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"We will work for you" – Social influence may suppress individual food preferences in a communicative situation in dogs

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ABSTRACT

The level of motivation (i.e. incentive power) is thought to be one of the most important factors affecting performance and learning in various tasks. We investigated whether reward quality has an effect on the performance of family dogs in a two-way object choice test in which they can find the hidden food by relying on distal momentary human pointing cues. In three experiments we varied (1) the type of food reward according to the subjects' own preference; (2) the quality of the reward offered at the same time in the indicated and not-indicated locations; and (3) the order of the high or low quality rewards in consecutive sessions. In Experiment 1, we first tested whether dogs prefer one kind of reward over another. Then one group was tested with the 'preferred' food as reward in the indicated bowl, while dogs in the other group received the 'non-preferred' food as reward. We did not find any difference between the performance and choice latencies of the two groups. In Experiment 2 for the first group, the indicated bowl contained a piece of carrot and the notindicated bowl was empty. In the second group the indicated bowl contained carrot, but the not-indicated bowl contained sausage. According to a preliminary preference test, most dogs prefer sausage over carrot invariably. After 20 trials, the two groups performed surprisingly similarly. There was no difference found between groups in the number of correct choices, incorrect choices and non-choices. However, the comparison between the first and last five trials revealed that subjects who found sausage when they chose the not-indicated bowl (did not follow the pointing) chose the non-indicated bowl significantly more often toward the end of their test session. In Experiment 3, each dog received two sessions with 12 pointing trials in each. For the first session, one group was rewarded with sausage and the other with carrot upon choosing the indicated bowl. In the second session, the indicated bowl contained dry dog food for both groups. We found that correct choices and response latencies did not change over two sessions in the 'sausage' group. In the 'carrot' group, the dogs chose faster in the second session, but their performance did not improve; in fact, they chose the not-indicated bowl more often than the indicated bowl. As a conclusion, we can say that reward quality had some effect on dogs' choice behavior in these experiments. The drop in their performance was not drastic, taking into account the general refusal to eat one of the 'rewards' (carrot) during the preference tests and also during the test

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trials. It seems that incentive contrast may play a relatively minor role in dog-human social interactions. Appropriate reward quality can be very important in asocial problem solving tasks, but, when interacting with humans, following human signals may override the effect of changed incentive power.

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Reward is considered a fundamental factor to the organization of behavior (for a review, see for example Cannon & Bseikri, 2004). Not only the presence and the quantity of the reward, but obviously its quality also can affect behavioral and mental performance. Although there is a vivid debate over the possible beneficial and detrimental effects of extrinsic rewards on human creativity and motivation (Deci, Koestner, & Ryan, 1999; Eisenberger & Cameron, 1996), the so-called 'natural rewards' like food, drink, and positive social interactions are considered almost unequivocally necessary for higher motivation and learning performance in animals. It has been known for some time that positive reinforcement (usually food reward) results in faster learning than punishment in operant conditioning tasks (for example Lawson & Watson, 1963), and that better quality rewards also speed up learning performance (Elliott, 1928). Norway rats (*Rattus norvegicus*) that developed a particular taste preference through social learning lost their preference faster after being exposed to an alternative food with a different taste, if that food had higher caloric content (Galef & Whiskin, 2001). Human children also show a preference for calorie rich food. They performed better in a social learning task if their mothers demonstrated the consumption of a 'nutritious' food in comparison to the 'light' variant of the same product (Jansen & Tenney, 2001).

The sensitivity of animals to food quality can be tested using the incentive contrast method (Flaherty, 1996). There is evidence that the performance of rats declines after they find a reward of lower quality then expected (see Papini & Dudley, 1997). Dogs are also show the incentive contrast effect during instrumental learning. Bentosela, Jakovcevic, Elgier, Mustaca, and Papini (2009) reported that switching from a high quality reward (beef liver) to a low quality reward (ordinary dog food) caused decreased duration of conditioned gazing at a human in dogs.

Testing the effect of reward quality on dogs proved to be surprisingly difficult according to the last decade's ethological research. Although dogs are definitely motivated to participate in tasks where food or object rewards are involved, their performance is often more strongly affected by social factors like the manifestation of human communicative actions than the quality, quantity or the presence of a reward. For example, dogs do not rely on their renowned sense of smell when the location of an odorous food item is misrepresented to them by a 'dishonest' human experimenter's pointing gesture (Szetei, Miklósi, Topál, & Csányi, 2003). Dogs also proved to be quite insensitive to being rewarded with low quality food while another dog was rewarded openly with high quality treats for the same behavior (Range, Horn, Virányi, & Huber, 2008). The importance of human ostensive communication was shown for example in simple object search tasks (Topál, Gergely, Erdőhegyi, Csibra, & Miklósi, 2009) and in social learning experiments (Pongrácz, Miklósi, Timár-Geng, & Csányi, 2004). In both cases, the behavior of dogs was more strongly influenced if the visible trajectory of the target object to be found later was accompanied by verbal attention from the human experimenter who carried the target. Prato-Previde, Marshall-Pescini, and Valsecchi (2008) found that the majority of dogs opt for the smaller amount of food after seeing their human partner choose it in a two-choice task. These results can be explained if we consider the evolutionary history of canines. Family dogs' attachment to their owners (Topál, Miklósi, & Csányi, 1998) and their dependency on humans as a source of information and support (Miklósi, Kubinyi, Topál, Gácsi, Virányi, & Csányi, 2003) are thought to be key factors in dogs when they face more or less difficult tasks. Therefore, it is possible that the performance of dogs does not always reflect the incentive value of a reward if the task requires cooperation with humans.

