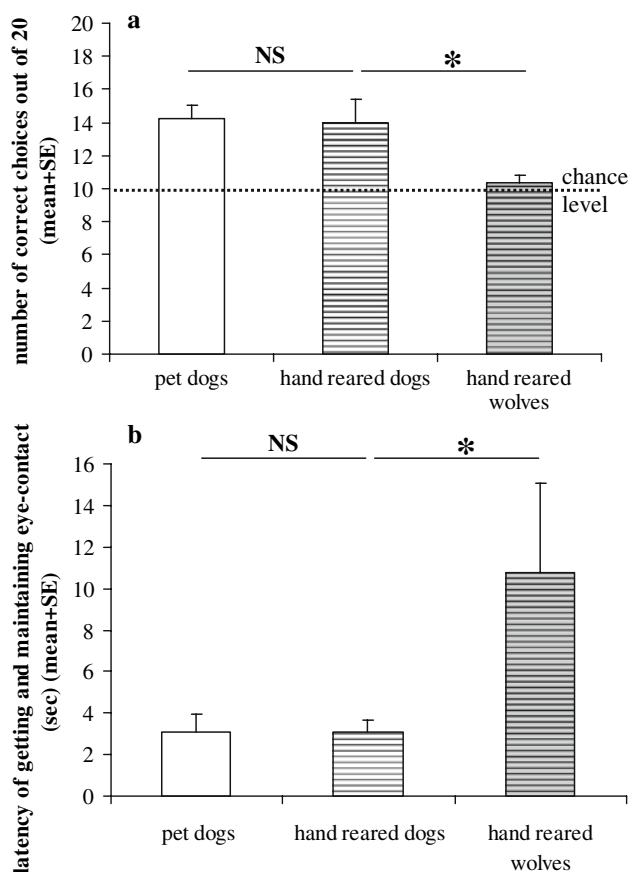


Fig. 1 Number of correct choices (a) and latency of establishing and maintaining eye contact with the pointing experimenter (b) in a two-way choice task comparing 4-month-old pet dogs ($N = 9$), hand-reared dogs ($N = 8$) and hand-reared wolves ($N = 9$) (mean + SE). Dotted line indicates random choice. * indicates significant difference between two groups (Mann–Whitney U test)

and Soproni 2006 for review). Since at the age of four months the wolves did not use the momentary distal pointing, as a next step, they were tested with a variation of five different human-given cues.

Methods

Subjects

Seven intensively and individually socialized wolf pups (five females and two males, from four litters—see Table 1) took part in this study between 7 and 11 months of age. Five of them had participated also in Study 1.

Procedures

The basic procedure of the tests (Fig. 2) was the same as described in Study 1 with the exceptions that the signalling experimenter was standing upright (instead of kneeling),



Fig. 2 Experimental arrangement in Studies 2 and 3. The extensively hand-raised wolves were tested in the same way as pet dogs are usually tested in object-choice tasks: they were held by leash in the same area where the pointing experimenter was standing

Table 1 The hand-raised wolf subjects of the four studies

	Name	Sex	Participation
Litter 1	Bence	Male	Study 1, 2, 4
Litter 2	Ursula	Female	Study 1, 2, 4
Litter 3	Léna	Female	Study 1, 2
	Bogi	Female	Study 1, 2, 4
	Tóbiás	Male	Study 2, 4
Litter 4	Zazi	Female	Study 2, 4
	Maja	Female	Study 1, 2, 4
Litter 5	Barnus	Male	Study 1, 3, 4
	Jimmy	Male	Study 1, 3, 4
	Rebeka	Female	Study 1, 3, 4
	Minka	Female	Study 1, 3, 4

and the tests were carried out in a run (4×4 m) at the wolf-farm where the animals lived.

Pre-testing with momentary distal pointing gesture: In the first phase of this study, the four individuals that had participated in Study 1 were tested again in a session of 20 distal pointing trials at the age of 7 months.

Probe testing: During the second phase all seven wolves were presented with five different gestures: (1) momentary distal pointing; (2) dynamic distal pointing; (3) momentary proximal pointing; (4) touching object; and (5) standing

behind object. In each session, the wolves were given 20 trials in a predetermined, semi-random order: five different trials were executed in a random order then they were repeated in a different order and so on two more times. With 1–3 weeks between the sessions each wolf participated in five sessions, hence it received 20 trials of each cueing type.

Re-testing with momentary distal pointing gesture: In the third phase of the study, the wolves were retested in a session of 20 momentary distal pointing trials on a separate occasion at their age of 11 months (with the exception of one individual that was unavailable at the time of this retesting).

Description of the cueing gestures

Momentary distal pointing: The experimenter enacted a short, definite pointing toward the baited bowl then placed her hands back to her chest. The gesture was presented for about 1 s. Just when the experimenter's hand returned to the starting position at her chest, the subject was released and allowed to make a choice. The distance between the tip of the pointing finger and the bowl was more than 50 cm.

