

Simple Mechanisms Can Explain Social Learning in Domestic **Dogs (Canis familiaris)**

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Abstract

Recent studies have suggested that domestic dogs (Canis familiaris) engage in highly complex forms of social learning. Here, we critically assess the potential mechanisms underlying social learning in dogs using two problem-solving tasks. In a classical detour task, the test dogs benefited from observing a demonstrator walking around a fence to obtain a reward. However, even inexperienced dogs did not show a preference for passing the fence at the same end as the demonstrator. Furthermore, dogs did not need to observe a complete demonstration by a human demonstrator to pass the task. Instead, they were just as successful in solving the problem after seeing a partial demonstration by an object passing by at the end of the fence. In contrast to earlier findings, our results suggest that stimulus enhancement (or affordance learning) might be a powerful social learning mechanism used by dogs to solve such detour problems. In the second task, we examined whether naïve dogs copy actions to solve an instrumental problem. After controlling for stimulus enhancement and other forms of social influence (e.g. social facilitation and observational conditioning), we found that dogs' problem solving was not influenced by witnessing a skilful demonstrator (either an unknown human, a conspecific or the dog's owner). Together, these results add to evidence suggesting that social learning may often be explained by relatively simple (but powerful) mechanisms.

Introduction

Dogs (Canis familiaris) are social animals and very skilful in using communicative cues provided by humans (Hare et al. 2002; Miklósi et al. 2003; Bräuer et al. 2006). Their readiness to use human gestures seems to be a side effect of an increased attention towards humans (Miklósi et al. 2003; Gácsi et al. 2009), which may form a basis for increased social learning from humans as social partners.

Social learning can reduce the costs (e.g. time, effort, risk) involved in the acquisition of resources or new skills. The capability to use information provided by others is a prerequisite for the evolution of culture (Tomasello 1999). The practical importance of social learning has been demonstrated for a number of species in food acquisition and processing (Itani & Nishimura 1973; Galef 1996; Terkel 1996; Biro et al. 2003), predator recognition (Curio 1988; Mineka & Cook 1988), mate choice (Dugatkin 1996; Galef 2001) and intraspecific communication (Catchpole & Slater 1995; West et al. 1996; Hile & Striedter

It seems that most often social learning mechanisms reflect rather simple forms of social influence (e.g. local enhancement, stimulus enhancement, social facilitation; Whiten & Ham 1992; Zentall 1996; Byrne & Russon 1998). Social facilitation, social support and mere presence effects are involved when the presence of another individual acts to either increase motivation or reduce fear; thus, through the mere presence of A, B is more likely to learn a similar act (Whiten & Ham 1992). Often, the movement of another individual or the location where this happens draws an observer's attention to a certain place or stimulus, thus facilitating individual learning of the observer (e.g. trial and error learning; Whiten & Ham 1992; Byrne & Russon 1998). We should like to clearly distinguish between 'local enhancement', as defined by drawing attention to a particular locale in the environment, and 'stimulus enhancement', where attention is drawn to an object or part of an object, irrespective of its location (Whiten & Ham 1992, p. 249). Neither form of enhancement causes specific learning from an observed action, speaking strictly the behaviour is not copied, and individual learning is required to perform the behaviour (Call & Carpenter 2002). In contrast to these forms of social influence, imitation or emulation involves learning something either about the other individual's goals and actions (e.g. imitation) or about the results of a performed action (e.g. emulation) (Whiten & Ham 1992; Tomasello 1996, 1999; Call & Carpenter 2002; Call et al. 2005).