The two-way choice task based on human pointing signals (for methodological review see Miklósi & Soproni, 2006; Reid, 2009) offers a promising opportunity for testing the relationship between the influence of social variables and reward quality on the behavior of dogs. This task consists of several trials (usually at least ten, and often many more) in which the dog has to find a reward, hidden in one of two bowls, indicated by the pointing gesture of a human. Although utilization of the human communicative signal is essential for being successful, the repetitive manner of the experiment may be demanding for most dogs unless their motivation is maintained by the incentive value of the food reward. Therefore one may assume that if the reward quality is manipulated, the performance of dogs will change according to the direction of incentive value modification.

Despite the considerable literature dealing with dogs' responses to human pointing signals, the role of reward quality has not been directly investigated until now. Learning as the main factor explaining the ability to comprehend human pointing became one of the main hypotheses (see Udell & Wynne, 2008; Wynne, Udell, & Lord, 2008), but these studies concentrated mostly on the period of ontogeny when dogs possibly learn the connection between hand signals and the location of food. However, if learning is critical during two-choice tasks, one should be able to detect performance changes over a succession of trials. Perhaps the studies most relevant to this issue are those experiments that investigated the effect of human 'deception' on dogs' performance. All these studies involved one or another form of deceptive human pointing, in which the indicated bowl did not contain food. Elgier, Jakovcevic, Mustaca, and Bentosela (2009) found that dogs eventually reach the level of 'extinction' when they stop responding to points that do not yield reward. Kundey, De Los Reyes, Arbuthnot,

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Allen, and Coshun (2010) reported that dogs keep on following deceptive human signals, especially if they are coupled with a human positioned near the indicated bowl. Finally, Petter, Musolino, Roberts, and Cole (2008) found that dogs can learn to differentiate between an 'honest' and a 'deceptive' human partner based on the reward found or not found at the indicated location.

In this paper, we investigated whether reward quality had an effect on dogs' performance in the two-way object choice test. We always placed food reward into the indicated bowl, and the quality of the reward was adjusted to the preference of the dogs. Rewards with high, moderate and almost no incentive value were used. Momentary distal pointing (for example Soproni, Miklósi, Topál, & Csányi, 2002) was used to cue dogs. Earlier research showed this cue to be a moderately demanding signal for the dogs to comprehend (Lakatos, Soproni, Dóka, & Miklósi, 2009; Pongrácz, Gácsi, Hegedüs, Péter, & Miklósi, 2013). We predicted that the incentive value of the reward would have a stronger effect on dogs' performance in the case of momentary distal pointing than in the case of sustained, proximal pointing (e.g. Kundey et al., 2010).

In Experiment 1, we tested dogs either with their preferred or non-preferred food rewards and predicted that dogs would perform worse when they received the non-preferred food as a reward. In Experiment 2, dogs participated in a 20-trial session in which a human indicated a bowl containing an almost non-palatable food (a piece of carrot). In one of the experimental groups, sausage (high incentive value) was placed to the not-indicated bowl; in the other group, the non-indicated bowl was empty. We predicted that dogs would learn to avoid the indicated bowl faster if they found a better incentive at the alternative location. In Experiment 3, dogs in two groups received two 12-trial sessions. In the first session, the indicated bowl contained either sausage or carrot. In the second session, the indicated bowl contained dry dog food (reward of moderate quality) in both groups. We predicted that in the second session dogs that found carrot earlier would improve with higher reward quality (positive contrast), while dogs that received the moderate quality reward after the high quality one (sausage) would perform worse (negative contrast). As an alternative hypothesis, reward quality of the first session could have a long lasting effect, leading to no performance change between the two sessions.

Materials and methods

Different dogs were used in each experiment. The specific details of the experimental procedure are presented below.

Subjects

Subjects were recruited from a Family Dog Project data base. There were no specific requirements for participating in the tests, but the dogs had to be older than one year. Additionally, dogs were not tested if they were not motivated enough to accept food in the experimental room (see pre-training phase below). Before the test, we explained to the owners the basic goal of the experiment and discussed with them how to behave during the test.

Experimental room

All experiments were performed indoors, at the Department of Ethology. Subjects were tested in an empty experimental $room(4 \text{ m} \times 6 \text{ m})$. During the tests, only the dog, the experimenter and the dog's owner were present. Each test was recorded by continuously running digital cameras, and the footage was analyzed later.

Testing for food preference

Food preference was established by offering two types of treats (one little piece of each) to the dog simultaneously. The food items were presented on a semi-transparent, rectangular plastic plate (20 cm wide and 30 cm long), approximately 20 cm apart from each other. During the preference test, the dog was unleashed and it was allowed to move freely in the experimental room. The experimenter crouched down and offered the plate with the food items to the dog, holding the plate in her hand. In Experiment 1, the pairs of food types were custom selected by asking the owner of the dog which treats his/her dog favored and did not favor. Some of the typical food types were: cheese, sausage, dry dog food, biscuits, etc. In Experiments 2 and 3, the preference test always involved sausage vs. little pieces of carrot. In every preference test, the food items were cut to $5 \,\mathrm{mm} \times 5 \,\mathrm{mm}$ cubes. The same two types of food were offered five times to the dog. The relative position of the two food items (left or right) was chosen randomly by turning the Plate 180°. The type of food the dog ate three or more times was considered 'preferred', and the other type was considered 'non-preferred'.