Dynamic distal pointing: The experimenter enacted a definite pointing toward the baited bowl and held her arm in the pointing position until the subject made its choice. The distance between the pointing finger and the bowl was more than 50 cm.

Momentary proximal pointing: The same short, 1 s-long cue as the distal pointing but the experimenter was sitting on her heels, so the bowl was about 10 cm from the tip of her pointing finger.

Touching: The experimenter was sitting on her heels, touched the closer rim of baited bowl with her fingers (without noise or moving it) for about 1 s and then retracted her arm back to her chest.

Standing behind: The experimenter stepped behind the baited bowl and stayed there still and looking at the subject till it made its choice.

Data analysis

For the different cues separate Wilcoxon rank sum tests were used for the group performance analyses and binomial tests for the individual performance.

In order to test for changes over time the number of correct choices (out of 20) was calculated for the probe-test sessions (irrespective of the types of trials) and compared across the five sessions (Friedman ANOVA). Also the number of successful wolves was calculated in the first and the fifth sessions of the probe testing, and similarly in the momentary distal pointing pretest and retest.

Results and discussion

Results of distal pointing pretest appear to be similar to that of Study 1. None of the four wolves performed above chance level (see first black columns in Fig. 3) suggesting that even at the age of 7 months socialized wolves do not rely spontaneously on human’s momentary distal pointing gestures.

In the probe-testing phase, however, the wolves’ performance was above chance level not only in cases of dynamic distal pointing ($T(-) = 0$, $df = 6$, $P = 0.016$), momentary proximal pointing ($T(-) = 1.5$, $df = 6$, $P = 0.031$), touching ($T(-) = 0$, $df = 6$, $P = 0.031$) and standing behind ($T(-) = 0$, $df = 6$, $P = 0.031$) but also in the case of momentary distal pointing trials ($T(-) = 1.5$, $df = 6$, $P = 0.031$).

Considering the individual results (Table 2) one wolf was outstandingly successful using four out of five cues, one wolf used two cues, two wolves performed above chance on one cue (different ones) and three individuals’ performance was at chance level on all cues. As for the cueing types, all cues were used by at least one wolf but by no more than three individuals. Touching the object was used by three individuals and the proximal pointing by two wolves, whereas only one wolf performed above chance on either standing behind the object or dynamic or momentary distal pointing to it.

The comparison of the wolves’ group-performance across the five sessions of probe-testing found no significant improvement (Friedman ANOVA: $\chi^2 = 6.18$, $df = 4$, $P = 0.19$). However, comparing the individual performances in the first and the fifth sessions revealed that only one of the seven wolves performed above chance level in the first session (taken all types of trials together), whereas three of them were successful in session 5 (Fig. 3).

Retesting with the momentary distal pointing gesture at the age of 11 months confirmed the results of the second phase. Though the wolves’ overall performance did not differ significantly from chance level ($T(-) = 0$, $df = 5$, $P = 0.063$), individually three out of six animals performed above chance (see last black columns on Fig. 3).

Although there is still a high interindividual variation, the results indicate that extensive socialization procedure and/or experimental training can increase the success of wolves to follow human cues. The somewhat elevated performance on hand-associated cueing trials (proximal pointing, touching) can be explained by our hand-raising procedure. Hand-feeding the animals might have been the basis to associate human hand with food. However, in case of momentary distal pointing this hand–food association cannot be used in such a straightforward way, and also the relatively higher number of successful wolves in the later sessions suggests learning during the course of the experiment.

Fig. 3 Number of correct choices (out of 20) of each wolf in the distal pointing pretest, five sessions of mixed cueing and distal pointing retest of Study 2. Broken line at 10 indicates random choice, line at 15 indicates significant deviation from chance level (binomial test, $P < 0.02$; max. 5 errors in 20 trials)

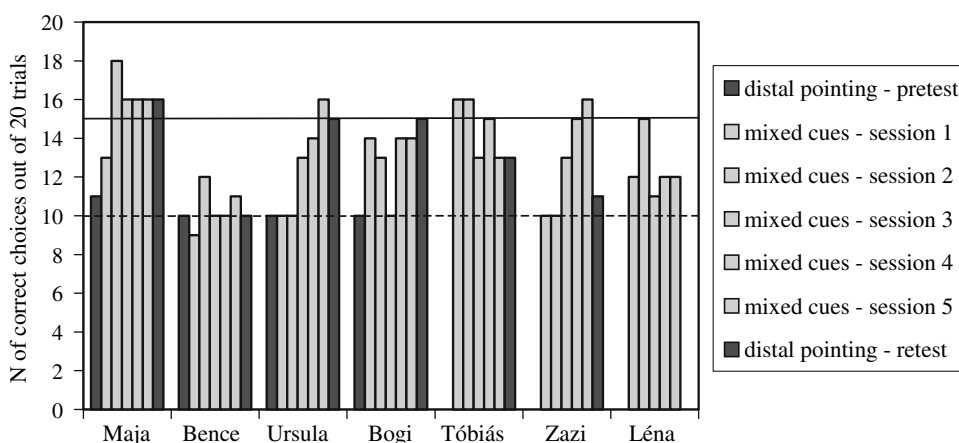


Table 2 Number of correct choices out of 20 trials of each cue for each wolf in the cue-mixing (second) phase of Study 2

