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A Simple Reason for a Big Difference: Wolves Do Not Look Back at Humans, but Dogs Do

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Summary

The present investigations were undertaken to compare interspecific communicative abilities of dogs and wolves, which were socialized to humans at comparable levels. The first study demonstrated that socialized wolves were able to locate the place of hidden food indicated by the touching and, to some extent, pointing cues provided by the familiar human experimenter, but their performance remained inferior to that of dogs. In the second study, we have found that, after undergoing training to solve a simple manipulation task, dogs that are faced with an insoluble version of the same problem look/gaze at the human, while socialized wolves do not. Based on these observations, we suggest that the key difference between dog and wolf behavior is the dogs' ability to look at the human's face. Since looking behavior has an important function in initializing and maintaining communicative interaction in human communication systems, we suppose that by positive feedback processes (both evolutionary and ontogenetically) the readiness of dogs to look at the human face has lead to complex forms of dog-human communication that cannot be achieved in wolves even after extended socialization.

Results and Discussion

Recent results have shown that dogs' (*Canis familiaris*) performance at some communicative task is surprisingly good in comparison to, for example, chimpanzees (*Pan troglodytes*) [1–4]. Dogs could use different or unusual forms of the human directional gestures (i.e., pointing) to find hidden food indicated by a human [5], and they could also inform humans about locations of hidden food by gazing at it and showing gaze alternation between the target location and the human subject [6]. We assume that the genetic divergence of the dog from its ancestor was accompanied by important behavioral changes that could have a genetic basis because of a selection pressure for dogs that were able to adapt better to the human social setting [7]. One way to investigate genetic effects on dog behavior is to compare dogs' behavior with that of the nearest living relative, the wolf (*Canis lupus*). Unfortunately, a recent comparative investigation [8] showing dog-wolf differences did not control for effects of the differential level of socialization to humans and thus resulted in potentially misleading interpretations.

In Study 1, we investigated how four socialized wolves perform in a two-way object choice task when the correct place of the hidden food is indicated by gestures of the experimenter standing between the two containers that are 1.5 m apart. Here, we report performance obtained for three different gestural cues: distal pointing (the index finger of the human is approximately 50 cm away from the object), proximal pointing (the index finger of the human is approximately 5–10 cm away from the object), and touching (the human touches the object physically). The data of the first and last 20 trials are analyzed (also see the Experimental Procedures). At the end of the test series, 20 control trials were staged without the use of any gestures. The overall results are presented in Figure 1; however, the performance of each wolf has been analyzed individually. The statistical analysis with a binomial test showed that the performance was at chance with "distal pointing" gestures at the beginning of the tests ($p > 0.12$ for all), but one wolf increased his performance significantly by the end of the experiment ($p < 0.01$) and was correct in 80% of the trials. (He achieved this level of performance after the fifth block of trials). Further, in the case of "touching," all individuals performed well over chance ($p < 0.01$ for all). Two individuals preferred to choose the container indicated by the "proximal pointing" gesture ($p < 0.01$ for both). In sum, our socialized wolves performed over chance in at least one condition; one wolf performed over chance with all gestures, and another one performed over chance in two conditions. Overall, it seems that when they experience appropriate rearing conditions, wolves can learn about human cuing, and this behavior is in contrast to the performance of "semisocialized" wolves [8].

Although these results indicate that given "dog-like" upbringing young wolves can learn about some human gestures that indicate the place of food, their performance is generally worse than that of the dogs' in a similar testing situation and there was a large individual variability. However, this finding in itself does not explain why wolves perform differently in some of the cuing conditions. In order to be correct in the case of the "touching" and "proximal pointing" gestures, subjects needed to look only at the vicinity of the container and to be sensitive to the moving hand. Correct performance in these situations can be explained by simple associative learning that was attenuated by previous experience with humans; that is, wolves had many opportunities to learn that the human hand is often associated (e.g., at feeding occasions) with the presence of food. To be able to utilize the "distal pointing" gesture, subjects need to look not only at the containers but also at the human informant's upper body. Therefore, if wolves avoid looking at humans (or they look only for a very short duration), they are not able to perceive the directionality of the gesture, and, as a result, the task is by design insolvable

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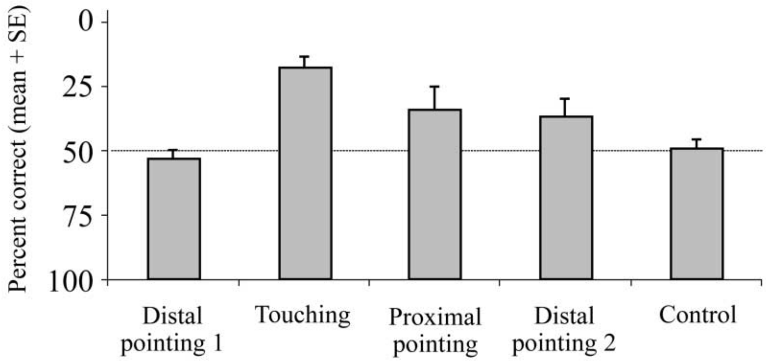

