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The early ontogeny of human–dog communication

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Although dogs, *Canis familiaris*, are skilful at responding to human social cues, the role of ontogeny in the development of these abilities has not been systematically examined. We studied the ability of very young dog puppies to follow human communicative cues and successfully find hidden food. In the first experiment we compared 6-, 8-, 16- and 24-week-old puppies in their ability to use pointing gestures or a marker as a cue. The results showed that puppies, independent of age, could use all human communicative cues provided; only their success at using the marker cue increased with age. In the second and third experiments we investigated the flexibility of the puppies' understanding by reducing the degree to which they could use local enhancement to solve these problems. Here, subjects could not simply approach the hand of the experimenter and follow its direction to the correct location because cups were placed next to the dog instead of next to the experimenter. Six-week-old puppies readily used all of the human communicative cues provided. These findings support the hypothesis that domestication played a critical role in shaping the ability of dogs to follow human-given cues.

Keywords: *Canis familiaris*; communication; dog; evolution; object choice task; social cognition

Domestic dogs, *Canis familiaris*, can follow a variety of human communicative cues. This ability has been extensively investigated using an object choice paradigm in which a human experimenter hides food outside the view of the dog in one of several distinct locations and then gives a social cue (such as pointing or gazing) to indicate the correct location of the food (Hare et al. 1998; Miklósi et al. 1998; Hare & Tomasello 1999; Agnetta et al. 2000; Soproni et al. 2001, 2002). Dogs are able to use most of these cues successfully, including the use of objects as markers for the location in which food has been hidden (Agnetta et al. 2000; Riedel et al. 2005). Their success appears to be based purely on the use of the social cues because several controls have ruled out alternative explanations, including using odour as a cue to find the food (Hare et al. 1998; McKinley & Sambrook 2000; Szetei et al. 2003) or pure local enhancement (Hare & Tomasello 1999). In this last experiment a human walked towards an empty container while pointing to the target location, and dogs consistently selected the location the human pointed towards rather than the location that had been enhanced because of the human's presence.

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In contrast to dogs, most nonhuman primates perform quite poorly in this kind of object choice paradigm if the cues are given in a cooperative context in which the humans attempt to help the subject by showing her the location of food (than a competitive context in which the subject and the experimenter are both attempting to acquire the food for themselves; Call & Tomasello 1994; Anderson et al. 1995; Tomasello & Camaioni 1997; Itakura et al. 1999; Bräuer et al. 2006). In direct comparisons between apes and dogs, dogs clearly outperform apes in the use of social cues (Hare et al. 2002; Bräuer et al. 2006). This is surprising given that nonhuman primates are more closely related to humans than are dogs. Moreover, wolves, *Canis lupus*, are also less skilful than dogs in using these kinds of communicative gestures, e.g. pointing (Hare et al. 2002), despite that dogs diverged from wild wolves very recently. This difference in performance remains even if wolves are hand-reared by humans in the same environments as dog subjects (Miklósi et al. 2003). Certain differences between dogs' and wolfs' attention towards humans tends to be apparent at a very early age (Gácsi et al. 2005; Topal et al. 2005). By the age of 5 weeks, dog puppies tend to gaze more towards humans than younger puppies and more than wolf puppies of the same age (Gácsi et al. 2005). Together, these results suggest that selection through domestication, a process

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ongoing for at least 15 000 years (Vila et al. 1997), has influenced the ability of domestic dogs to use the social gestures of humans (Hare & Tomasello 2005). The domestication hypothesis claims that either direct (Miklósi et al. 2003) or indirect (Hare & Tomasello 2005) selection processes that occurred during domestication influenced dog's social-cognitive skills.

The alternative to the domestication hypothesis, however, is that dogs acquire their skills mainly during ontogeny through constant exposure to and interaction with humans. Some evidence suggests that exposure to humans alone does not account for the different behaviours of wolves and dogs because both species perform differently in the object choice task if reared under identical conditions (Miklósi et al. 2003). However, Frank (1980) hypothesized that a major difference between dogs and wolves are the different levels of trainability in the two species. An extension of this hypothesis is that early development plays a critical role in dogs' ability to use social cues and they therefore show a higher degree of skilfulness because of their higher degree of trainability relative to that of wolves.

A powerful way to test these two opposing explanations for the origins of dogs' social-cognitive skills is to examine the behaviour of dog puppies, specifically puppies with limited or no human contact. In their study, Hare et al. (2002) tested a group of puppies with an age range of 9–24 weeks. They found that puppies, like adult dogs, are able to use human communicative cues. However, 9–24 weeks is a wide age range, and major changes in dogs' cognitive abilities may occur even earlier. Most notably, in a longitudinal investigation of socialization of dogs with humans, Freedman et al. (1961) showed that at 7 weeks of age puppies are most receptive to socialization with humans. To determine whether human exposure influences dogs' behaviour, it is therefore necessary to investigate dogs' response to human communicative cues before the age of 7 weeks. We therefore conducted a series of experiments investigating the ontogeny of cue reading in dogs by comparing different age groups from 6 weeks on.

EXPERIMENT 1

In this first experiment we systematically investigated the performance of four different age groups in the object choice paradigm across three different human communicative cues (dynamic cross point, dynamic cross point move and marker).

Methods

Subjects

Sixty-four domestic dog puppies of various breeds participated in the experiment. We tested 16 subjects per age class and there were four specific age classes: 6 weeks, 8 weeks, 16 weeks and 24 weeks. All puppies were reared by their mothers until 8 and 9 weeks of age. There were 30 females and 34 males; 41% were herding dog breeds, 28% were hunting dog breeds, 19% were mongrels, 9% were terrier and 3% were working dogs (we used the breed classification defined by the Fédération Cynologique Internationale; this classification includes 10 breed groups). In the 6- and 8-week-old puppy groups some individuals were littermates which can be seen in Table 1, for the 6-week-old group we tested four different litters with a maximum of five subjects per litter and for the 8-week-old group we tested six different litters with a maximum of six subjects per litter.