During each preference test, the experimenter always handled one kind of food with the same hand, and on the plate there was an assigned spot for a particular kind of food item to prevent the mixing of odor traces, both on the food items and on the plate. Between tests with different dogs, the plate was cleansed with water and dish soap.

Pre-training phase

to test whether the subjects were motivated to eat food at the test location. At first we asked the O (O = owner) to unleash

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This phase served a dual purpose: (a) to familiarize the dogs with the testing location and the experimental setup; (b)

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the dog and allow it to explore the experimental site for 1.5–2 min. Then the O moved to the start point, restrained the dog by its collar and positioned the dog at the start point 2.5 m from the E (E = experimenter). The E placed two identical brown bowls (round, plastic flower pots, 20 cm tall and 20 cm wide) on the ground, 1.5–1.6 m away from each other. The E stood in the middle between the two bowls, and dropped a little piece of food into one of the bowls, conspicuously enough so that the dog observed this action. After the experimenter had dropped the food into the bowl, the O let the dog free and verbally encouraged it to eat the food. If the dog ate the food from the bowl, then the E put another piece of food into the other bowl, and the dog was again encouraged to eat it. Between two such trials, the dog was not called back to the O and the E remained in the middle between the two bowls. This pre-training was repeated once more by dropping food into both bowls in the same order as was done previously. The type of food that was used for pre-training the dogs is described at each test.

If a dog failed to take food from the bowls and/or did not eat more than one piece of food during the pre-training phase, we considered it as not food motivated and we excluded it from the experiment. Only two dogs failed to pass this criterion, one in Experiment 2 and one in Experiment 3.

The experiments started right after the pre-training phase.

Pointing procedure

At the beginning of each trial, the dog was held by its owner by the collar at the start point. The experimenter stood 2.5 m away from them. The type and arrangement of the two plastic bowls were the same as described at the pre-training phase. The E stood 20-30 cm behind the imaginary connecting line, equal distance from the two bowls. In each experiment, we used momentary distal pointing (see also Gácsi, Kara, Belényi, Topál, & Miklósi, 2009; Lakatos et al., 2009; Pongrácz et al., 2013; Soproni et al., 2002).

The E first held both bowls with one hand in front of her body, then put a piece of food conspicuously into one of them. and then exchanged the two bowls between her hands a few times in order to confuse the dog about the exact location of the food. After this, E crouched down and with stretched arms put the two bowls simultaneously on the floor on her left and

The E stood up and, while holding her two hands bent in front of her chest, attracted the dog's attention by calling its name. When E managed to establish eye contact with the dog, she pointed with extended ipsilateral arm and index finger in the direction of the correct location (the baited pot). The distance between the end of the pointing finger and the bowl was 1 m. The cue was displayed for approximately 1 s, and then E brought her hand back to the front of her chest. During the pointing gesture, E kept looking at the dog. If the dog did not leave the start position for 3 s after the pointing gesture was finished, E repeated the pointing gesture one more time.

It is important to note that the O kept the dog restrained during the pointing. The dog was released only after E's hand was again in front of her chest. If the dog approached the baited bowl first, it was allowed to consume the food. After this, E quickly picked up both bowls, preventing the dog from examining the other bowl. If the dog visited the empty bowl first, E did not allow it to examine the other (baited) bowl by picking up both bowls. After the dog had made a choice and E had picked up the bowls, the O called the dog back to the start point and the next trial started. A dog was considered to have 'made a choice' if it approached one of the bowls at least as close that it lowered its head over the bowl.

If the dog did not choose between the two bowls, but for example sat down in front of E, or went back to O, no score was given, and the trial was repeated once more. If the dog did not choose again, the trial was recorded as 'no-choice' and the next trial started. The time limit for no-choice was 20 s; that is, if a dog arrived at one of the pots with latency longer than 20 s, the trial was scored as no-choice.

Testing consisted of different numbers of consecutive pointing trials (see the exact numbers at the test descriptions). An equal number of pointing trials was performed to the right and the left sides. The order of left and right pointing was semi-random: no more than two consecutive pointing trials were performed to the same side (to avoid the development of side bias), and E did not start the session with two pointing trials to the same side (to avoid the tendency to commit perseverative errors).

Data collection and analysis

The following parameters were collected or calculated from the video recordings: strength of preference (the number of times a dog chose the preferred food in the preference test); number of choices of the indicated bowl (the dog went to the bowl that was pointed to by E, and either ate the food or lowered its head to the level of the top of the pot); number of choices of the not-indicated bowl (the dog went to the not-indicated bowl and either put its nose into the bowl, or lowered its head to the level of the top of the bowl); number of no-choices (the dog did not leave the owner's vicinity, or went back to the owner without visiting any of the bowls for the 20-s duration of the trial); relative number of choices of the indicated bowl (the number of choices of the indicated bowl divided by the number of all trials); number of dogs that performed above the chance level (the chance level was always at 33% of the total number of the trials, as no-choices can be regarded as a third option besides choosing one or the other bowl – see also Hare et al., 2010); latency of

As in most cases, the data followed the Gaussian distribution and the error variances were also equal across groups (Levene test for homogeneity of variance), we used parametric tests. A one-sample t-test was employed to compare the

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number of successful choices against chance performance within a particular group. GLM for repeated measures was used when we compared correct choices or latencies between the first and last three or five trials and among the experimental groups. Pair-wise comparisons were performed with unpaired or paired *t*-tests. The proportion of dogs that performed above chance level was compared among the experimental groups with Chi-square tests. Statistical analyses were performed using SPSS 16.0 and InStat.