Several studies have indicated the ability of dogs to use diverse social learning mechanisms (Brodgen 1942; Slabbert & Rasa 1997; Christiansen et al. 2001; Kubinyi et al. 2003; McKinley & Young 2003; Heberlein & Turner 2009; Miller et al. 2009). Dogs have been shown to imitate selectively (Range et al. 2007), automatically (Range et al. 2011) and to be able to master 'do as I do' relations (Topál et al. 2006). In a detour paradigm (Köhler 1926), which has been used most extensively in the study of social learning in dogs, they were shown to benefit from human as well as conspecific demonstration (Pongrácz et al. 2001, 2003a,b, 2004, 2008). In these experiments, dogs were tested to detour around a V-shaped fence in various conditions. Dogs that witnessed a skilful demonstration decreased their latency, whereas dogs without a demonstration failed to improve over the next few trials (Pongrácz et al. 2001, 2003a). Inexperienced dogs did follow the demonstrated route when the demonstrator, carrying the food, passed the same end of the fence for bating and coming back (Pongrácz et al. 2003b). In most of those experiments, dogs were tested for their ability to detour on their own, i.e. prior to demonstration, and only dogs were chosen as subjects for subsequent trials that detoured successfully within 10-60 s (Pongrácz et al. 2001, 2003a, 2004). Pongracz and coworkers suggested that dogs benefit directly from seeing another individual detouring a fence to obtain a reward. However, the exact mechanism involved remained obscure. Possibilities range from local enhancement (Pongrácz et al. 2003a) to response facilitation (Pongrácz et al. 2001) and it was also suggested that human verbal attention might play a key role in the interaction (Pongrácz et al. 2004).

Here, we aim to unravel the mechanisms underlying the behaviour of dogs in two social learning paradigms, focusing on the influence of stimulus enhancement (Spence 1937). The most extensively used social learning paradigm, the detour task, served to unravel which cues dogs will use if they can benefit from observing a demonstration. Therefore, we compared the effect of two forms of demonstration by a human experimenter, and in contrast to previous studies, compared this also with a partial demonstration by an inanimate object, testing mainly for (A) local enhancement vs. (B) stimulus enhancement or emulation via affordance learning. In a second experiment, we controlled for local and stimulus enhancement and other forms of social influence and explored whether dogs dispose of more complex social learning skills such as emulation and imitation. For this, we chose a towel task in the two-action, one-outcome paradigm (Dawson & Foss 1965; see also Voelkl & Huber 2000).

Experiment 1: Detour Test

Detour tests have been extensively used recently to test social learning abilities in dogs (Pongrácz et al. 2001, 2003a,b, 2004, 2005, 2008). Our study was developed parallel to the studies of Pongracz and colleagues and did not intend to replicate theirs. Instead, we developed a set-up allowing us to explore the learning mechanisms involved in more detail. The aim was to test whether dogs can learn from a demonstration in either direction (towards a target or the reverse, i.e. the way back from a target to the dog), as proposed by Pongrácz et al. (2003a). Therefore, we used a straight and not a V-shaped fence. A straight fence is the simplest geometrical form of an obstacle and represents a basic form of the classical detour problem (Köhler 1926). It allows varying the side of demonstration (left or right) and also the direction of demonstration (towards target or back), with all demonstrations representing the same geometrical shape. Our aim was further to test whether stimulus enhancement could explain the dogs' enhanced performance found in slightly different demonstration conditions of previous studies. Thus, we introduced an object as demonstrator,

which was pulled past one end of the fence instead of demonstrating the whole path towards the target. For critically testing stimulus enhancement, it was also necessary to use a procedure different from previous studies. Most importantly, we tested naïve dogs (i.e. without experience to detour around the fence prior to demonstration) and provided balanced information to test and control dogs. In contrast to earlier studies (Pongrácz et al. 2001, 2003b, 2004, 2005), dogs of all conditions (both experimental and control) were provided with a demonstration prior to their first trial. The demonstration to the 'control dogs' allowed controlling for alternative forms of learning mechanisms (e.g. social facilitation, response facilitation), as these dogs witnessed a walking human in that condition, too. Further differences to the set-up of previous studies were intended (1) to minimize the likelihood that dogs would follow the demonstrator because of the latter's carrying of food; therefore, baiting was completely separated from the demonstration and even performed by two different experimenters; (2) to prevent dogs from using cues that were not part of the experimental paradigm; therefore, we performed the tests without the owners present. We expected dogs to be able to learn from a human demonstrator in a detour task, as has been suggested by previous studies. We chose a human instead of a conspecific as demonstrator, because demonstrations could be conducted more precisely (see procedure) and without extensive training.