All puppies were recruited by phone from owners in a medium-sized German city. The puppies had not participated in experiments previously. We recruited six additional puppies that were not included in the experiment because they either did not pass the warm-up phase (two dogs) or refused to participate after a certain number of trials (four dogs).

Procedure

The test was conducted during October 2004 and September 2005. For the 16- and 24-week-old puppies testing took place in a quiet room of approximately 20 m^2 in the dog research center of the Max-Planck Institute Leipzig with the owners present throughout the test. For the 6- and 8-week-old puppies testing was conducted at their breeding home because these puppies were too young to be separated from their mothers for a longer time. To control for effects of environment the young puppies were tested in a controlled room in their home environment. This room was unfamiliar to them, cleaned and emptied from all distracting objects. Each puppy was tested individually; therefore each puppy had to be separated from its littermates and mother for approximately 10 min per session, totaling 40 min of separation per day. The puppies and the mothers showed no signs of stress during the periods of separation nor any changes in behaviour after returning to the litter. The owners of the puppies were present and waiting in an adjacent room during the entire time of testing.

The basic setup was identical for all age groups (see Fig. 1 for details). In each trial, one experimenter (E2) stood behind the dog and held it by the collar. A second experimenter (E1) sat on the ground 150 cm away from the dog, between two identical cups placed 100 cm apart from each other and oriented upside down so that the puppies could not see the food underneath. A trial started when E1 got the dog's attention by showing a piece of food (dog treat). Then E1 hid the food, placing it under one of two plastic cups (blue coloured, diameter = 13 cm, height = 7 cm). To ensure that the subject could not determine the final location of the food during the hiding process, E1 always touched both cups starting with the left cup and followed by the right cup. E2 was always unaware of the location of the food at the beginning of each trial. E2 was not blindfolded but behaved neutrally to the highest degree possible and did not cue the dogs in any way. This was to rule out that unconscious cueing could take place. A control condition was conducted to control for odour as a cue for the dog, but we equalized the smell of both cups also by ensuring that both had been in contact with food before the experiment began.

Before the test trials began, each puppy first participated in six warm-up trials where it received complete information

Table 1. Individual data and number of correct choices in experiment 1 (total number of trials per condition = 8)

Age group	Subject	Litter	Breed group	Gender	Dynamic cross point move	Dynamic cross point	Marker	Control
Six weeks	Emma	1	Mongrel	F	5	7*	8*	4
	Kleine	1	Mongrel	F	2	5	6	2
	Nils	1	Mongrel	M	6	5	7*	7*
	Filu	1	Mongrel	M	6	4	5	3
	Hanna	1	Mongrel	F	5	5	3	6
	Calvin	2	Herding	M	6	6	8*	5
	Calypso	2	Herding	M	7*	7*	8*	2
	Clara	2	Herding	F	7*	6	8*	4
	Conzalis	2	Herding	M	7*	6	7*	2
	Drei	3	Hunting	M	6	6	8*	5
	Vier	3	Hunting	F	8*	8*	8*	7*
	Jacek	4	Herding	M	6	5	5	3
	Janosch	4	Herding	M	6	5	6	3
	Jessica	4	Herding	F	8*	8*	7*	5
	Jojo	4	Herding	M	7*	7*	7*	3
	Jorko	4	Herding	M	8*	5	8*	5
Eight weeks	Frank	1	Mongrel	M	3	5	8*	5
	Lara	1	Mongrel	F	5	6	8*	6
	Kaja	8	Herding	F	5	6	8*	5
	Kara	8	Herding	F	6	7*	8*	3
	Koko	8	Herding	F	7*	7*	8*	2
	Fünf	3	Hunting	F	7*	8*	8*	3
	Sechs	3	Hunting	M	6	5	8*	2
	Acht	3	Hunting	M	8*	7*	8*	2
	Adam	5	Hunting	M	4	8*	6	2
	Asta	5	Hunting	F	5	5	8*	2
	Bello	5	Hunting	M	6	6	7*	4
	Ella	5	Hunting	F	7*	8*	8*	3
	Mobby	5	Hunting	M	5	6	7*	1
	Quietschie	5	Hunting	M	7*	7*	7*	2
	Candel	6	Hunting	F	7*	6	6	3
	Dienne	7	Herding	F	8*	7*	8*	5
Sixteen weeks	Balou	9	Hunting	M	6	8*	8*	4
	Bolle	10	Hunting	M	8*	7*	8*	3
	Cantor	11	Herding	M	6	5	8*	5
	Dusty	12	Terrier	M	8*	8*	8*	4
	Enja	13	Herding	F	8*	4	8*	5
	Fenja	14	Herding	F	6	7*	5	6
	Ingwin	15	Working	M	8*	8*	8*	3
	Lenny	16	Mongrel	M	7*	7*	8*	2
	Lucy	17	Terrier	F	8*	7*	5	2
	Nemo	18	Mongrel	M	4	5	8*	5
	Paula	19	Herding	F	6	7*	8*	1
	Phil	20	Mongrel	M	7*	6	8*	4
	Reika	21	Herding	F	8*	7*	8*	3
	Sherly	22	Hunting	F	7*	8*	8*	6
	Toby	23	Hunting	M	8*	7*	8*	5
	Yahra	24	Terrier	F	8*	7*	8*	6
Twenty-four weeks	Angie	25	Herding	F	6	6	8*	0
	Anna	25	Herding	F	4	3	8*	4
	Anne	25	Herding	F	7*	7*	8*	6
	Arthur	25	Herding	M	8*	8*	8*	7*
	Balu	26	Herding	M	6	5	8*	3
	Higgins	27	Terrier	M	7*	8*	8*	3
	Jessy	28	Herding	F	8*	7*	8*	4
	Joshua	29	Hunting	M	8*	7*	8*	5
	Kessy	30	Terrier	F	7*	8*	8*	5
	Leni	31	Working	F	6	5	8*	3
	Lina	32	Terrier	F	7*	7*	8*	3
	Necki	33	Hunting	M	8*	8*	8*	3
	Nemo	34	Mongrel	M	7*	8*	8*	4
	Odin	35	Mongrel	M	7*	7*	8*	3
	Sandy	36	Herding	F	8*	6	8*	3
	Theo	37	Herding	M	6	8*	8*	5

*Data points that are significantly above chance (two-tailed binominal test).