Experiment 1: The effect of treat quality on the choice performance of dogs

This experiment tested whether dogs perform better (or worse) if they find their preferred (or non-preferred) food in the bowl, after making a choice based on the experimenter's pointing gesture.

Subjects and methods

The subjects were represented by several dog breeds (see the details below). After a food preference test (see the description above), the dogs were assigned to one of the two experimental groups: preferred food (PF), N=15 (one Belgian Malinois, one Fox Terrier, one French Bulldog, one German Shepherd dog, one Golden Retriever, one Labrador Retriever, one Poodle, one Rough Collie, one Transylvanian Hound, two Mudis and four dogs of mixed breed. They ranged in age from 1 to 10 years – Mean age = 4.73 years; SD = 2.94); and non-preferred food (NF), N=15 (one Doberman, one German Shepherd dog, one Giant Schnauzer, one Labrador Retriever, one Poodle, one Puli, one Siberian Husky, one Whippet, one Wirehaired Vizsla, two Border Collies, two Mudis and two dogs of mixed breed. They ranged in age from 1 to 11 years – Mean age = 4.47 years; SD = 2.77). The pre-training was always performed with that type of food, which we used in the test trials for that particular dog. After pre-training, each dog participated in ten test trials. Dogs in the PF group received their preferred food, while dogs in the NF group received their non-preferred food.

Results and discussion

We first analyzed the strength of preference by comparing the number of choices toward the preferred type of food in the preference test using the Mann–Whitney U-test. We found that dogs in the PF and the NF groups did not differ in the strength of preference for one of the two types of food (medians of choosing one type of food over the other were 3 in both groups, U(14) = 107.50; p = 0.85). With Wilcoxon signed rank tests, we analyzed whether one type of food was chosen significantly more often than the other (W(15) = 120.00; p < 0.001 for both groups). This result is important because it shows that dogs in both groups had an equally strong preference for one of the offered treats. Therefore, we could predict the same strength of positive contrast in the PF group as negative contrast in the NF group.

In the two-way object choice test, dogs performed significantly above the chance level in both the PF and the NF groups (one-sample t-test, PF: t(14) = 9.28; p < 0.001; NF: t(14) = 7.25; p < 0.001, respectively). Comparing the number of choices to the indicated bowl between the two groups (mean \pm SE – PF: 7.47 \pm 0.45; NF: 6.40 \pm 0.42), we did not find a significant effect (t(28) = 1.74; p = 0.09) of the type of food.

Of the 15 subjects, nine chose the indicated bowl at least eight times in the PF group, while only three dogs did so in the NF group. The proportion of the dogs that chose the indicated bowl above the chance level was, however, only marginally different between the two groups (Fisher's exact test = 3; p = 0.06).

We also looked for a possible learning effect during the trials by comparing the number of choices to the indicated bowl in the first three and last three trials. Using a GLM for repeated measures (with food type as a fixed factor and first three vs. last three trials as a repeated factor), we did not find any significant effect (repeated factor (F(1,28) = 0.001; p = 1.00), food type (F(1,28) = 1.40; p = 0.28), interaction (F(1,28) = 0.13; p = 0.73)), which means that the number of choices of the indicated bowl did not change significantly during the course of the experiment with any of the reward types (Fig. 1).

The choice latencies did not differ between the two groups (t(28) = 1.38; p = 0.18). We also analyzed whether there was a change in the choice latencies during the ten trials by comparing the latencies on trials 1–3 with the latencies on trials 8–10 (Fig. 2). We used GLM for repeated measures (with food type as a fixed factor and first vs. last three trials as a repeated factor). We found no significant effect of the repeated factor (F(1,28) = 2.98; p = 0.10), again no significant effect of the food type (F(1,28) = 2.16; p = 0.15), and the interaction between the two factors was also not significant (F(1,28) = 0.36; p = 0.55).

These results suggest that companion dogs show robust performance in two-way object choice tests if they are rewarded with palatable food. Despite displaying detectable preference for one or the other reward type, they kept on making choices even when they could obtain only the non-preferred food. It is worthy to note here that each dog in both groups ate the reward in each trial, regardless of its quality. However, individual dogs that were rewarded with their preferred treats were more likely to perform over the chance level. Note that the dogs were not food restricted before the testing in any way, similar to other dogs that have been tested with the pointing task. Thus it may be advantageous for experimenters to use high incentive food rewards suggested by the owners because this can have a stabilizing effect on a dog's performance, especially if the test consists of multiple trials.

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E

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100 NS NS 90 NS Indicated bowl choices (percentage+SE) 80 70 60 50 ■ Non-preferred food ■ Preferred Food 40 30 20 10 0 Ten trials First 3 trials Last 3 trials

Fig. 1. Dogs' choices of the bowl indicated by the human pointing gesture in Experiment 1. Based on an *a* priori preference test, dogs found preferred or non-preferred food reward in the indicated bowl. There was no difference between the two groups' performance throughout the test (10 trials), or at the beginning and the end of the tests (first and last three trials). NS, not significant.

Experiment 2: Does an alternative (good quality) food affect dogs' performance when the experimenter points at a food reward with very low incentive value?

In previous experiments, researchers used deceptive pointing to investigate whether dogs can learn to choose the container not pointed at by the experimenter (Elgier et al., 2009; Kundey et al., 2010; Petter et al., 2008). Using different training methods and pointing gestures, these studies found that dogs showed a preference for the non-indicated location after some experience. However, in all of these studies humans pointed at an unbaited location. In the present experiment, we wanted to find out whether dogs would continue to approach the indicated container if they found unpalatable food (which they do not eat), and whether they are able to change their preference if they find an alternative more attractive food source. Based on the results of Experiment 1 and the observations by Kundey et al. (2010), we predicted that dogs will show a preference for the container pointed at by the experimenter if the alternative container is empty; however, after repeated exposures, they may learn to choose the alternative container if it contains food with higher incentive value.