We should like to point out that in the context of the social learning mechanisms 'local enhancement' and 'stimulus enhancement', the whole fence as such is neither the 'locale' nor the 'stimulus' that is the subject of demonstration. Rather, the important feature is the end of the fence on either side of the dog at the starting position (i.e. left or right). We predict that if dogs use local enhancement, they will pay more attention to the one end of the fence that is highlighted by a demonstration (locus). This would help dogs under all demonstration conditions to improve their performance in comparison with dogs under control condition. Furthermore, as dogs merely pay more attention to the demonstrated end (locus), they should detour around the same end. In contrast to this, if dogs apply stimulus enhancement, they should be able to make a stimulus generalization (Zentall 1996, Hoppitt & Laland 2008) and therefore react to stimuli of the same type regardless of their location (Spence 1937; Hoppitt & Laland 2008). Hence, we expect if dogs use stimulus enhancement in the Detour test, they would show an improved performance by generalizing, causing them to detour around *either* end (stimulus) of the fence. In a similar fashion, improved performance and taking either end to pass the fence is also expected by dogs utilizing affordance learning (Tomasello 1990, 1996; Whiten & Ham 1992). We further predict that if dogs use emulation (in the strict sense; Call & Carpenter 2002), they should only benefit from demonstrations providing actions, goals and results that are congruent with those of the dogs to solve the experimental problem; when emulation is involved, dogs should not benefit from a partial demonstration of the solution.

Materials and Methods

Subjects

Fifty-four dogs (27 female, 27 male) of various breeds (see Appendix Table S1 for details) participated in the test. All dogs except one Beagle lived as pets with their owners and received the training typical for a family dog (the mentioned Beagle lived in a pack of Beagles at the Faculty of Veterinary Medicine in Leipzig and had frequent contact with people). The prerequisites for dog recruitment were that dogs were food or toy motivated, felt comfortable without their owner, were older than 1 yr and were not fed 2 h prior to the testing. Dog owners were not present during testing. The dogs were randomly assigned to one of the four test conditions.

Materials

The Detour test took place in a dog training hall of the German Red Cross Rescue Dog Section in Leipzig. The hall was divided into a waiting area (approx. 5×20 m) and a testing arena (ca. 40×20 m) in which a straight fence (11 × 1.2 m) was set up (Fig. 1). The fence units consisted of a metal frame with several thin vertical bars, spaced approx. 10 cm apart. The target (food or toy) was located on the side opposite to the dog's starting position. Two plastic boxes $(49 \times 35 \times 35 \text{ cm})$ on wheels served as object demonstrators in the object condition; a rope was attached to the boxes to pull them. When moved, the boxes produced a sound because small bells were attached to the rope. There were occluders on both sides of the fence so that the demonstrator could get out of view before and after all demonstrations. Furthermore, they allowed blocking the test dog's view of the preparation prior to each trial. Two additional occluders were placed 2.5 m

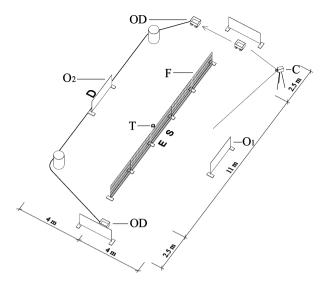


Fig. 1: Set-up of the detour test. C, camera; D, demonstrator; E, experimenter 1; F, fence; O_1 , occluder 1; O_2 , occluder 2; OD, object demonstrator; S, subject; and T, target. Experimenter and subject stand in the middle of the fence during demonstration, while the target is in the bowl on the other side of the fence. The test dog gets unleashed and is encouraged to take the target after demonstration, when the demonstrator is hiding behind an occluder.

away from both ends of the fence to provide a similar and even background behind both endings. Thus, they allowed test dogs to perceive both endings equally distant and therefore prevented a potential side bias by dogs choosing a seemingly shorter way to the food (Dumas & Pagé 2006).

Procedure

Testing took place in Jan. and Feb. 2002. For all but one dog, D.M. served as the experimenter (E) handling the dog. A second experimenter acted as the demonstrator (D). Subjects were divided into four groups by experimental condition.