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Figure 1. General setup for the different experiments with the containers being placed next to the experimenter in experiment 1 (top) and next to the dog in experiments 2 and 3 (bottom).

about the location of the food while it was being hidden by E1. The procedure of the warm-up trials was as follows: E1 showed the food to the subject and then while lifting one of the two cups totally from the ground E1 placed the food under full view under this cup and without touching the other cup the dog was released and allowed to chose. Virtually all dogs met the criterion of six correct warm-up trials in a row. After subjects passed the warm-up phase, they participated in the actual test. Here, E1 first hid the food and then gave one of three possible human communicative cues that indicated the location of the food. To underline the communicative nature of each cue it was always presented with the human gaze alternating between the location of the food and the dog. Evidence that dogs distinguish between gestures given with and without gaze alternation comes from a study by Bräuer et al. (2006) in which dogs would follow a human pointing and gaze alternating more than a human reaching for the correct cup but not looking at the dog at any time.

Dynamic cross point. E1 pointed to the correct cup once and in full vision of the subject and with the extended index finger of her contra lateral hand. In addition E1 alternated her gaze between the subject and the cup four times. The distance between index finger and cup was about 23 cm. E1 remained in the pointing position until the dog made a choice. Following Miklósi & Soproni (2006), this gesture can be defined as dynamic, proximal, cross body and symmetric.

Dynamic cross point move. E1 pointed repeatedly towards the correct cup four times with the extended index finger of her contra lateral hand. Additionally, she alternated her gaze between the subject and the cup. The distance between index finger and cup was about 23 cm.

Marker. E1 obtained the dog's attention by showing it a marker (black and white coloured piece of wood; $11 \times 7 \times 3$ cm). E1 then placed the marker on top of the cup with food, looking at the cup as she placed the marker. E1 removed her hand and adopted the relaxing position with only the gaze alternation still being present between subject and cup plus marker on top.

Control. E1 turned towards the subject but remained still with head and gaze straight down.

E1 continued to give the cue in all conditions until E2 released the dog and the dog had made its choice. As in previous studies, dogs almost always made their choice immediately by approaching one of the cups and nudging it with the nose.

If the subject chose the correct cup, it was allowed to eat the food; if it chose the incorrect cup, E1 took the food from the correct cup with the dog watching and put it back in a bag.

We used a within-subject experimental design, with each of the 64 subjects experiencing each of the four conditions. Each subject received eight trials per condition, totaling 32 trials. All trials were presented in a single session (with breaks after a set of eight trials). Conditions were presented in a randomized order with the stipulation that the same condition was not presented in more than two consecutive trials. The location of the food was counterbalanced and randomized with the stipulation that food appeared in the same location for not more than two consecutive trials.

Scoring and analyses

The two experimenters scored the dog's choice live, but E2 also coded 100% of their performance from videotapes. For reliability purposes a third coder coded 20% of the video material. Interobserver reliability was excellent (Cohen's kappa = 1.0, $N = 406$). We used ANOVAs and t tests to make comparisons across age groups and conditions and one-sample t tests (with 50% expected probability) to assess the deviation from chance responding. The majority of puppies in our sample could be grouped in two breed groups (herding dogs and hunting dogs). For further comparisons we also looked at the two breed groups to determine whether they behaved differently. All tests were two tailed.

Results

Figure 2 shows the mean per cent correct responses of all four age groups in each condition (see also individual data in Table 1). Each condition was first compared to chance using a one-sample t test. The puppies of all age groups showed above-chance selection of the correct container in all conditions ($P < 0.0001$) except the control condition (6 weeks: $P = 0.769$; 8 weeks: $P = 0.029$; 16 weeks: $P = 1.00$; 24 weeks: $P = 0.646$), (control: 6 weeks:

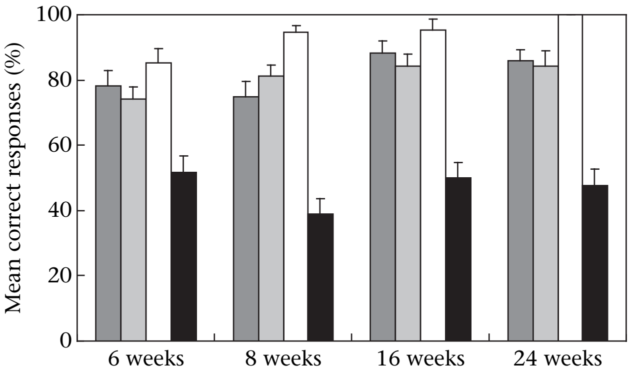

Figure 2. Mean correct responses (%) shown by each of the four test groups (age groups) in the dynamic cross point move, dynamic cross point, marker and control conditions with SE. All comparisons of experimental condition against the control condition are significant with $P \leq 0.001$. (■) Dynamic cross point move; (■) dynamic cross point; (□) marker; (■) control.

$t_{15} = 0.30$; 8 weeks: $t_{15} = -2.41$; 16 weeks: $t_{15} = 0.00$; 24 weeks: $t_{15} = -0.47$; marker: 6 weeks: $t_{15} = 7.65$; 8 weeks: $t_{15} = 19.59$; 16 weeks: $t_{15} = 14.15$; 24 weeks: 100% correct; dynamic cross point: 6 weeks: $t_{15} = 6.56$; 8 weeks: $t_{15} = 9.68$; 16 weeks: $t_{15} = 9.29$; 24 weeks: $t_{15} = 7.65$; dynamic cross point move: 6 weeks: $t_{15} = 6.07$; 8 weeks: $t_{15} = 5.66$; 16 weeks: $t_{15} = 10.37$; 24 weeks: $t_{15} = 10.57$).