Figure 1. The Mean Performance of the Group of Four Wolves in the Two-Way Choice Task When a Human Experimenter Provides the Cue

The results for the first and last 20 trials are presented for the distal pointing cue ("distal pointing 1" [at the beginning of the test series] and "distal pointing 2" [at the end of the test series]), and the results of the first 40 trials for "touching" and "proximal pointing" are shown. In the "control" condition (no cues were given), individual wolves chose at random ($p > 0.2$ for all individuals).

for wolves (performance bias) because of species-specific differences of looking at the human.

Recently, Hauser [9] suggested that looking/gazing behavior is relatively independent of species-specific performance characteristics, and therefore it is a good indicator of species differences in cognitive/communicative abilities (also see [10]). Our idea was based on the observation that in a problem situation dogs show a preference for looking at their owner that could be interpreted as initialization of communicative interaction [6, 11].

Study 2 consisted of two behavioral tests ("bin-opening" and "rope-pulling") in which such gazing/looking behavior was tested directly. Both dogs and socialized wolves were given the opportunity to learn how to solve the problem situation in six repeated trials ("training trials") over an approximate 10 min period. After the animals had mastered the task, that is, they opened the bin (which contained a piece of meat) or pulled out a rope (with a piece of meat attached to its end) from a cage within a few seconds, we presented the animals with the same problem, but this time the problem was insoluble ("blocked test trials": bin was closed mechanically; a hidden end of the rope was fastened to the cage). The direction, duration, and latency of looking/gazing behavior were recorded. There was no difference (two-way ANOVA with repeated measures) between how fast dogs and wolves could obtain the food during the training phase for either of the tasks (bin-opening: $F(1,60) = 0.12$, $p = 0.73$; rope-pulling: $F(1,70) = 0.52$, $p = 0.47$), but the mean latency for getting the reward decreased over the six trials in both species (bin-opening: $F(5,60) = 2.71$, $p = 0.03$; rope-pulling: $F(5,70) = 10.11$, $p < 0.01$; no interaction was found). This suggests that both dogs and socialized wolves were equally motivated to solve the task and had all the abilities and physical means to achieve their goal.

However, during the blocked test trial, in both tasks dogs looked back earlier and spent more time gazing at the human than did socialized wolves (Figures 2 and 3). In the bin-opening task, dogs tended to spend more time gazing at the human ($U = 11$, $p < 0.056$), and their first look at the owner took place significantly earlier ($U = 9$, $p < 0.03$) than it did in wolves. Only two out of seven wolves looked in the direction of the human at all during the blocked trial, while this ratio was the reverse in dogs. Similar results have been obtained in the rope-pulling task. Dogs looked at the human after they tried for approximately 1 min (median) to get the piece of meat, while wolves seemed to ignore the human present ($U = 11.5$, $p < 0.03$); seven out of nine dogs looked back at the owner, in contrast to only two wolves out of seven. There was also a significant difference in gazing duration between the species ($U = 8.5$, $p < 0.025$); dogs spent more time gazing at the human.

The observations in both tasks suggest that, after facing problems of getting the food in the insoluble blocked trials, dogs initialized communicative face/eye contact with the human earlier and maintained it for longer periods of time compared to the socialized wolves. Since there were no motivational differences in obtaining the food, dogs were more likely to interrupt their own efforts to obtain the reward. This indicates that, in the present context, dogs are bound to a lesser degree to the "attracting" effects of the food.

Based on these two studies, we suggest that the failure of the socialized wolves to perform well in the pointing trials of the choice task can be attributed to their decreased willingness to look at the human. Preferential looking at the human seems to be a genetic predisposi-

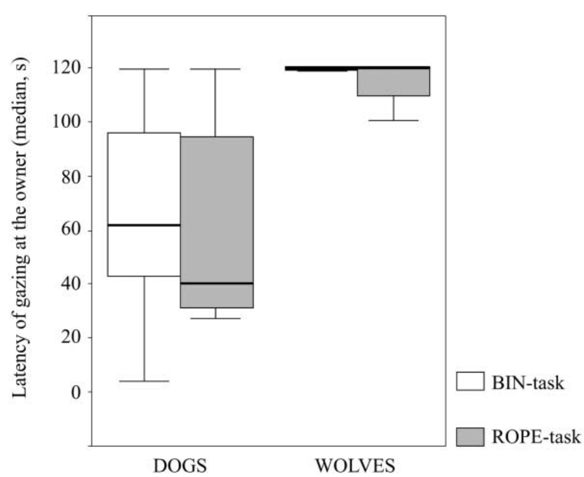

Figure 2. The Latency of Looking at the Human in Both Problem-Solving Tasks in Dogs and Wolves

Nonparametric data are represented as median, and the box indicates the interquartile range of 50% of the data. Whiskers extend to the smallest and largest values and exclude outliers. In both tests, dogs look significantly longer at the human than do the wolves ($p < 0.03$).