At the beginning of each experimental day, D walked around the perimeter of the fence twice to prevent asymmetric olfactory cues by D later in the test. Before the test, dogs were habituated to the unfamiliar experimenters and the unknown testing hall in a 30-min warm-up period in the waiting area, while the experimenters interacted with it in a friendly manner (i.e. playing, petting). Later for the first trial, E and the dog entered the testing arena. E led the dog on a leash to the starting position in the middle of the fence, guiding the dog with the target (food or toy) in her hand. The fence was always approached from a perpendicular direction. With the dogs' attention still on the target, E reached through the metal bars of the fence and placed the target in

the bowl on the other side. The fence allowed for visual and olfactorial access to the target. While still on the leash, the dog then witnessed one of four possible demonstrations to reach the target.

Path towards target (Pt, N = 13)

D started her detour from the dog's side of the fence. D walked perpendicularly towards the middle of the fence. Being close to the dog, she called the dog's attention by saying 'Hallo Hund' (i.e. German for 'Hello dog') and then walked around one end of the fence (sides were randomized between the dogs) to the target's side. D approached the target, stopped and looked at it. She then walked towards an occluder and hid behind it.

Path back from target (Pb. N = 14)

D started her detour from the target's side. She walked perpendicularly to the fence towards the target. She stopped, looked at the target, called the dog's attention as described previously and walked around one end of the fence towards the dog (sides were randomized between test dogs). She passed E and the dog and hid behind an occluder.

Object demonstration (Od, N = 13)

While hiding behind an occluder, D pulled the rope to move the demonstration box. The box was pulled in a straight line at an angle of ca. 80° to the fence. The box's starting position was on the dog's side of the fence, and the ending position was on the target's side of the fence (see Fig. 1). The bells attached to the rope produced a noise that attracted the dog's attention.

Control (C, N = 14)

D started from behind the occluder on the target's side. She walked perpendicularly to the fence towards the target. She stopped, looked at the target and called the dog's attention as described previously. Then, she turned around, walked the same way back and hid behind the occluder.

After the demonstration, E unleashed the dog and twice encouraged the dog to reach the target by saying 'Na hol's Dir' (i.e. German phrase for 'Come on, get it'). E did not react to the dog's behaviour nor did she cue the dog in any way. To prevent unintended gaze cues, E wore sunglasses and kept her head straight and oriented towards the target. The

trial ended when the dog had successfully walked around the fence and received the reward or if 45 s had elapsed (an interval of 45 s was chosen, because we expected unsuccessful dogs to become uneasier and less motivated for further trials with longer test phases during which no human–animal interactions occurred). Each dog was tested four times in the condition to which it had been assigned (i.e. 4 times 45 s). Half of the dogs saw the demonstrator/object passing the fence on the left side, and the other half saw the demonstrations at the right side of the fence.

Data Collection and Analysis

All trials were videotaped and later coded from tape by D.M. We coded whether the target was reached and the latency until this happened. For all analyses except for the 'overall latency', only latencies of successful trials were included. (For the overall latency, the 45 s of previous unsuccessful trials were added to the latency of the first successful trial, e.g. if a dog was first successful in trial number 3 after 25 s, the overall latency was $2 \times 45 \text{ s} + 25 \text{ s} = 115 \text{ s}$). We also coded which end the dog chose to pass around the fence. To test for the reliability of coding, a second person, blind to the hypothesis, coded the number of successful trials and the latencies of the first and second successful trials of 29.6% of all tested dogs. Concordance between observers was excellent [number of successful trials: Cohen's $\kappa = 0.905$ (Cicchetti & Sparrow 1981), latency of first successful trial: intraclass correlation coefficient for single measures (ICC) = 0.948; latency of second successful trial: ICC = 0.992, (Landis & Koch 1977)].