To determine whether there was an interaction of age with the conditions, we ran a mixed-model ANOVA with condition as a within-subjects factor and age group as a between-subjects factor. There were significant effects of condition ($F_{3,180} = 119.739$, $P < 0.0001$) and age group ($F_{3,60} = 2.852$, $P = 0.045$) with subjects being significantly more successful in the experimental than in the control condition. This effect was independent from age as there was no significant interaction between condition and age group ($F_{9,180} = 1.594$, $P = 0.12$). To specifically examine the influence of age on the puppies' performance, we conducted one-way ANOVAs for each condition (all Bonferroni corrected) with age group as a between-subjects factor. This analysis indicated that the only significant difference between dog age classes was in the marker condition ($F_{3,60} = 4.232$, $P = 0.009$). Post hoc analysis (Bonferroni corrected) revealed that the 6- and 24-week-old puppies significantly differed in their ability to use the marker as a social cue ($P = 0.006$): the older puppies were more successful than younger puppies in this condition.

To test for learning within the experimental session, we conducted a mixed-model ANOVA comparing the first four trials of each experimental condition against the last four trials of each experimental condition, with age group as a between-subject factor. There was no evidence for learning whatsoever because performance in the experimental conditions did not improve over time ($F_{2,120} = 0.284$, $P = 0.753$) and this was true for all age groups ($F_{6,120} = 0.596$, $P = 0.733$).

To test for differences in performance due to breed, we conducted a final ANOVA comparing the two major breeds (hunting versus herding; $N = 18$ versus $N = 26$) across the three experimental conditions. As age did not have an effect in most of the experimental conditions (recall that there was only a minor effect in the marker condition) we looked at these two main breed groups (see Methods for further explanation for what constitutes the breed groups) independent of age. Although there was the expected significant effect of condition ($F_{2,84} = 15.14$, $P < 0.0001$), breed group did not have a significant effect on the performance of the puppies because there was no interaction between condition and breed group ($F_{2,84} = 2.09$, $P = 0.130$).

Discussion

The results of this experiment indicated that dogs as young as 6 weeks old can use a variety of human communicative gestures to locate hidden food. Indeed, even the youngest of puppies were as skilful at using these cues as the older puppies, which suggests that dogs do not acquire these skills mainly because of their experiences in ontogeny. The youngest dog age class (6 weeks) examined in this experiment still lived in their breeding home with their littermates and had not yet reached the most sensitive period of socialization with humans. Thus, human interaction and influence on their behaviour was reduced to a minimum. These results therefore strongly support the hypothesis that an understanding of human social cues is a dog-specific adaptation that is a functional aspect of dogs' behavioural repertoire from an early age. This experiment also suggests that the two breed groups tested (hunting and herding dogs) do not differ in their abilities to use human social cues, at least at younger ages.

Overall, the young dogs' behaviour in this paradigm was very successful. However, our observations during the tests indicated that many puppies had a tendency to approach the hand of the human experimenter before they made their choice, which may have helped the puppies to choose correctly without actually using the pointing gestures as social cues because they could have simply followed the direction of the hand to the correct location. Notably, comparisons between dogs and wolves indicate that dogs show an increased tendency to approach humans and would even prefer to do so over approaching a conspecific (Topal et al. 2005). More specifically, the dogs' tendency to especially attend to the humans' hand (Soproni et al. 2002; Riedel et al. 2005; Miklósi & Soproni 2006) may partially account for the puppies' successful behaviour in this experiment. In this experiment and others it is not clear whether puppies or dogs in general understand the triadic nature of pointing gestures in the way that even young human children do (Behne et al. 2005). Specifically, it is unknown whether dogs would follow human pointing gestures to outside events. Although some evidence indicates that local enhancement alone cannot account for adult dogs' behaviour in object choice tasks (Hare et al. 1998; Soproni et al. 2002), there is no evidence that dog puppies understand the pointing gesture as being directed to some outside event. To investigate this possibility, we altered the general setup of the experiment so that puppies had to move away from the experimenter's hand to solve the problem successfully and could not simply approach their hand and follow its position to the correct location.

EXPERIMENT 2

To investigate the flexibility of the puppies' behaviour, we changed the setup from the previous experiment so that the cups were placed beside the dog rather than beside the experimenter. This allowed us to investigate whether dog puppies understand the triadic nature of pointing gestures or whether a preference for the hand accounts for the successful behaviour of the puppies in this type of task. We also changed the gesture itself to reduce the possibility of local enhancement as much as possible.

Methods

Subjects

We tested 48 domestic dogs of various breeds (29 females and 19 males). Subjects were classified into one of three groups based on their age and experiential backgrounds: 6-week-old puppies, naïve adults (mean age (years) $\pm$ SD $= 4.2 \pm 3.1$), and experienced adults (mean age (years) $\pm$ SD $= 4.7 \pm 3.2$). We tested 16 subjects per age group. The experienced adults had already participated in an object choice experiment and were able to successfully use human pointing gestures (see Table 2 for individual performance in former object choice tasks within the pointing condition), whereas naïve adults and the 6-week-old puppies had not previously participated in object choice experiments. Fifty per cent of the dogs were herding dog breeds, 29% were mongrels, 10.5% were terrier and 10.5% were hunting dogs. In the 6-week-old puppy group some individuals were littermates (see Table 2). We tested four different litters with a maximum of six subjects per litter. As before, dogs were recruited by phone from owners in a medium-sized German city.