Name	Momentary distal pointing	Dynamic distal pointing	Momentary proximal pointing	Touching	Standing behind
Maja	15*	15*	16*	19*	14
Bence	11	11	9	10	11
Ursula	12	13	12	13	13
Bogi	12	12	11	14	15*
Tóbiás	14	12	17*	18*	12
Zazi	13	11	13	14	13
Léna	9	12	13	17*	10
Average	12.3	12.3	13	15	12.6

* Marks above chance success according to binomial probability

Nevertheless, the possible effect of developmental maturation cannot be excluded with this experimental design.

Study 3: longitudinal investigation on young wolves' use of human cues

The short-term procedure of Study 2 provided only suggestive but unequivocal indications of learning effect but a more extended training regime may confirm these results. Accordingly, the other four animals of Study 1 were tested longitudinally for 6.5 months in 22 sessions of momentary distal pointing trials in parallel with the other four cue-types (dynamic distal pointing, momentary proximal pointing, touching, standing behind).

Methods

Subjects

Four intensively and individually socialized wolf pups (littermates, two females and two males—see Table 1) participated in this study. At the time of testing they were between 4.5 and 11 months of age.

Procedures

The basic procedure of the tests was the same as described in Study 1 with the exceptions that after the fourth test session—in accordance with the higher eye level of the growing animals—the signalling experimenter was standing upright instead of kneeling, and the tests were carried out in an outdoor run (4 × 4 m) at the wolf-farm where the animals lived. The wolves were tested once a week.

During this study, the same five cues were presented as in Study 2 but in blocks in a predetermined order: (1) momentary distal pointing (henceforth tested continuously); (2) standing behind; (3) dynamic distal pointing; (4) touching object; and (5) momentary proximal pointing (see Table 3). On each session, wolves were given ten momen-

tary distal pointing trials that were followed by ten trials of another cue from the third session on. Subjects were tested on 22 occasions with momentary distal pointing (total number of trials: 220). With dynamic distal pointing and proximal pointing wolves were tested in six consecutive sessions (60 trials). There were only four sessions (40 trials) for the cues standing behind and touching because all individuals achieved at least 15 correct choices in either the first or the last two sessions.

To examine whether only the deliberate cues influenced the behaviour of the wolves control trials were staged on the last two sessions (ten trials in each). In these trials the experimenter did not produce any signals. She remained still and waited in this relaxed posture orienting to the subject for similar duration as in the cued trials after which the wolf was allowed to choose in a similar manner as described above.

Data analysis

Since for this experiment there were only four wolves available the emphasis of the statistical analysis was on individual performance. The overall performance of each individual was calculated for each cue based on the total number of trials experienced by the animal (binomial test). For further analysis—similarly as in Study 2—the trials were arranged in 20-trial blocks and above chance performance was recorded in a block in case of five or less errors according to the binomial distribution. Friedman ANOVA was used to test for changes over time in the performance of the animals as a group.

Results and discussion

Based on their overall performance across all trials, two wolves followed all cues significantly above chance, one wolf performed above chance level on all cues except dynamic distal pointing and one wolf could use three cues but not dynamic distal pointing and momentary proximal pointing (Table 4).

Table 3 Number and order of sessions with different human-given cues in Study 3

Test sessions	Momentary distal pointing total <i>N</i> : 220	Standing behind <i>N</i> : 40	Dynamic distal pointing <i>N</i> : 60	Touching <i>N</i> : 40	Momentary proximal pointing <i>N</i> : 60	Control (no cue) <i>N</i> : 20
1–2	10					
3–6	10	10				
7–12	10		10			
13–16	10			10		
17–22	10				10	
23–24						10

In sessions 1 and 2, ten trials were executed with momentary distal pointing; in sessions 3–22, ten trials of distal pointing were followed by ten trials of another cue; and finally in each of the last two sessions, ten control trials were run

Table 4 Number and percentage of correct choices of each wolf in cases of the different human-given cues in Study 3

Name	Momentary distal pointing Total N: 220	Standing behind Total N: 40	Dynamic distal pointing Total N: 60	Touching Total N: 40	Momentary proximal pointing Total N: 60	Control Total N: 20
Jimmy	157 (71%)*	37 (93%)*	49 (82%)*	30 (75%)*	44 (73%)*	9 (45%)
Barnus	126 (57%)*	31 (78%)*	33 (55%)	32 (80%)*	34 (57%)	11 (55%)
Minka	132 (60%)*	34 (85%)*	31 (52%)	30 (75%)*	50 (83%)*	11 (55%)
Rebi	138 (63%)*	32 (80%)*	44 (73%)*	35 (88%)*	38 (63%)*	12 (60%)
Average	138.3 (63%)	33.5 (84%)	39.3 (65%)	31.8 (79%)	41.5 (69%)	10.8 (54%)