Subjects and methods

We formed two experimental groups for this experiment in which dogs from various breeds participated (see the details below). During the testing, the experimenter always pointed to the bowl containing the carrot. In the 'Empty alternative' (EA) group, the opposite (not indicated) bowl was always empty, but in the 'Sausage alternative' (SA) group the opposite bowl contained a piece of fresh sausage. In the EA group the following dogs were used as subjects: one Bull Terrier, one

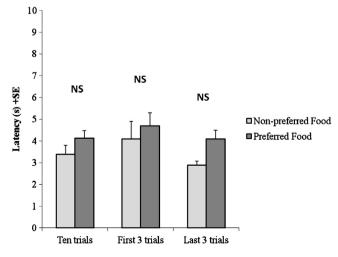


Fig. 2. Latency of choices in Experiment 1. Dogs' latencies to choose did not differ between the two groups in Experiment 1. Maximum choice latency was 20 s; if a dog did not arrive at one of the two bowls within this interval, its performance was considered as 'no-choice'. NS, not significant.

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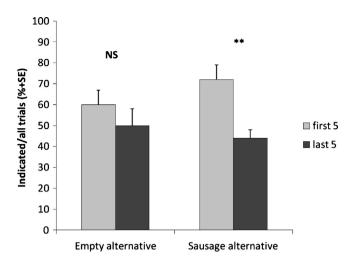


Fig. 3. Relative number of choices (indicated choices/all choices) of the indicated bowl for of first five trials and last five trials of the 20 trial long session in Experiment 2. In the Empty Alternative group, the indicated bowl contained carrot and the not-indicated bowl was empty. In the Sausage Alternative group, the indicated bowl contained sausage. In this latter group, dogs started to opt for the not-indicated bowl towards the end of the experiment. (*Note*: the interaction between the two factors was not significant, only showed a near-significant tendency (p = 0.12)). NS, not significant; **p < 0.01 (paired t-test).

German Shepherd dog, one Greyhound, one Groenendael, one Havanese, one Miniature Pinscher, one Poodle, one Vizsla, two Labrador retrievers and five dogs of mixed breed. They ranged in age from 1 to 9 years – Mean age = 4.07 years; SD = 2.52. In the SA group the following dogs were used: one Beagle, one Tervueren, one English Cocker Spaniel, one Mudi, one Vizsla, two Labrador Retrievers and eight mixed breed dogs. They ranged in age from 1 to 10 years – Mean age = 3.13 years; SD = 2.75.

After the preference test (sausage vs. carrot), the pre-training was done with sausage (two times to each bowl) in both groups, and then all dogs received 20 test trials according to the previously described rewarding/baiting regime.

In this experiment it was important that the carrot should serve as a food 'reward' with only minimal palatability for the dogs. Therefore, we excluded those subjects from further analysis that ate pieces of carrot more than once during the preference test. Therefore, the initial N = 15 was reduced to N = 12 in the EA group and to N = 13 in the SA group.

Results and discussion

The mean choice latencies did not differ between the groups (unpaired t-test, t(28) = 0.27; p = 0.74). There was no difference between the relative number of choices of the indicated bowl in the two groups (unpaired t-tests: t(23) = 0.67; p = 0.51). We found the proportion of the individually successful dogs (11 or more correct choices from 20) also very similar between the two groups (8 successful dogs in both groups; Fisher's exact test = 0.92; p = 1.00).

However, we found differences when we compared the performance of the dogs between the first five and the last five of the 20 trials. We analyzed the relative number of choices of the indicated bowl in the first five and last five trials with GLM (with group as a fixed factor and first five vs. last five trials as a repeated factor). We found that repetition had a significant effect (F(1,23)=11.56; P<0.01). We did not find a significant effect of group (F(1,23)=0.22; P=0.64), and there was no significant interaction between the two factors (F(1,23)=2.55; P=0.12). However, as the between-factor interaction showed a near-significant tendency, we compared the relative number of choices of the indicated bowl between the first five and last five trials separately in the two groups with paired t-tests (Fig. 3). We did not find significant differences in the EA group (t(11)=1.15; P=0.28). However, in the SA group the relative number of choices of the indicated bowl was higher in the first five trials (t(12)=3.96; t>0.01).

We also compared the choice latencies between the two groups (Fig. 4). We did not find a significant difference in any of the comparisons (unpaired t-test, first five trials: t(23) = 0.95; p = 0.35; last five trials: t(23) = 1.16; p = 0.26; all 20 trials: t(23) = 0.10; p = 0.92).

This experiment showed that dogs did not stop making choices during a prolonged session of trials with a 'reward' of minimal incentive value. Offering them a high value alternative food in the non-indicated bowls did not make a difference when we compared the performance of dogs over the 20 trials. However, having a high incentive food as an alternative choice caused a noticeable learning effect. These dogs started to abandon the indicated bowl in favor of the non-indicated one towards the end of the session. The results therefore reflect a conflict in the subjects: they preferred to follow human pointing even with almost no reward for it. However, if there was a better choice available, they were tempted to disregard human signals sooner.