Procedure

We conducted this experiment between August 2005 and August 2006. The adult dogs were tested in the same room as the 16- and 24-week-olds in the first experiment, whereas the 6-week-olds were again tested at their breeding home because these puppies were too young to be separated from their mothers for a longer time. To control for effects of environment the young puppies were tested in a controlled room in their home environment. This room was unfamiliar to them, cleaned and emptied from all distracting objects. Each puppy was tested individually; therefore we briefly separated each puppy from its littermates and mother for approximately 10 min per session, totaling 20 min of separation per day. The puppies and the mothers showed no signs of stress during the periods of separation nor any changes in behaviour after returning to the litter.

The warm-up trials and basic procedure of the experimental trials were conducted in the same way as in the first experiment. Again E2 was never aware of the location of the food. However, trials in this experiment differed from those in experiment 1 in the placement of the two cups (see Fig. 1). As before, the cups were placed 100 cm apart, but in this experiment they were located next to the dog rather than next to E1 (see Fig. 1). After baiting the cups, we presented two different conditions.

Distal point middle. E1 pointed to the correct cup with the extended index finger of her contra lateral hand (see Fig. 1) but with her arm extended from the centre of her body. Only the index finger indicated the correct cup; the position of the experimenter's arm did not provide information about its location. E1 alternated her gaze between the subject and the cup four times. The distance between index finger and cup was about 100 cm. Following Miklósi & Soproni (2006), this pointing gesture is defined as dynamic, distal, cross body and symmetric.

Control. E1 turned towards the subject and oriented her head and gaze direction straight down without giving any cue.

E1 resumed giving her cue until E2 released the dog and the dog had made its choice. If after 1 min the dogs did not make a choice, the trial was not used. Two puppies did not choose in one trial of the control condition.

If the dog chose the correct cup, it was allowed to eat the food; if it chose the incorrect cup, E1 took the food while the dog watched and put it back in the food bag. The experimental design was within-subjects, with each subject receiving eight trials in each condition for a total of 16 trials in a single session; subjects received a break after a set of eight trials. Conditions were presented in a randomized order with the stipulation that the same condition was not presented in more than two consecutive trials. The side on which the food was hidden was counterbalanced and randomized, with the stipulation that food was not in the same location for more than two consecutive trials.

Scoring and analyses

The two experimenters coded the choice of the dogs live, and all choices of the dogs were also coded by E2 from the videotaped recordings. For reliability purposes a second coder coded 20% of the video material. Interobserver reliability was excellent (Cohen's kappa $=$ 0.975, $N = 160$). In addition to the dogs' choices, we also scored whether the dog approached E1's hand before it made a choice of one of the cups. The hand-visiting behaviour was defined as follows: after E2 released the dog, the dog did not approach the cups directly but went instead to the hand and arm of E1 and then approached the cups to make its choice. The dog could visit the hand once per trial (or not at all). The number of visits per condition was coded from the videotapes. For further analysis we used only the hand-visiting behaviour in the pointing conditions because it was much more frequent than in the control condition. Statistical analysis was similar to that in experiment 1. However, breed comparisons in this experiment were not possible due to the small number of individuals in each breed group.

Table 2. Individual data and number of correct choices in experiment 2 (total number of trials per condition = 8)

Age group	Subject	Litter	Breed group	Gender	Distal point middle (DPM)	Control	Visit hand during DPM	Performance before in point
Six weeks	Kara	39	Herding	F	5	0	0	Not tested
	Karina	39	Herding	F	4	4	1	Not tested
	Khan	39	Herding	M	5	3	1	Not tested
	Kiku	39	Herding	F	7*	2	0	Not tested
	Kira	39	Herding	F	5	3	1	Not tested
	Kyrus	39	Herding	M	6	3	0	Not tested
	Adam	40	Herding	M	4	3	1	Not tested
	Eva	40	Herding	F	3	2	3	Not tested
	Locke	40	Herding	F	5	3	3	Not tested
	Panda	40	Herding	F	5	3	3	Not tested
	Paule	40	Herding	M	6	3	2	Not tested
	Pünktchen	40	Herding	F	3	4	2	Not tested
	Kimi	41	Herding	F	6	2	6	Not tested
	Lisa	41	Herding	F	3	3	2	Not tested
	Molly	41	Herding	F	4	4	6	Not tested
	Pit	42	Terrier	M	4	6	5	Not tested
Naïve adults	Amy		Hunting	F	5	3	2	Not tested
	Couper		Herding	M	4	4	0	Not tested
	Dasso		Herding	M	3	2	1	Not tested
	Galina		Herding	F	3	4	6	Not tested
	Luka		Mongrels	F	4	4	2	Not tested
	Luna		Herding	F	3	6	5	Not tested
	Luna		Mongrels	F	4	3	1	Not tested
	Luna2		Terrier	F	3	6	0	Not tested
	Lupo		Mongrels	M	6	3	1	Not tested
	Maddie		Herding	F	4	4	2	Not tested
	Pasko		Herding	M	3	4	0	Not tested
	Quincy		Herding	M	3	4	1	Not tested
	Tisza		Mongrels	M	5	3	1	Not tested
	Tony		Mongrels	M	3	4	5	Not tested
	Tracy		Mongrels	F	4	4	5	Not tested
	Zadek		Herding	M	3	2	5	Not tested
Experienced adults	Akira		Mongrels	F	4	4	0	87.50%
	Alice		Herding	F	3	5	0	87.50%
	Ambula		Hunting	M	2	4	0	87.50%
	Auguste		Mongrels	F	3	5	3	100%
	Ben		Mongrels	M	4	4	0	100%
	Dusty		Terrier	M	4	4	1	100%
	Higgins		Terrier	M	5	3	6	100%
	Jonas		Mongrels	M	6	4	1	100%
	Kessy		Terrier	F	5	4	0	100%
	Lotte		Hunting	F	4	4	0	100%
	Lucy		Hunting	F	6	3	2	87.50%
	Lucy2		Mongrels	F	4	4	1	87.50%
	Mora		Mongrels	F	4	2	0	100%
	Necki		Hunting	M	7*	3	8	100%
	Ronja		Mongrels	F	4	3	1	100%
	Ronja2		Mongrels	F	7*	4	0	100%

*Data points that are significantly above chance (two-tailed binominal test).