* Marks above chance success according to binomial probability

Based on the total number of momentary distal pointing trials all four wolves' success was significantly over chance (157/220; 138/220; 132/220; 126/220; binomial test—the lowest number of correct choices out of 220 which results in a significant P value 0.037 is 126). After arranging the data into eleven 20-trial blocks the group performance was found to improve over time (Friedman ANOVA: $\chi^2 = 19.89$, $df = 10$, $P = 0.03$). However, the individual data clearly show large variability in the wolves' performance across the testing period (see Fig. 4). Only one wolf's performance remained relatively stable choosing the correct location from the seventh block of trials onwards. Comparing the number of blocks with at least 15 correct choices out of the first five and the last five blocks of each individual we found a growing tendency in three individuals (no successful block among the first five blocks and two or five successful blocks among the last five ones, or one successful block of the first ones and two of the last five blocks). Only one individual had reduced number of successful blocks out of the last five blocks compared to the first five ones (change from 1 to 0).

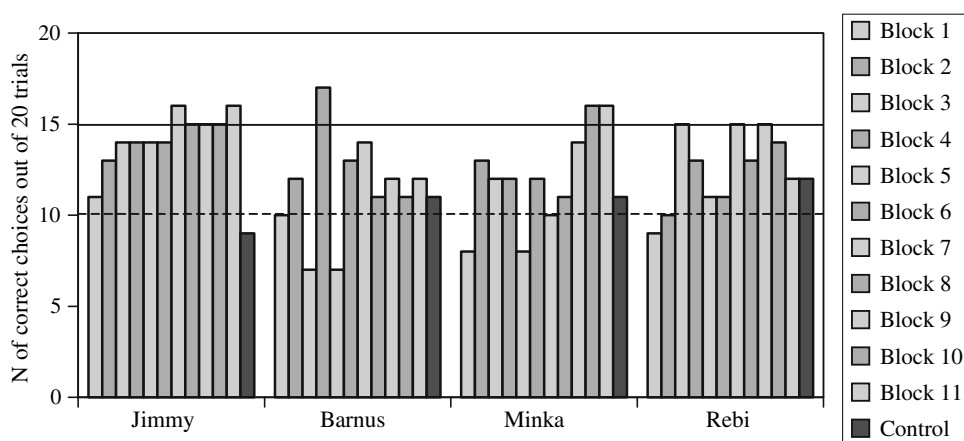
When displaying the *standing behind* cue all wolves showed a significant preference for the baited bowl (37/40; 34/40; 32/40; 31/40; binomial test—the lowest number of correct choices out of 40 which results in a significant P value 0.040 is 27). One wolf displayed significant preference already in the first block, and two others only missed

out by one incorrect choice (Fig. 5a). By the second block of trials all wolves reached over-chance performance. At the group level it resulted in a significant improvement over time (Friedman ANOVA: $\chi^2 = 4.00$, $df = 1$, $P < 0.05$).

In contrast, only two out of four wolves performed significantly over chance in the *dynamic distal pointing* trials (49/60; 44/60 but 33/60; 31/60; binomial test—the lowest number of correct choices out of 60 which results in a significant P value 0.028 is 39). These two wolves reached significance already in the first block but this level of success was maintained by only one of them for the next two blocks of trials (Fig. 5b). At the group level no sign for significant improvement was found (Friedman ANOVA: $\chi^2 = 0.15$, $df = 2$, $P = 0.93$).

In trials utilizing the *touching* gesture the wolves were similarly successful as in the standing behind trials: taking all trials into account all four wolves were better than chance (35/40; 32/40; 30/40; 30/40; binomial test—the lowest number of correct choices out of 40 which results in a significant P value 0.040 is 27). Three wolves performed over chance level already in the first block of trials. There was a slight decrease in their preference in the second block however, because only two individuals were over chance level, the other two were just below it (14/20) (Fig. 5c). Accordingly, at the group level no change in the performance could be detected over time (Friedman ANOVA: $\chi^2 = 0.00$, $df = 1$, $P = 1.00$).