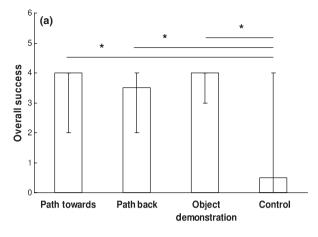
All analyses were calculated with SPSS 8.0, 10.0 (SPSS Inc., Chicago, IL, USA) or StatXact 5 (Cytel Software Corp. Cambridge, MA, USA). If data met the assumptions of parametric testing (i.e. normality and homoscedasticity of variances), we performed between-group and within-group analyses of variance (ANOVAs) to compare several samples (e.g. the four conditions). If the assumptions were not met, we used Kruskal-Wallis ANOVAs for the comparison of several independent samples and Mann-Whitney *U*-tests for pairwise comparisons. To further test each of the three demonstration conditions singly against the control condition, we applied Holm's sequentially rejective Bonferroni method (Shaffer 1995) to adjust for multiple testing in these pairwise comparisons. To test whether a binary distribution differed from random, we used a binomial test. Following Mundry & Fischer (1998), we applied the exact version of the respective statistical test when sample sizes were small. Generally, two-tailed tests were used unless otherwise stated. As dogs had been shown to be more skilful in a detour test after witnessing a skilful demonstrator (Pongrácz et al. 2001, 2003b, 2005), we expected the dogs from our experimental conditions to be more successful than dogs from the control group in our detour test. Therefore, we used one-tailed tests for comparing the dogs' success between control and demonstration conditions.

Results

A comparison of the different conditions showed that dogs were more successful in some conditions than in others (Kruskal–Wallis test: $H_3 = 8.126$, N = 54, p = 0.043). Pairwise comparisons showed that dogs in all three demonstrations (path towards, path back and object) were more successful than dogs in the control condition (*U*-tests: path towards: U = 49, $N_{Pt} = 13$, $N_C = 14$, p = 0.028; path back: U = 58, $N_{Pb} = 14$, $N_{C} = 14$, p = 0.027, object: U = 43.5, $N_{\text{Od}} = 13$, $N_{\text{C}} = 14$, p = 0.024; one-tailed, corrected by the Holm's sequentially rejective Bonferroni method (Shaffer 1995), Fig. 2a). There was no significant difference between the three demonstration conditions (Kruskal–Wallis test: $H_2 = 0.584$; N = 40, p = 0.747). The four conditions differed also in the number of dogs that were successful in their first trial (exact $\chi_3^2 = 8.718$, p = 0.034). Only 36% dogs of the control condition where successful in their first trial, whereas this was true for 77% of the dogs in the path towards target condition, 57% of dogs in the path back condition and 85% of dogs in the object demonstration condition.

Even though dogs were more successful when they saw a demonstration to reach the target, there was no evidence that they followed the specific route taken by the demonstrator. In the trial in which the dogs first successfully passed around the fence, only 17 of 36 dogs took the same end as the demonstrator (binomial test: p = 0.868). This is unlikely to be the result of a general side bias, as neither end was used preferentially in the first successful trial ($N_{\text{Left}} = 16$, $N_{\text{Right}} = 27$, binomial test p = 0.126).

We also checked whether latency to successful solving of the task decreased over time. Dogs with only one (N = 4) or no successful trials (N = 11) were excluded from this analysis. A comparison of the first and second successful trials revealed that dogs solved the problem faster over time (ANOVA $F_{1,35} = 14.142$, p = 0.001), regardless of the



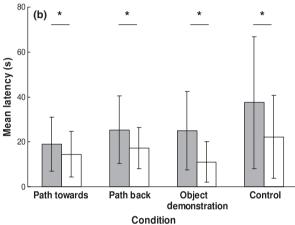


Fig. 2: Results of the detour test: (a) Overall success (median \pm quartiles) reflecting the number of trials out of four in which the dogs detoured around the fence and reached the target in the four experimental conditions. Test dogs were more successful in all demonstration conditions than in the control condition. (b) Latencies $(\bar{X}\pm SD)$ to reach the target in the four conditions. Dogs improved the latency from their first successful trial (grey bars) to their second successful trial (white bars), regardless of the condition. The time required to reach the target did not differ significantly between conditions. *p < 0.05; see text for statistical details.

condition (ANOVA: $F_{3,35} = 0.844$, p = 0.48, Fig. 2b). In addition, this analysis revealed that the time required to reach the target did not differ significantly between conditions (ANOVA $F_{3,35} = 1.679$, p = 0.19), which was also true for the overall latency (ANOVA $F_{3,42} = 0.819$, p = 0.491).