Results

Figure 3 presents the mean per cent correct responses of the three dog groups across conditions (see also individual data in Table 2). Each condition was first compared to chance using a one-sample *t* test. In the experimental condition, only the 6-week-old puppies chose the correct cup above chance ($t_{15} = 2.3$, $P = 0.036$) and not the two adult groups (naïve adults: $t_{15} = -1.07$, $P = 0.30$; experienced adults: $t_{15} = 1.41$, $P = 0.178$). The performance in the control condition was not above chance for the two adult groups (naïve adults: $t_{15} = -0.89$, $P = 0.388$; experienced adults: $t_{15} = -1.29$, $P = 0.216$) and the 6-week-old puppies were significantly below chance ($t_{15} = 3.09$, $P = 0.007$).

To examine how puppies, naïve adult dogs, and experienced adult dogs performed on the test, we conducted a 3 (dog group) × 2 (condition) ANOVA. Dogs were more successful at finding the food in the experimental condition than in the control condition ($F_{1,45} = 9.157$, $P = 0.004$). In contrast, there were no significant differences between groups ($F_{2,45} = 1.319$, $P = 0.277$). However, there was a significant condition × group interaction ($F_{2,45} = 3.25$, $P = 0.048$). Consequently, we analysed the behaviour of the different age groups separately, conducting

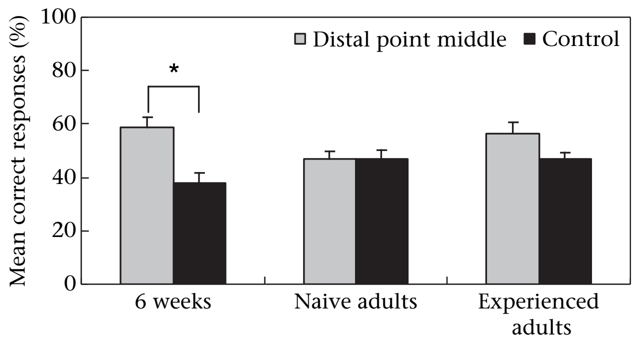

Figure 3. Mean correct responses (%) shown by each of the three test groups (age groups) in the distal point middle and control conditions with SE and asterisks to mark statistically significant results for the distal point middle against the control condition: $*P < 0.05$.

a paired-sample *t* test to compare the experimental and control conditions. The comparison indicated that the 6-week-old puppies were significantly better at locating the food in the experimental condition ($t_{15} = 3.364$, $P = 0.004$); the performance of the naïve adults ($t_{15} = 0.0$, $P = 1.0$) and the experienced adults ($t_{15} = 1.627$, $P = 0.125$) did not statistically differ between the experimental and the control conditions.

Subjects of each group visited the hand of the experimenter before actually making their choice. This behaviour occurred in the 6-week-old puppies ($\overline{X} \pm SD = 29.7 \pm 26.2$, $N = 16$), the naïve adults (29.7 ± 27.7, $N = 16$) and the experienced adults (18.8 ± 29.6, $N = 16$). We next further examined whether approaching the experimenter's hand prior to making their choice actually helped them locate the food. To do so, we performed separate nonparametric correlations for each dog group. We tested whether dogs' success rate in the experimental condition was correlated to the rate at which the puppies would approach the hand before making their choice. There was no correlation between these two variables for any of the groups (puppies: $r_S = -0.309$, $N = 16$, $P = 0.245$; naïve adults: $r_S = -0.199$, $N = 16$, $P = 0.461$; experienced adults: $r_S = 0.333$, $N = 16$, $P = 0.207$).

Finally, we examined whether there were any learning effects within the experiment. We conducted an ANOVA comparing the first four trials of the experimental condition against the last four trials of the experimental condition, with age group as a between-subject factor. There was no evidence for learning as within the experimental condition ($F_{1,45} = 0.011$, $P = 0.918$) and this was true for all dog groups ($F_{2,45} = 0.462$, $P = 0.633$).

Discussion

The results of this experiment show that 6-week-old puppies use human pointing gestures by following them to an outside entity. Approaching the experimenter's hand did not influence their success in using the communicative cue provided, ruling out low-level interpretations such as local enhancement. Surprisingly, the experimentally naïve and experienced adult dogs failed to use the pointing gesture in this new setup. That puppies use a human communicative cue that adult dogs do not use may indicate that puppies are more sensitive to human communicative cues than adult dogs. However, this is unlikely given the results of the first experiment, which showed no effects of age on the puppies' ability as might be expected if ontogeny and exposure to humans plays a major role in the development of these skills. The adult dogs' low success in using the given cue is even more surprising given that the gesture was accompanied with gaze alternation, a cue which alone is used by adult dogs to find food (Bräuer et al. 2006). Potentially the two stimuli (gaze and hand cue) may give conflicting information for the dogs. While the gaze cue is clearly directed towards the cup, the hand cue may not be readable. To further test this we conducted a third experiment in which we introduced a less ambiguous cue.

EXPERIMENT 3

We conducted a follow-up experiment in which the general setup was comparable to that of experiment 2, but a more natural pointing gesture was provided. This gesture included extension of the arm, a feature lacking in the gesture used in experiment 2. This is one feature that older dogs might expect to be present in human social cues due to their more extensive interactions with humans; by using a gesture that lacked this cue, experiment 2 may have obscured adults' flexible use of human cues.

Methods

Subjects

Thirty-two domestic dogs of various breeds participated in the experiment (18 females and 14 males). The dogs were either 6-week-old puppies or experimentally naïve adult dogs (mean age (years) $\pm$ SD $= 6.6 \pm 3.9$). We tested 16 subjects per age group. Fifty per cent were herding dog breeds, 41% were mongrels, 3% were terrier and 6% were toy dogs. In the 6-week-old puppy group some individuals were littermates which can be seen in Table 3; we tested four different litters with a maximum of six subjects per litter. Recruitment was similar to the other experiments. None of the dogs had participated in the other two experiments or in any other object choice experiment.