Fig. 4 Number of correct choices (out of 20) of each wolf in 11 blocks of distal pointing trials and in the control trials. *Broken line* at 10 indicates random choice, line at 15 indicates significant deviation from chance level (binomial test, $P < 0.02$; max. 5 errors in 20 trials)



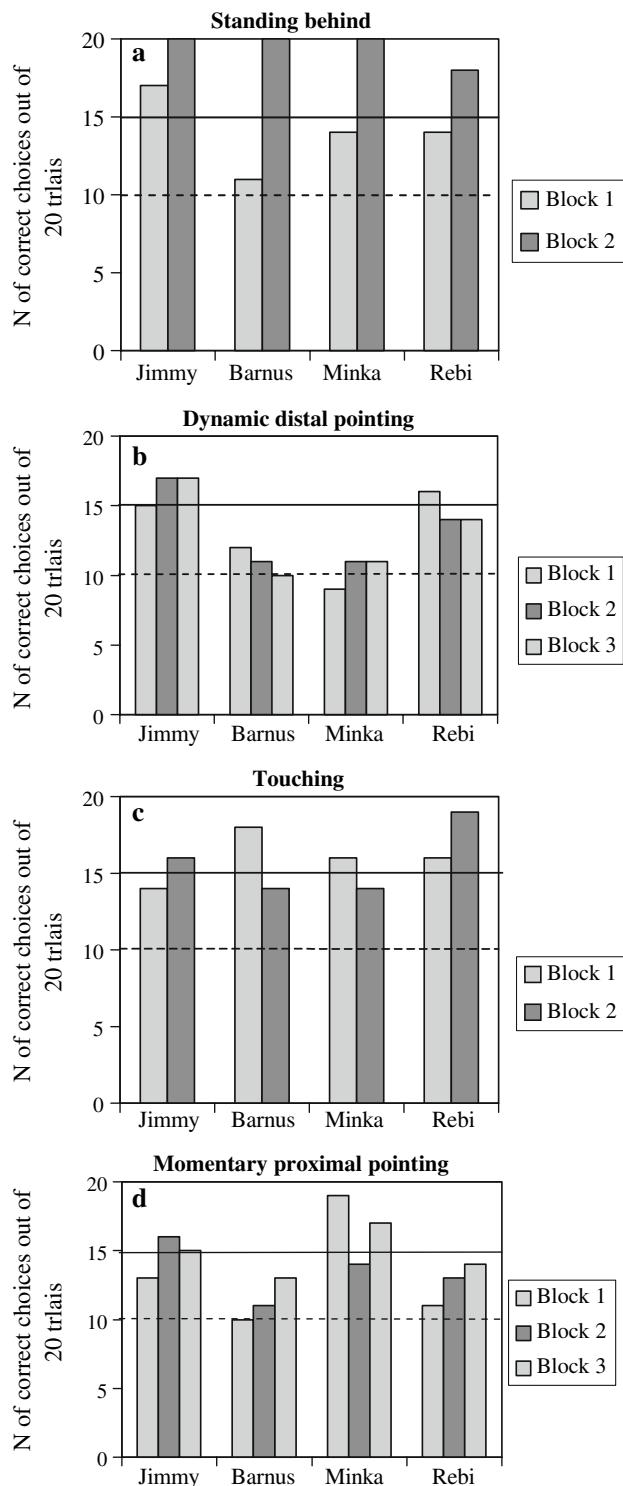


Fig. 5 a–d Number of correct choices of each wolf in case of the different cues. *Broken line* at 10 indicates random choice, *line* at 15 indicates significant deviation from chance level (binomial test, $P < 0.02$; max. 5 errors in 20 trials)

The *momentary proximal pointing* was the second most effective type of gestures based on the wolves' overall success: two individuals achieved significance for this gesture

and one only missed out by one incorrect choice (50/60; 44/60 but 38/60; 34/60; binomial test—the lowest number of correct choices out of 60 which results in a significant P value 0.028 is 39). Examining their performance in 20-trial blocks one wolf was found to be over chance in blocks one and three while another showed significant preference for the baited container in blocks two and three (Fig. 5d). Friedman ANOVA did not confirm improvement in group-performance ($\chi^2 = 2.00$, $df = 2$, $P = 0.37$).

In the control trials each wolf performed at chance level (12/20; 11/20; 11/20; 9/20) (see black columns in Fig. 4) showing that neither the asymmetrical presence (e.g. smell) of the food in the bowls nor possible unconscious cues of the experimenter had an effect on the animals' choices.

These results show that socialized wolves can spontaneously follow some human gestures and/or learn to do so. The correct choices in the standing behind (utilized early in sessions 3–6) and touching trials also provide positive control that the task itself was soluble for our animals.

Wolves were most successful with gestures in which the experimenter's hand or body was close to the baited container. This can be attributed to local enhancement effects (e.g. standing behind: the food is there where the human is) or to using gestures displayed close to the container as associative signals for the presence of food. Although in case of these cues we found little evidence for learning during the training (which could be due to our small sample size) these wolves' previous every day experiences with humans could have facilitated such learning. For instance many times they had experienced humans providing them with their feeding dish or food by hand. With the given cues and experimental design it also cannot be excluded that the similar types of gestures had a mutual facilitative effect on learning to follow them.

Study 4: comparing the wolves after extensive training and naïve dogs of same age in momentary distal pointing trials

Observing the increasing performance of the wolves in studies 2 and 3 we wondered whether after this extensive training, at the age of 11 months their final performance reaches the level of success of dogs of the same age. Accordingly 11-month-old dogs with no previous experimental training to use human pointing were tested in 20 trials of momentary distal pointing. For comparison, we used the last 20 distal pointing trials of the wolves from studies 2 or 3. In addition, we also investigated whether the improvement in following the pointing gesture is paralleled by increased readiness to establish and maintain eye-contact with the human experimenter.