Discussion

This experiment showed that dogs are better able to solve a detour task after witnessing a demonstration of a human, but also after witnessing a partial demonstration by an object being pulled past the end of the fence. Contrary to a previous study (Pongrácz et al. 2003a), the dogs did not follow the same trajectory as the demonstrator. Therefore, option (A) local enhancement and also other learning mechanisms that would predict the observer to detour around the fence at the demonstrated end can be ruled out (i.e. imitation, mimicry; see Call & Carpenter 2002). Regarding option (B), following Call & Carpenter (2002), the dogs probably did not use emulation either, as they succeeded also in the object condition, in which the whole trajectory towards the object was missing, and the object movement did not provide any information regarding its intended target.

As dogs are generally capable of detouring around an obstacle, and the test animals thus did not need to learn a new type of action to solve the problem, it might seem that response facilitation could have been involved in reaching the target. Response facilitation means that an action that has already been part of the observer's repertoire will be more likely to occur if the observer sees another individual gaining a reward while performing this action, because as Byrne & Russon (1998, p. 670) suggest 'the corresponding brain record would be primed'. However, even if one considers it possible that any moving object could potentially evoke such priming, the object demonstrator did neither show the actual path nor was the demonstration of the object linked to the reward in any obvious way. Therefore, response facilitation is unlikely to explain the results. Furthermore, social facilitation (Zajonc 1965), which might have increased motivation or activity, is also very unlikely to account for the differences between the human demonstrator conditions and the control condition, as the control dogs witnessed a walking demonstrator as well. For the same reason of a walking demonstrator in the control condition, we rule out contagion as possible reason for differences between control and demonstration conditions.

One might argue that the dogs might have learnt something about the general properties of a fence (e.g. that it has ends that could be circumnavigated) and that they altered their behaviour contingent on this newly learned affordance, which could be attributed as affordance learning or emulation in a broad sense (Tomasello 1990, 1996; Whiten & Ham 1992). However, as dogs are generally familiar with fences and other obstacles, it seems rather unlikely that they would learn something completely new here (i.e. that the fence has ends and can be circumnavigated). Instead, it seems plausible that the observers' attention was drawn to the fence end (stimulus) by

the demonstrator, which then facilitated passing the fence regardless of side, corresponding to stimulus enhancement (Spence 1937; Zentall, 1986, Hoppitt & Laland 2008). The fact that the object demonstration resulted in a similar success rate as the human demonstration might suggest that the social component of the demonstration was unimportant, even though it is unclear whether dogs differentiate between humans and inanimate objects in this context.

One could argue that a demonstration involving anything going around the barrier just increased the subjects' general exploration of the environment, especially of the fence, which subsequently led to individual trial and error learning. Nevertheless, even if increased exploration was shown towards the fence, this would not be contradictory to stimulus enhancement, which 'is the tendency to pay attention to, or aim responses towards a particular place or object in the environment after observing [an] action at that place or in conjunction with those objects... the mechanism that generates this apparent copy [being] individual trial - and - error learning' (Byrne & Russon 1998, p. 669). However, in our detour paradigm, stimulus enhancement is special for two reasons: (1) in the object demonstrator treatment, it was not a conspecific but a moving object drawing the attention to an end of the fence and (2) trial and error learning at the place of enhanced attention was not really necessary for the dogs, as once they had reached the end of the fence, the solution of the task may have been obvious to them. Hence, enhanced attention to the stimulus may have been sufficient for dogs to overcome the detour problem, which is a component of stimulus enhancement in which the subject does not need to learn a new action. However, enhanced attention is also underlying affordance learning and more generally, it is a prerequisite of most mechanisms of social learning.