Procedure

We conducted this experiment between November 2005 and August 2006; as before, adults were tested in the experimental room and puppies were tested in their breeding homes because these puppies were too young to be separated from their mothers for a long time. To control for effects of environment the young puppies were tested in a controlled room in their home environment. This room was unfamiliar to them, cleaned and emptied from all distracting objects. During the test, puppies were separated from their littermates and mother for 20 min per day. The warm-up trials were conducted as in the two other experiments. The basic procedure of the experimental trials and the materials were similar to those

Table 3. Individual data and number of correct choices in experiment 3 (total number of trials per condition = 8)

Age group	Subject	Litter	Breed group	Gender	Distal point side (DPS)	Control	Visit hand during DPS
Six weeks	Sechs	43	Herding	F	7*	6	3
	Acht	43	Herding	F	5	6	3
	Drei	43	Herding	M	5	4	0
	Vier	43	Herding	M	4	3	3
	Zwei	43	Herding	F	8*	4	2
	Neun	43	Herding	M	5	6	2
	Fatima	44	Herding	F	6	4	6
	Felica	44	Herding	F	4	5	1
	Ferres	44	Herding	M	6	3	3
	Finja	44	Herding	F	5	5	0
	Fion	44	Herding	M	4	4	3
	Fiscus	44	Herding	M	5	3	4
	Flecki	41	Herding	F	7*	5	7
	Nicky	41	Herding	F	5	4	6
	Susi	41	Herding	F	4	5	7
	Eddy2	42	Terrier	M	6	6	2
Adults	Arne		Mongrels	M	5	4	0
	Asta		Mongrels	F	5	5	1
	Balou		Mongrels	M	8*	4	0
	Bella		Mongrels	F	4	2	3
	Eddy		Mongrels	M	6	4	1
	Fritz		Mongrels	M	3	3	3
	Gustav		Terrier	M	7*	3	5
	Hugo		Mongrels	M	5	3	0
	Kurt		Working	M	6	4	7
	Luna		Mongrels	F	6	5	8
	Malve		Mongrels	F	5	3	4
	Maxi		Mongrels	F	5	3	0
	Nera		Herding	F	5	0	1
	Paula		Mongrels	F	5	3	0
	Tina		Mongrels	F	5	4	1
	Wilma		Toy	F	6	3	7

*Data points that are significantly above chance (two-tailed binominal test).

in experiment 2. Again E2 was never aware of the location of the food. Dogs experienced two different conditions.

Distal point side. E1 pointed to the correct cup with the extended index finger of the ipsilateral hand, so that the index finger and the position of the arm indicated the correct cup. E1 alternated her gaze between the subject and the cup four times. The distance between index finger and cup was about 100 cm. Following Miklósi & Soproni (2006), this pointing gesture can be defined as dynamic, distal and symmetric.

Control. After baiting, E1 turned towards the subject and looked with head and gaze straight down for 4 s without giving any cue.

E1 resumed giving her cue until E2 released the dog and the dog had made its choice. If the dog chose the correct cup, it was allowed to eat the food; if it chose the incorrect cup, E1 took the food while the dog watched and put it back in the food bag. The experimental design was within-subjects, with each subject receiving eight trials in each condition for a total of 16 trials in a single session; subjects received a break after a set of eight trials. Conditions were presented in a randomized order with the stipulation that the same condition was not presented in more than two consecutive trials. The side on which the food was hidden was counterbalanced and randomized, with the stipulation that food was not in the same location for more than two consecutive trials.

Scoring and analysis

The two experimenters coded the choice of the dogs live, and all choices of the dogs were also coded by E2 from the videotaped recordings. For reliability purposes a second coder coded 20% of the video material. Interobserver reliability was excellent (Cohen's kappa = 1.0, $N = 112$). In addition to the dogs' choices, we also scored whether the dog approached E1's hand before it made a choice of one of the cups (the hand-visiting behaviour was defined for the video coding as in experiment 2). Statistical analysis was similar to that in experiments 1 and 2. However, breed comparisons in this experiment were not possible due to the small number of individuals in each breed group.

Results

Figure 4 shows the mean per cent correct responses of the two age groups in each condition (see also individual data in Table 3). Each condition was first compared to chance and the dogs used the human communicative

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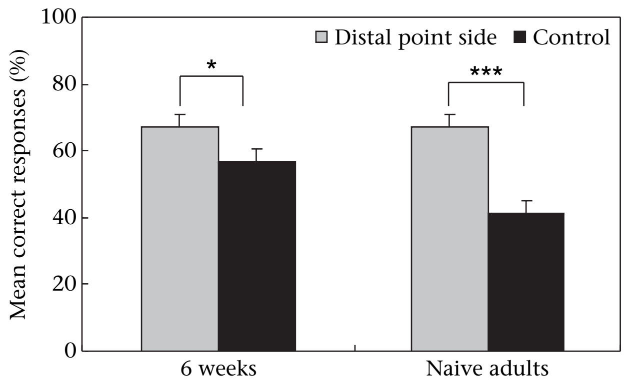

Figure 4. Mean correct responses (%) shown by each of the two test groups (age groups) in the distal point side and control conditions with SE and asterisks to mark statistically significant results for the distal point side against the control condition: $*P < 0.05$ and $***P < 0.001$.

cue well above chance (puppies: $t_{15} = 4.568$, $P < 0.0001$; adults: $t_{15} = 4.793$, $P < 0.0001$).