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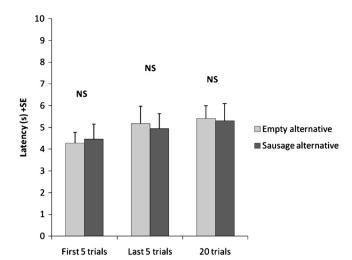


Fig. 4. Latencies of choices in Experiment 2. Mean latencies are shown for first five trials and the last five trials and for the whole test (20 trials). There was no difference between the two groups' latencies in any of the cases. NS, not significant.

Experiment 3: Does the previous experience of reward incentive value affect the performance of dogs?

In this experiment we wanted to see whether a change in reward quality between two sessions affected dogs' performance. In the first session, dogs in one group were rewarded with high quality food (sausage) and dogs in the other group were rewarded with low quality food (carrot). In the second session, both groups were switched to dry dog food. Based on the incentive contrast theory we hypothesized that subjects in the positive contrast group would improve their performance in the second session. At the same time for the negative contrast group we predicted a slight drop in performance in the second half of the experiment because sausage is considered to be a slightly higher quality food than dry dog food.

Subjects and methods

In this experiment we tested the dogs in two separate sessions, with 12 trials in each session. We formed two groups of dogs from various breeds. In the 'Carrot first' (CF) group, dogs received carrot in the indicated bowl during the first 12 trials, and then they received dry dog food as reward in the second 12 trials (positive contrast). In the 'Sausage first' (SF) group, dogs were rewarded with sausage during the first 12 trials and then were switched to dry dog food in the last 12 trials (negative contrast). The non-indicated bowl was always empty for all dogs. The following dogs were used in the CF group: one Fox Terrier, one Havanese, one Hovawart, one Rottweiler, one Samojed, three Border Collies, three Mudis and three mixed breed dogs. They ranged in age from 1 to 16 years – Mean age = 5.53 years; SD = 4.79. The SF group consisted of the following subjects: one Australian Kelpie, one Malinois, one French Bulldog, one Jack Russell terrier, one Labrador Retriever, one Puli, one Wirehaired Vizsla, three Border Collies and five mixed breed dogs. They ranged in age from 1 to 12 years – Mean age = 4.93 years; SD = 3.86.

All dogs participated at first in a preference test, where they had to choose between a piece of carrot and sausage five times. Again, only those dogs were included in the analysis that did not eat carrot more than once during the preference test (N=15 in both groups). After this preference test, all of the dogs received a piece of sausage twice from each bowl. Next the dogs were divided randomly into the two experimental groups and received either carrot or sausage as reward. Then all dogs had a 5 min long break, during which they left the experimental room with their owner, and the owner was asked to complete a short demographic questionnaire about the dog. Then we performed further pre-training trials with all dogs using dry dog food, after which they were tested for a further 12 test trials with dog food hidden in the indicated bowl.

Results and discussion

We analyzed the effect of group and repetition of sessions with GLM on the relative number of choices of the indicated bowl, the number of the choices of the not-indicated bowl, and the choice latencies. As only one dog made a no-choice in the SF group, occurrence of no-choices was compared only between the two sessions of the CF group.

The GLM did not find any significant effects on the relative number of choices of the indicated bowl. There was only a near-significant trend in the group comparisons (repetition: F(1,28) = 0.09; p = 0.77; group: F(1,28) = 3.59; p = 0.07; interaction: F(1,28) = 0.78; p = 0.39). In the case of the choices of the non-indicated bowl, repetition showed a significant effect (F(1,28) = 6.28; p < 0.05), but the effect of group (F(1,28) = 0.14; p = 0.71) and the interaction (F(1,28) = 0.90; p = 0.35) were not significant. In the CF group, dogs made significantly more non-choices in the first session than in the second session

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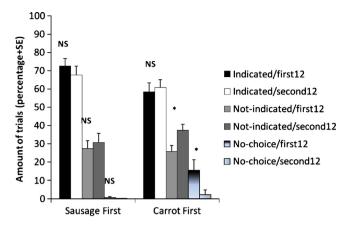


Fig. 5. Percentage of trials that ended with choices of the indicated or not-indicated bowl, or ended with no-choice in Experiment 3. Dogs in the 'Sausage First' group received 12 trials rewarded with sausage in the indicated bowl, followed by 12 trials with dry dog food as reward. Dogs in the 'Carrot First' group were rewarded with carrot first and then received dry dog food in the second half of the experiment. Number of trials with similar outcomes was compared in pairs between the first and second sessions. Dogs in the 'Carrot First' group chose the not-indicated bowl more often and performed less no-choices in the second session. NS, not significant; *p < 0.05 (paired *t*-test).

(Wilcoxon, W = 28.00; p < 0.05). The GLM found a significant effect on choice latencies in the case of both factors (repetition: (F(1,28) = 7.67; p < 0.01; group: F(1,28) = 5.48; p < 0.05)), and the interaction was also significant (F(1,28) = 7.05; p < 0.05).

As a post hoc analysis, we compared the choices of the not-indicated bowl between the first and second sessions with paired t-tests (Fig. 5). We did not find a significant difference in the SF group (t(14) = 1.07; p = 0.30). However, in the CF group, dogs chose the non-indicated bowl significantly more often in the second session than in the first session (t(14) = 2.51; p < 0.05). In the case of latencies, we performed post hoc analyses between the two 12-trial sessions and between the two groups (Fig. 6). We did not find a significant difference between the latencies of the first and second sessions in the SF group (t(14) = 0.18; p = 0.85), but the dogs chose significantly faster during the second session in the CF group (t(14) = 2.85; p < 0.05). An unpaired t-test showed that dogs in the SF group chose significantly faster than dogs in the CF group during the first session (t(28) = 2.88; p < 0.01). There was no significant difference between the two groups during the second session (t(28) = 1.07; t = 0.29).