Our results seem to disagree with earlier findings of Pongrácz et al. (2003a) in two ways, both of which are probably due to differences in the set-up of the studies. In their experiment, inexperienced dogs took the demonstrated end of the fence, while experienced dogs used either end (Pongrácz et al. 2003a). Copying of the demonstrated end was taken as support for local enhancement, while the behaviour of the experienced dogs was interpreted as evidence for response facilitation. However, it seems possible that dogs in their experiment were more prone to following because they had witnessed the demonstrator carrying the target around the fence.

Experiencing a toy or food being carried around one end of the fence might have released a following response or make the dog follow a scent trail of the bait or demonstrator, which is not necessarily (social) learning (cf. Hoppitt & Laland 2008).

The fact that dogs in our experiment got faster even in the control condition is not surprising, because a significant acceleration from the first successful to the second successful trial can be a result of trial and error learning or something similar to response facilitation (because of priming through own experience of detouring). However, this result is contradictory to earlier findings by Pongracz and collaborators (Pongrácz et al. 2001, 2003b, 2004) and suggests new interpretations. Dogs of their control condition did not get faster in detouring, indicating that even for experienced dogs, it was still hard to overcome the detour problem with a V-shaped fence. This difference between studies is most likely due to the different shape of the fence (straight vs. V-shaped), as variations in the geometrical circumstances of an obstacle are of great importance and may drastically change the difficulties to detour around it (Köhler 1926; Scott & Fuller 1965; Pongrácz et al. 2001). One reason why the dogs of the demonstration conditions were able to get faster in these studies might again be attributed to the demonstrator carrying the target around the fence. Newer results showing different effects of a talking vs. non-talking, food-carrying demonstrator suggest that other components may be additionally involved (Pongrácz et al. 2004). In conclusion, the differences between studies might suggest that to check whether the underlying mechanism is stimulus enhancement, naïve dogs should be tested.

Experiment 2A: Towel Test with Unfamiliar Demonstrator

In this experiment, we investigated the propensity of dogs to show mimicry, imitation or emulation by investigating whether they copy action of a model to solve an instrumental problem. We presented a task that could be performed by two different actions (two-action/one-outcome procedure, Voelkl & Huber 2000). While all dogs were provided with social support and stimulus enhancement, dogs in the demonstration conditions witnessed one of the two ways to solve the problem, whereas control dogs were kept naïve in this respect. We predict dogs that use imitation or emulation in this test to be more successful under demonstration conditions than under the control condition. Imitation and mimicry (the latter

meaning to copy the demonstrator's actions without understanding the demonstrator's goals, Call & Carpenter 2002) would result in an increased number of dogs using the same or a similar technique as demonstrated, whereas emulation would not.

Materials and Methods

Subjects

Sixty-two dogs (34 females, 28 males) of various breeds (see Appendix Table S1 for details) participated in the test. Thirty-four of these dogs had already participated in test 1. All dogs except three Beagles lived as pets with their owners and received the training typical for a family dog (the three Beagles lived in a pack of Beagles at the Faculty of Veterinary Medicine in Leipzig and had frequent contact with people). Dog owners were not present during testing. The prerequisites for dog recruitment were that dogs were food or toy motivated, felt comfortable without their owner, were older than 1 yr and were not fed 2 h prior to the testing. The dogs were randomly assigned to one of the four conditions of the test.

Materials

The test was conducted in a test room $(3 \times 1.9 \text{ m})$ separated from an observation room $(3.7 \times 2.8 \text{ m})$ by a Plexiglas door panel $(76 \times 141 \text{ cm})$ to ensure that dogs could observe the demonstrations. In addition, we attached a cardboard box (40 cm width) to the door to reduce the space for the dog to look through and to ensure test dogs to stand behind the Plexiglas panel in the best position to watch the demonstration. A hole (7 cm diameter) was cut into the Plexiglas to allow presenting the target to the dogs. When the experimental procedure required the dog's view to be blocked, we placed a cardboard sheet in front of the glass.