Again we conducted a mixed-model ANOVA to determine whether there was an interaction of age with the conditions. There was a significant effect for condition ($F_{1,30} = 31.302$, $P < 0.0001$) with dogs performing significantly better in the experimental than in the control condition and no overall effect of age ($F_{1,30} = 3.812$, $P = 0.06$). However, age had an effect on the behaviour of the dogs in the different conditions ($F_{1,30} = 5.917$, $P = 0.021$). We therefore analysed both age groups separately. A paired-sample *t* test of the experimental against the control condition showed that both the puppies ($t_{15} = 2.145$, $P = 0.049$) and the adults ($t_{15} = 5.94$, $P < 0.0001$) used the human communicative cue provided.

Subjects of the two groups visited the hand of the experimenter before actually making their choice. This behaviour occurred in the 6-week-old puppies ($\overline{X} \pm SD = 48.4 \pm 27.7$, $N = 16$) and in the naïve adults (32.8 ± 35.6, $N = 16$). We next further examined whether subjects' approaches to the experimenter's hand prior to making their choice actually helped them locate the food. Dogs' success rate in the experimental condition was not correlated to the rate at which they would approach the humans' hand before making their choice for either puppies ($r_S = 0.126$, $N = 16$, $P = 0.642$) or adults ($r_S = -0.250$, $N = 16$, $P = 0.351$).

To test for learning during the experiment, we conducted an ANOVA comparing the first four trials of the experimental condition against the last four trials of the experimental condition, with age group as a between-subject factor. There was no evidence for learning within the experimental condition ($F_{1,30} = 0.062$, $P = 0.805$) and this was true for all age groups ($F_{1,30} = 0.556$, $P = 0.462$).

Discussion

In experiment 3, both adult dogs and 6-week-old puppies were able to follow the pointing gesture to locate hidden food. The adult dogs may have been more successful here than in experiment 2 because the experimenter's gesture was less ambiguous. As in experiment 2, approaching the experimenter's hand before making a choice did not improve the dogs' performance. This is strong evidence that even very young dogs can use pointing gestures even when they cannot depend on simpler strategies (such as local enhancement of the correct location).

GENERAL DISCUSSION

Based on this set of results we conclude that dogs' ability to follow human communicative cues is a skill present in dogs before exposure to humans can have ontogenetically major influences on dogs' behaviour. The dog puppies tested in these experiments were successful in using human-given communicative cooperative cues from the age of 6 weeks on with no major differences between age classes. As dog puppies by the age of 6 weeks had not yet reached the most sensitive period of socialization with humans (Freedman et al. 1961), human exposure as a factor driving the communicative skills of the puppies was excluded as much as possible. This is therefore strong evidence that human exposure has no major effect on dogs' ability to use human-given communicative cues and that this skill therefore represents a special adaptation in dogs which is present from early age. These results have several important implications to both evolutionary and cognitive perspectives.

From an evolutionary perspective the results support the idea that dogs' communicative skills are a special adaptation and the result of selection processes during domestication. However, these experiments do not allow further specification of which evolutionary events led to dogs' ability in this domain. One possible scenario is that humans directly selected a certain population of wolves for the ability to use human-given cues. As humans needed other animals with which they could interact over a distance (hunting, herding, etc.) they may have directly selected for their ability do so (Coppinger & Coppinger 2002). A second possible scenario is that dogs' communicative skills develop as result of indirect selection and as a by-product of selection for other behaviours. Hare & Tomasello (2005) hypothesized that changes during domestication in the system mediating social reactivity may have led to changes in certain social skills in dogs. This hypothesis is based mainly on research with foxes selected for tame behaviour, which means selection against fear and aggression (Belyaev 1979), which were more skilful in using cooperative communicative cues than their unselected counterparts (Hare et al. 2005).

Changes in dog temperament by humans selecting against fear and aggression can be seen as one prerequisite for the successful approach between humans and wolves (Coppinger & Coppinger 2002). This leads to the third possible scenario of a combination of both indirect and direct selection, which assumes two waves of domestication. After a first wave of domestication which led to certain temperamental changes, a subgroup of dogs was put under additional selection for their skills in using

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human-given cues (Coppinger & Coppinger 2002). As humans needed dogs for certain functions they may have selected certain populations more specifically. Following this hypothesis we predict that working dogs, selected for specific functions (e.g. herding, hunting, etc), should be especially skilful in using human-given communicative cues compared to nonworking dogs (e.g. toy dogs). V. Wobber, J. Koler-Matznick, B. Hare, R. Wrangham and M. Tomasello (unpublished data) tested this hypothesis by comparing adult individuals of various breeds of dogs. Their data suggest that what predicts dogs' social skills best is whether the dog belonged to a working breed.

From a cognitive perspective the overall results are interesting as they give first evidence that when dog puppies use the human pointing gesture they do so by actually following the pointing and not by using simpler mechanisms, e.g. approaching the human's hand and then the cup closest to it. Puppies here also did not appear to follow simple visual stimuli, such as the hand and index finger protruding from the human's body contour, as has been suggested to be the factor driving dogs' behaviour in these situations (Soproni et al. 2002; Miklósi & Soproni 2006). To be able to perceive the arm as protruding from the body, dogs would have had to approach the human sideways and then follow the cue. However, approaching the human did not affect the dogs' success in our experiments. To be successful in some of the tasks that we provided in our experiments, the dogs had to move away from the hand instead of towards it. This suggests that the dog puppies understand the relation between the pointing gesture and the outside referent. The dogs therefore appear to understand the communicative nature of the pointing gesture. However, the results of these experiments and others give no indication of whether dogs take into account the communicative intent of the human (see for a review Miklósi & Soproni 2006). Therefore we cannot conclude whether dogs understand the pointing gesture as referential because this would require both comprehension of the relation between the gesture and its outside referent and comprehension of the signaller's communicative intent. Human children from an early age clearly understand the intentional aspects of the pointing gesture and do not simply follow it and use it as a visual cue (Behne et al. 2005). They for example make a clear distinction between pointing gestures given with a communicative intent and situations in which some of the visual features of a pointing gesture appear accidentally, e.g. because the experimenter is checking her watch (Behne et al. 2005). Whether dogs make this same distinction is yet unknown and should be the subject of further experimentation.

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