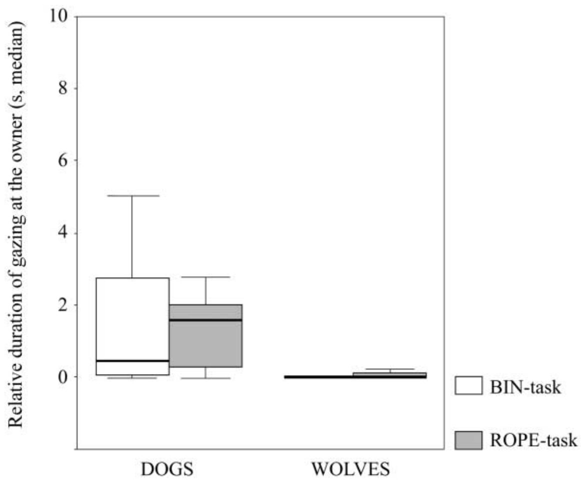

Figure 3. The Duration of Looking at the Human in Both Problem-Solving Tasks in Dogs and Wolves

Nonparametric data are represented as medians, and the box indicates the interquartile range of 50% of the data. Whiskers extend to the smallest and largest values and exclude outliers. The difference was significant in the rope-pulling task ($p < 0.025$) and approached significance in the bin-opening task ($p < 0.056$).

tion in dogs, as it was difficult to induce this behavior in wolves even after intensive socialization. We assume that one of the first steps in the domestication of the dog was the selection for "human-like" communicative behaviors [6, 12]. As we found some behavioral variability in our wolves, this species might have been predisposed for successful selection to take place. Since in humans taking up eye/face contact is understood as initialization and maintenance of a communicative interaction [13–17], we suppose that the corresponding behavior in dogs provides the foundation on which developmentally canalized complex communicative interactions can emerge between man and dog. This relatively subtle change in the behavior of dogs could have wide-ranging consequences, as it provides a potential starting point for the integration of dog and human communication systems. This hypothesis is further supported by other recent evidence showing that in many other respects dog behavior can be used as an analog model of corresponding human behavior [18], as in the case of attachment [19–20], cooperation [21], or social learning [22].

Experimental Procedures

Subjects

In 2001 and 2002, we individually raised two groups of wolf puppies ($n = 4$ and $n = 9$) from day 4 with 24 hr human contact in family homes. At 3 months of age, we transferred the animals to a farm where they lived together in a large garden around a house. Apart from the owners of the farm, who had daily contact with the wolves, the caretakers (the persons who reared the wolves after their birth) visited them at least twice a week and spent about 4–5 hr in close contact with regular exercises (i.e., walking on leash, basic obedience training). In general, this means that our wolves have experienced a very similar rearing environment and were familiar with the testing situation(s), just as dogs living in families. Dogs for Study 2 were recruited from visitors of puppy classes in dog schools. Participation was voluntary, and there were no preconditions.

Procedures

Study 1

The tests were carried out in a kennel (4 m $\times$ 4 m) at the farm where the animals lived. The test sessions started when the wolves ($n = 4$) were 4 months old and were staged once a week for the following 7 month period. Subjects underwent 20 trials in two 10-trial sessions and had a short break between sessions.

Two bowls (brown plastic flower pots; 15–20 cm in diameter, 15–20 cm high) were used for hiding the bait. We used small pieces of raw meat. There were no strict restrictions on the feeding regime of the animals; however, they had not eaten at least 1 hr prior to the training session. Previous studies have shown that olfaction does not play a role in this context, but prior to starting the experimental trials, both bowls were rubbed inside with a piece of meat.

The two bowls were placed 1.5 m apart, and the female experimenter stood on her knees 30 cm back from the middle line between the pots (she was standing upright after the fourth session, when the pups became 5 months old). The subject and its caretaker stood facing the experimenter at a distance of 2.5 m. Before the first two sessions, subjects were familiarized with the experimental procedure. The experimenter showed a piece of food to the subject and then placed it into one of the bowls with slow movements so that the animal could see the baiting. Then, the subject was allowed to go to one of the bowls and was encouraged to eat the food. This procedure was repeated two times for each bowl on the left and right.