Methods

Subjects

The result of ten intensively and individually socialized wolves (four males and six females from five litters) was combined for this study (see Table 1). Six of them participated in Study 2. They received 20–40 trials of momentary distal pointing and 80 trials of other human-given cues in the last 4 months prior to the sessions analysed in this study (see “Methods” of Study 2). The other four wolves had participated in Study 3 during which they had experienced 200 trials of momentary distal pointing and 200 trials of other human gestures between the ages of 4.5 and 11 months (see “Methods” of Study 3). All wolves were 10.5–11.5 months old (mean age 11 ± 0.5 months) at the time of testing. Eight of them participated also in Study 1.

For comparison ten pet dogs (reared by their natural mothers together with their littermates and adopted by a human family at the age of 6–9 weeks) (four males and six females, two Labrador Retrievers, two mongrels, one Golden Retriever, Sheltie, Great Dane, Pumi, Belgian Shepherd, Beagle; mean age 10.7 ± 1.3 months) were tested with the same procedure. They had no previous experimental experiences with human pointing gestures. They were recruited on voluntary basis from the dog-school they attended.

Procedures

The basic procedure of the tests and the pointing gesture were the same as described in Study 1 with the exceptions that the signalling experimenter was standing upright (instead of kneeling). The dogs were tested in a room in their dog school and the wolves were tested in a run (4×4 m) at the wolf-farm where they lived.

Data analysis

Similarly to Study 1 the number of correct choices out of the 20 trials and the latencies of attending to the pointing experimenter were recorded for each individual. The two groups were compared with Mann–Whitney U tests. The number of correct choices was analysed also by Wilcoxon signed rank tests at group level and with binomial tests at individual level.

To test for improvement with training and/or age the performance of the 8 wolves participating in both Studies 1 and 4 was compared with Wilcoxon matched pairs tests between the ages of 4 and 11 months. The performance of the 11-month-old pet dogs of Study 4 was compared to that of the 4-month-old pet dogs of Study 1 with Mann–Whitney U tests.

Results and discussion

No significant difference was found between the trained wolves and the naïve dogs either in the number of their correct choices ($U = 47$, $N_1 = N_2 = 10$, $P = 0.853$; Fig. 6a) or their latency of establishing and maintaining eye-contact with the pointing experimenter ($U = 33$, $N_1 = N_2 = 10$, $P = 0.218$; Fig. 6b). This finding was confirmed by the Wilcoxon signed rank tests showing that both the dogs ($T(-) = 2.5$, $df = 9$, $P = 0.023$) and the wolves ($T(-) = 0$, $df = 9$, $P = 0.004$) chose the baited bowl significantly above chance level. The analyses of the individual performances showed similar results: five wolves (50%) and five dogs (50%) had correct choices above significance level.

When we compared the performance of the eight wolves that participated in both Study 1 (at the age of 4 months) and Study 4 (at the age of 11 months) its improvement became clear. The number of correct choices significantly increased ($T(-) = 0$, $df = 7$, $P = 0.017$) and in parallel the latency of establishing and maintaining eye-contact significantly decreased ($T(+) = 2$, $df = 7$, $P = 0.025$).

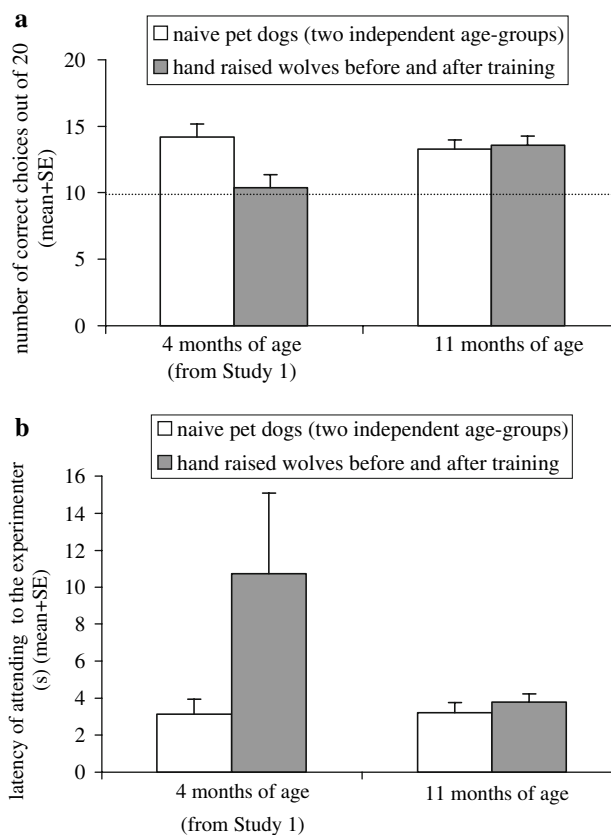


Fig. 6 Number of correct choices (a) and latency of establishing and maintaining eye contact with the pointing experimenter (b) in an object-choice task. The hand-raised wolves before and after the 7-month-long training with various pointing gestures were compared to two independent groups of naïve pet dogs of corresponding age (mean + SE). Dotted line indicates random choice