The results of this experiment showed that dogs performed surprisingly well when rewarded with food of very low or zero incentive value, as the number of choices of the indicated bowl did not differ between groups or between sessions. However, dogs in the CF group chose the non-indicated bowl significantly more often in the second session, when they were rewarded with a higher quality food. At the same time, the number of their non-choices dropped, as well as their choice latencies. This pattern suggests that these dogs noticed the positive change in the incentive value of the reward, although this was not manifested in their performance as they only chose more willingly. In general, dogs tended to react to the low-quality reward with more hesitation (long latencies) and refusal to choose (more non-choices), but when they actually chose, they usually opted for the indicated bowl. There was also an interesting difference between those CF dogs that refused

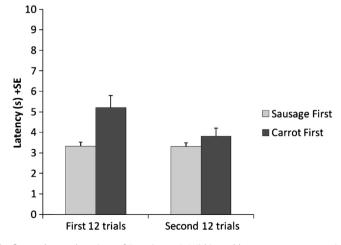


Fig. 6. Mean choice latencies in the first and second sessions of Experiment 3. Within and between group comparisons were performed, based on the significant result of a GLM analysis. Dogs chose significantly faster when they were tested with sausage during the first 12 trials. Dogs in the Carrot First group chose significantly faster during the second 12 trials (when they were rewarded with dry food). *p < 0.05 (paired t-test); **p < 0.01 (unpaired t-test).

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to choose in the first session and those that chose one of the bowls in each trial with the carrot. From the seven dogs that made non-choices in the first session, six chose the non-indicated bowl more often in the second session than in the first session, and only one dog made the same number of choices of the non-indicated bowl. Among the eight dogs that did not make any non-choices in the first session, four increased the number of choices to the non-indicated bowl, and the other four chose the non-indicated bowl fewer or equal times in the second session than in the first session. Thus there might be a connection between opting for not choosing and following human pointing less accurately in dogs, when a low quality reward is involved.

General discussion

We conducted three experiments in order to reveal the influence of reward quality on the performance of dogs in a food searching task that was based on human cueing. We found that the reward quality had in general only a subtle effect on the performance of the dogs unless the food was almost inedible. Carrot proved to be a food that most dogs refused to eat. However, in Experiment 2, most dogs kept on choosing it during 20 trials when the human indicated the bowl with carrot, If the other (non-indicated) bowl contained highly motivating food, the dogs learned gradually to disregard the human cueing in favor of the more motivating alternative choice. In Experiment 3, we found that experience with a good or poor quality reward (sausage vs. carrot) had only a slight effect on dogs' motivation and performance in a following session in which a medium quality reward was offered. Dogs that received the carrot reward in the first session chose faster and more willingly in the second session, but interestingly they had a worse success rate at the same time, while those dogs that were rewarded first with sausage kept on performing similarly with the lower quality food.

Many years ago, the two-choice task used in this study was introduced as a measure of dogs' ability to rely on human cueing (Hare, Call, & Tomasello, 1998; Miklósi, Polgárdi, Topál, & Csánvi 1998), The performance of dogs was contrasted with that of apes that did not seem to be very successful under relatively similar conditions (see Miklósi & Soproni, 2006, for review, but also Mulcahy & Call, 2009). Further experiments also revealed that this ability emerges relatively early in dogs and is quite stable over development (Gácsi, Kara, et al., 2009; Riedel, Schumann, Kaminski, Call, & Tomasello, 2008 – but see Wynne et al., 2008 for a learning effect during development); nevertheless, breed and experience may also affect the performance of individuals (e.g. Gácsi, McGreevy, et al., 2009).

Although most of the early studies emphasized the social-communicative component of this task, that is, how the dogs recognize and process human communicative behavior and use provided information for localizing hidden food (see also Bräuer, Kaminski, Riedel, Call, & Tomasello, 2006; Téglás, Gergely, Kupán, Miklósi, & Topál, 2012), another line of recent investigation aimed to reveal the contribution of learning to this interaction. In agreement with other earlier discussions (e.g. Hare, Rosati, Kaminski, Bräuer, Call, & Tomasello, 2010; Miklósi & Topál, 2011; Udell, Dorey, & Wynne, 2011), both social experience and learning are undoubtedly necessary for successful performance in the two-choice task when dogs can find the hidden food only on the basis of human cueing, just as learning and experience are a prerequisite for the proper development of intra-specific communication based on species specific signals (Ginsburg, 1975).

Experiment 1 supports the idea that food quality is of secondary importance in dogs because their performance was independent of the incentive value of the obtained reward. Note that dogs in the preference tests had the chance to taste the preferred food, so one might have expected that dogs' performance would drop in the 'Non-preferred Food' group if they encountered the less preferred food in the pointing experiment (negative contrast see Bentosela et al., 2009 and below). However, it is also possible that dogs would have developed a differential response toward the non-preferred or preferred food if the experiment had lasted longer.

The lack of effect in Experiment 1 also can be explained by ultimate causes. Researchers have argued that during evolution, dogs were selected for scavenging behavior (Coppinger & Coppinger, 2002) and for the use of human cueing (Reid, 2009; Gácsi et al., 2009a). The role of human cueing could be especially important for dogs living in human families. Several experiments found that dogs' choice behavior in such situations is influenced by human cueing. For example, Erdőhegyi, Topál, Virányi, and Miklósi (2007) reported that dogs are able to solve an inferential reasoning task only if the human cueing is carefully balanced (see also Topál et al., 2009). A recent study reported that dogs are able to select specific types of food based on nutrient content (Hewson-Hughes et al., 2012); however, despite these findings, dogs do not seem to be very selective in laboratory experiments. For example, food quality did not play a role in a food inequity aversion task in which dogs were tested, which was in contrast to primates tested under similar conditions (Range et al., 2008).