In a testing trial, the standing experimenter took both bowls in her hands and put a small piece of meat into one of them. Then, she exchanged the bowls in her hands twice and placed them on the floor at the same time. Next, she stood with hands bent in front of her chest and tried to make gaze contact with the subject prior to signaling. The owners restrained their animals gently by holding them on a leash until the end of the cueing. If the subject did not look in the direction of the face of the experimenter within 2 s, she called it by its name or produced some sounds (i.e., clapping with hands) to direct the pup's attention. As soon as the gaze contact was achieved, the experimenter enacted a distal pointing gesture (see below). If the subject changed his direction of orientation during the presentation, or did not leave the starting point within 2 s, the cueing was repeated no more than twice. The experimenter looked at the subject while displaying the cueing. When the experimenter's hand returned to the resting position at her chest, the subject was released and was allowed to make a choice. After choosing the baited bowl, it was allowed to eat the food and could be praised verbally. If the subject visited the empty bowl first, it failed to get the food.

For the 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 (total number of trials: 220). The proximal pointing gesture was enacted the same way, but now the distance between the bowl and the tip of the experimenter's index finger was 5–10 cm (number of trials: 60). The experimenter physically touched the containers for the "touching" gesture (number of trials: 40). There were no gestures presented in the control trials (number of trials: 20).

In half of the trials, the baited bowl was placed on the right side; in the other half, it was on the left. The order of baiting was defined randomly with the restrictions that one side could be rewarded only two times in a row and that this could not happen at the very beginning of the trial.

The wolves were tested continuously during the whole period with the distal pointing gesture. On the 17^{th} week of training, the touching gesture was introduced and was followed by testing with the proximal pointing gesture on the 23^{rd} week. Control trials were staged on the last 2 weeks of testing.

Study 2

Both the wolves and the dogs were tested at an outside area at the dog school. For the bin-opening test, we used a 30 cm high plastic container with a diameter of 20 cm (commercial container for household litter). In all training trials, the subjects were (wolves: $n = 9$; dogs: $n = 9$) taken on a leash and were directed at a distance of 1.5 m from the experimenter standing next to the bin. Their owner or caretaker was standing 1 m behind them holding the end of the leash. A piece of meat was hidden inside the bin before the trial, but the subject could not see it (it was turned around by the owner/caretaker). When the subject was looking, the experimenter opened the lid of the bin, and the subject was allowed to eat the food. This procedure was repeated ten times. In the next six trials, the experimenter ceased to demonstrate the opening action. After hiding the food (with the subject out of view), the subject returned to his starting positions, and it was allowed to open the bin on his own. We measured the latency for getting the meat (the time elapsed between the release of the subject and when he got the meat in his mouth). For the 2 min blocked test trial, we mechanically fixed the top of the bin; thus, it could not be opened by the subject.

In the rope-pulling task, the subjects (wolves: $n = 9$; dogs: $n = 9$) were positioned at a distance of 1.5 m from a wire mesh cage (100 cm $\times$ 50 cm $\times$ 50 cm) with their owner or caretaker standing 1 m behind them holding the end of the leash. In a warm up trial, the experimenter crouched into the cage and offered a piece of meat to the subject through the mesh to familiarize it with the situation. The owner or caretaker allowed the subject to eat the food. Then, as the subject was led out of view, a piece of meat was attached to the end of a 40 cm long rope inside the cage. The rope was positioned in such a way that a 15 cm long part of the other end was placed outside of the cage. Then, the subject was brought back to its starting position. As soon as it oriented toward the cage, it was released when a sign was given by the experimenter. The latency of obtaining the meat was measured. Six such training trials were staged in a row. For the 2 min blocked trial, the rope was inconspicuously fixed to the cage, so pulling it did not cause the rope to move. (For both tasks, two wolves and two dogs tested in the bin-opening task had to be excluded from the analysis because they did not retrieve the food in the final sixth trial of the training within the 2 min period.)

All trials were recorded on tape by a video camera positioned 2 m to the side of the cage. For analysis of looking behavior, we reviewed the tapes recorded during the trials. Since the subjects were engaged in trying to solve the problem in the blocked trials, they were facing generally toward the task in front of them. As the owner/caretaker stood 1 m behind them, they could look at them only if they turned their head to the side. An orientation by the subject's head/nose toward the caretaker/owner was taken as an act of gazing. Two trained observers independently recoded the occurrence of gazing (one of them was naïve with respect to the aim of the experiment). The latency, duration, and direction of gazing were noted.

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