Apparently, however, the dogs' performance in using human momentary distal pointing does not further improve with age. Four-month-old and 11-month-old dogs showed the same readiness to maintain eye-contact with the experimenter ($U = 37$, $N_1 = 9$, $N_2 = 10$, $P = 0.513$; Fig. 6b) and the same success to find the hidden food based on momentary distal pointing ($U = 39.5$, $N_1 = 9$, $N_2 = 10$, $P = 0.651$; Fig. 6a).

According to these results during extensive training socialized wolves acquired the ability to base their choice on human momentary distal pointing similar to that of dogs of the same age with no specialized training. However, interestingly both the wolves and the dogs showed large interindividual variations in their performance. Further on, although the everyday life of dogs provides various possibilities to learn about human gestures they proved to rely on distal pointing similarly at the age of 4 and 11 months.

General discussion

Comparisons between similarly reared wolf and dog puppies (Study 1) indicate heritable differences in their communicative behaviour when they are provided with human-given cues. We should note that only this study has served with unambiguous evidence for such a difference as earlier experimental evidence (Agnetta et al. 2000; Hare et al. 2002) can be criticized on methodological grounds either for comparing dogs and wolves with different every-day and situation-related experiences, or for using methods and apparatuses potentially eliciting neophobic reactions in wolves.

Further on, we have shown that dog puppies as young as 4-month-old are able to perform well with a more difficult version of the pointing gesture (momentary distal pointing) without any special, intensive and early socialization to humans. "Momentary distal pointing" provides a difficult scenario for finding hidden food (in comparison to pointing gestures used by Hare et al. (2002) or Riedel et al. (2007) because (1) the pointing finger is more than 50 cm far from the baited bowl, (2) the subjects cannot see the pointing hand during their approach to the bowl, and (3) the hand-cue is not accompanied by gazing at the bowl. In the case of momentary pointing gestures, the subject has to remember a short and relatively distant signal for some time before making a choice. This makes the situation more similar to a communicative interaction where behaviour of the receiver is influenced by a short discrete signal emitted by the sender.

In contrast to earlier observations (Hare et al. 2002) we have found that wolves, enculturated similarly to dogs, are able to rely on some human-given gestures spontaneously. These cues have a conspicuous local enhancement or food-

hand association component (e.g. touching, proximal pointing). Also farm-foxes without intensive hand-rearing or special selection for approaching humans have been found to use such a human gesture (proximal pointing with gazing) (Hare et al. 2005), which seems to confirm that former negative results in wolves (Agnetta et al. 2000; Hare et al. 2002) may be due to methodological problems.

However, in contrast to dogs, wolves failed to use more difficult human pointing gestures (e.g. momentary distal pointing) spontaneously and only after months of training they reached the same level of success which dogs reached promptly. To explain the difference between the wolves and the dogs we should investigate two different aspects of the experimental situation.

The two-choice task is often viewed as a typical communicative situation where the human signals the place of hidden food to the animal. Correct choice on the part of the subject is interpreted as an ability to rely on the signal. However, analogue situations are extremely rare in nature, and it has been argued that chimpanzees' poor performance is the consequence of their inability to collaborate in such inherently cooperative situations (Hare et al. 2000). Wolves' inferior performance could be viewed in parallel with that of the chimpanzees, since pointing to a food source with the intention of food-sharing can be comparably rare among pack mates.

As opposed to the communicative interpretation a more parsimonious view explains the correct choice of the subjects by invoking simple learning processes, as the place of the hidden reward can be indicated by any physical means. Based on this interpretation the position of the human or its body parts (hand, fingers, etc.) could be used as potential discriminative cues for choosing the correct bowl. The subject learns that the hand indicates the location of food. This may be the basis to follow simple human cues (e.g. touching, proximal pointing) either in the hand-raised wolves, the captive foxes or pet dogs. During hand-raising the wolves had numerous opportunities to form this association between the food and the human hand and also the farm-foxes might have learnt it during feedings. This explanation, however, has its own problems when the gestures are performed at some distance from the baited place (e.g. distal pointing). Chimpanzees for instance fail to choose correctly if the distance between the cue and the baited location is increased to approximately 20 cm (Murphy and Miller 1955). This suggests that understanding of the distal pointing gesture escapes the associative interpretation. Results showing that dogs follow the pointing even when the pointing experimenter is moving away from the baited location (McKinley and Sambrook 2000), or is standing behind the empty location (Soproni et al. 2002) also seem to be against the associative interpretation, but even in these cases one can argue that appearance of the pointing

hand on one side of the body may be used as a more powerful discriminative cue indicating the food-location. Further research is needed to clarify this question. Interestingly, the wolves performed poorly in this condition, and could approach the level of success of the dogs only months later after extensive training.