There have been reports that dogs learn to avoid the indicated container after repeated exposure (e.g. Elgier et al., 2009). Our Experiment 2 is most similar to the procedure applied by Kundey et al. (2010), in which the human experimenter displayed 'dishonest' pointing for the dog (food was in the alternative container). They found that in the course of 24 experimental trials, dogs became biased (60%) toward the location of the (not indicated) hidden food if the experimenter displayed a momentary point toward a location where no food was hidden. The main difference between their method and our method (Experiment 2) is that in our "Sausage alternative" group, the experimenter pointed to the bowl which contained a piece of carrot (non-preferred food). Interestingly, the presence of a non-preferred (and not eaten) food item at the indicated location seems to inhibit dogs from switching to the preferred alternative. In our case, dogs chose the sausage around 30% of the time overall, although there was some effect of experience as dogs more often went for the non-indicated container toward the end of the session. These observations strengthen the impression that in some cases social influences may override simple reward-based rules of learning (e.g. Topál et al., 2009). Given the fact that dogs did not eat (obtained a

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reward) from the indicated container either in Kundey et al. (2010) or in our Experiment 2, we expected similar performance. One possible interpretation is that dogs considered pointing at the non-preferred food an indicative ('honest') act performed by the human, despite the fact that they did not like (and eat) the food indicated by the experimenter. The experience of the experimenter pointing at a potentially edible item that turned out to be not edible did not lower their expectancy that the human may actually indicate a more preferable food in the future.

Dogs' failure to avoid the ('dishonestly') indicated container seems to parallel the performance of children in a similar task. Couillard and Woodward (1999) reported that children at 4 years of age chose randomly (50%) when deceptive pointing was used. The authors explained this by the habitual use and communicative role of the pointing gesture which overshadows the cognitive processes that may recognize the cheating. Because family dogs are also exposed to a large number of pointing gestures during their life, the corresponding finding in dogs and children may reflect similar environmental influences.

Similar conclusions could be drawn from an evolutionary perspective assuming that dogs have been selected for abilities that enhance cooperation with humans. In individual groups, cooperative interactions can be maintained on a long-term basis only if both parties benefit from it, that is, the obtained resource is shared according to certain rules (Cheney, 2011).

The results obtained in the first phase of Experiment 3 replicated the findings of Experiment 1; that is, dogs performed similarly whether they received preferred or non-preferred food. It should be noted, however, that dogs in the "Carrot first" group did not actually obtain a reward if they followed the pointing because they did not consume the food that they found. These dogs also had longer latencies in comparison to dogs in the "Sausage first" group, indicating that the meat had a strong motivating effect on them. The change in reward quality (incentive contrast effect, Papini & Dudley, 1997) also affected the behavior of dogs. In the case of positive contrast (improvement in reward quality), dogs made faster choices (but their performance worsened), probably because their higher motivation to obtain the reward had a negative impact on their attention to the pointing experimenter.

However, we detected no change in the case of negative contrast ("Sausage first group"). This observation contrasts with the report by Bentosela et al. (2009), who showed that in the case of negative contrast (learning to gaze at the experimenter for receiving liver which is then followed by dog food as reward), dogs decreased gazing toward the experimenter when they received the lower quality food. These differences could be explained by the difference between the two tasks. The reliance on human gesturing (shown also in the previous experiments) was sufficient to maintain motivation (latency) and choice of the indicated container in the negative contrast group.

Without disputing the presence of an incentive contrast effect in dogs (Bentosela et al., 2009), similar to other mammals, one could assume that the selective history of dogs acts against their sensitivity to negative contrast. As argued above, ecological factors, such as a scavenger life style, may cause resistance to such effects (see Coppinger & Coppinger, 2002 for such arguments in dogs); moreover, the strong social bond between humans and dogs may predispose dogs to be less sensitive to food quality, especially in communicative/cooperative interactions (see also Range et al., 2008).

There are a few important insights that should be considered in order to put the present results into a wider ethological context. The present, and most other studies, utilize (well-socialized) family dogs that have a wide range of socio-communicative experience with humans. In the case of these dogs, there are no strong intrinsic or extrinsic incentives that would force the dog to participate in these experiments. For example, dogs are not starved before the investigation and thus the food provided as a result of correct choice does not play a significant role in their caloric intake on that day. Also, they can stop cooperating at any time during the experiment. These factors could also explain the relatively small effect of the food quality (or the very modest effect of literally inedible 'reward').

In everyday life, communicative interactions (which are mimicked by the two-choice test) between family dogs and humans are incidental and may happen in several different contexts. The need for a large amount of data on choice behavior for statistical reasons resulted in a design in which the dog's performance had to be rewarded. Ethologically speaking, this means that the socio-communicative aspects of the interaction are more dominant than the fact that dogs receive some incentive for their collaboration.

In summary, dogs showed some sensitivity to the quality of the obtained reward in the two-choice task when they could find food on the basis of human cueing. However, the (lack of) effect of reward quality on the performance of dogs should be viewed in the context of an essentially social interaction, in which the dogs' bias may have been promoted by both ultimate and proximate factors.

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