According to our results in young wolves extensive experience with human is sufficient to elicit the use of only simple, proximal human-given cues, but extended formal training is necessary to make them follow the momentary distal pointing gesture. It means that ontogenetic manipulation of systems mediating fear and aggression toward humans during the process of hand-raising may facilitate the use of simple human-given cues. It is in line with Hare et al. (2005) results showing that experimentally selected foxes whose emotional systems are changed outperform control foxes in relying on proximal human-given cues. The ontogenetic manipulation of these systems in wolves, however, is insufficient to enhance the comprehension of more difficult human gestures like momentary distal pointing. On the other hand, unfortunately there is no data whether selection for tameness can influence these skills of experimentally selected foxes. Accordingly at present there is no experimental evidence supporting the hypothesis that in any species changes in emotional systems could result in higher success in using those human pointing gestures that are less prone to be based on direct associations.

Our results, however, show that another aspect of the wolves' behaviour changed in parallel with their increasing success in following momentary distal pointing. In the test situation the wolves did not establish and maintain eye-contact with human spontaneously, but they learnt to do it over extended training. It may have a special relevance due to an important aspect of object choice tasks that has received relatively little attention. When the experimenter is giving a signal, the animal has to look at the human (body and face) instead of looking at the general area around the bowls. This is even more important when gestures do not fall close to the bowl, as it is the case for example with distal pointing or nodding (Soproni et al. 2001). For the 'standing behind', 'touching' or 'proximal pointing' gestures the animal needs only to look at the bowls and check which is indicated by the discriminative stimulus. As it has been shown above, this situation is easily dealt with by the human(hand)–food association explanation. However, for the distal pointing gesture the wolves need to look at the human for extended time to be able to observe at which side of the body the pointing hand is indicating the bowl. Even our extensively socialized wolves did not search for eye-contact with humans spontaneously either in this or in other experimental situations (Miklósi et al. 2003). This could partially explain why wolves performed relatively poorly with distal gestures at the beginning of testing. It is also suggestive

that after extensive training their success improved in parallel with increased readiness to look at the pointing human.

The present results also point to the importance of using appropriately designed experiments in comparative research. It has been known for long that wolves can only be socialized if they are separated before eye opening from the mother (Klinghammer and Goodmann 1987) and they are raised separated from other wolves (and dogs) for the first few months after birth. Frank et al. (1989) reported that their wolf puppies that were fostered both by a wolf and humans and received less than 20 h of daily contact with humans were nearly as wary of humans as were pups reared without human contact. This means that wolves having received less extensive human contact and having been exposed too early to conspecifics (even if they tolerate the presence of humans) cannot be regarded as having comparable experience and being in the same arousal and motivational state as dogs when tested in such experimental situations. Such socialization is perhaps especially important for wolves among other wild-living animals since this species has suffered high levels of depredation by humans that resulted in selection for avoidance of humans. So it is less surprising that for a wolf to be socialized at a comparable level to that of a dog, it needs a more extensive exposure to humans than an average dog would require.

It has been suggested that in human evolution the change in communicative behaviour has played a determining role (Csányi 2000; Donald 1991). As an analogy one could assume that the domestication process of dogs had to affect their ability to communicate with humans. Previous results have shown that, compared to wolves raised identically, dogs have an increased tendency to have eye contact with humans in various situations (Miklósi et al. 2003; Gácsi et al. 2005). Since in human communication the dynamics of eye-contact plays a crucial role (Carpenter et al. 1995; Gomez 1996; Tomasello 1995; Trevarthen 1979) also dogs in human groups might have gained an advantage if they had acquired the ability to use this communicative skill flexibly (Miklósi et al. 2003). Our results in wolves suggest that an enhanced tendency to establish eye contact with humans may lead to higher success in locating hidden food based on human gestures pointing to objects far from the human's body. Also selection reducing fear and aggression toward humans in farm-foxes has been proposed to have an indirect effect on the foxes' ability to follow human-given cues (Hare et al. 2005). Based on this single study, however, effect of this selection on fox–human communication is unclear because simply local enhancement or hand–food association can explain following the cues utilized in this study and/or selection simply for approaching the human hand might have been in work. Further on, even when comparable behavioural performance of the two species will be found generalization of the underlying selective processes

of the farm-foxes to domestic dogs will remain essentially speculative.

Considering their relatively poor performance and the high variation of our wolves' behaviour (despite of being relatives and being reared under basically identical conditions) one could suggest that in the wolf population there is little selection in favour of this ability that seems to be strongly selected for in dogs. This variation assumed also in ancient wolves could have been a basis for selecting 'prospective' companions out from the existing wolf or the derived ancient dog populations during a relatively early (but not necessarily initial) phase of domestication.

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