The test apparatus consisted of a wire basket $(40 \times 30 \times 18 \text{ cm})$ attached upside down to a wooden panel $(44 \times 60 \text{ cm})$ (Fig. 3). A towel was placed under the basket, and two pieces of food (i.e. dry kibble and rawhide), which were inserted through a hole (3.5 cm diameter) at the top of the basket, were placed on the towel. To ensure that the food was always placed in the same position, we used a clear plastic tube $(21 \times 3 \text{ cm})$ for placing it. The towel had to be pulled out from the basket to make the food accessible to the dog. As the basket was made of wire mesh, the food could be seen and smelled from

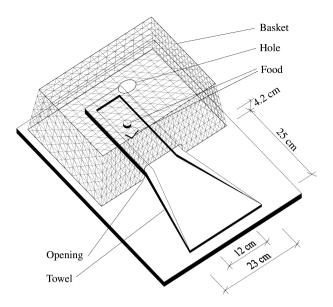


Fig. 3: Apparatus for towel tests A and B, showing the basket, the food, the towel and the hole for inserting the food. The food gets inserted through the hole and can only be reached by pulling out the towel

all sides, but it could only be reached from the front of the basket by pulling the towel.

One dog, a 7-yr-old male castrated mixed breed (Appenzell Cattle Dog/Pharaoh Hound), served as the demonstrator for all subjects in the dog demonstration and control conditions. The dog was easily trainable, very motivated and well socialized (i.e. not causing conflicts with other dogs). He was trained to pull the towel consistently according to the type needed in the different conditions. A woman who was unfamiliar to all test subjects served as human demonstrator for all dogs in the human demonstration group. We chose one demonstrator over several demonstrators to reduce noise in the data caused by potential individual demonstrator effects.

Procedure

For all dogs, D.M. served as the experimenter (E) handling the dog. Every dog was familiarized with the test apparatus before the session began. During this phase, the towel was placed completely inside the basket and was thus not accessible. Thereafter, the test subject was sent to the observation room to observe the demonstration. While the subject was watching, E placed the food on the towel in the basket and then allowed the demonstrator to access the food demonstrating on request one of the following

actions corresponding to each of four experimental groups.

Muzzle demonstration (Md, N = 18)

The dog demonstrator took the towel with his mouth and pulled the towel out. He ate the food and went back to the waiting room.

Paw demonstration (Pd, N = 16)

The dog demonstrator pulled the towel out with his left paw. He ate the food and went back to the waiting room.

Human demonstration (Hd, N = 14)

The human demonstrator pulled the towel out with her right hand, using similar actions as the demonstrator dog did (e.g. scratching movements). She then pretended to eat the food and went back to the waiting room.

Control (C, N = 14)

In this condition, the food was placed in front of the basket, not inside it. The demonstrator dog ate the food and went back to the waiting room. This baiting position caused the demonstrator dog to take the food close to the opening of the basket, like in the other conditions, but without any manipulation of the towel.

After the demonstration, E let the subject enter the test room and placed the food on the towel, ensuring that the dog was attending. The latter was then encouraged twice to get the food by saying 'Na hol's Dir' (i.e. German for 'Come on, get it'). E then turned around and ignored the dog deliberately for 45 s or until she heard the dog eating. The dog was addressed by talking in a friendly manner and led back to the observation room. E blocked the subject's vision with the cardboard sheet and prepared the towel for the next trial. Each dog was tested in four successive trials of the same condition, completed within one session. Each trial consisted of an observation and a test phase.

Data Collection and Analysis

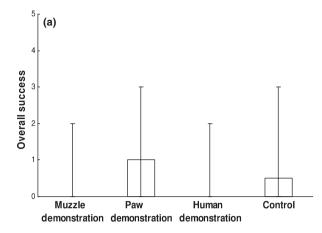
All trials were videotaped and later coded from tape by D.M. We coded whether the dogs pulled out the towel and which action was used to do so. A trial was coded as successful if the dog managed to eat the food. We also coded latency until success. In the rare cases that a dog pulled the towel out but the food fell off the towel, we also considered this trial as successful and measured the latency until the towel was pulled out. For all analyses except for the overall latency, only latencies of successful trials were included. (For the overall latency, the 45 s of previous unsuccessful trials were added to the latency of the first successful trial; e.g. if a dog was first successful in trial number 3 after 25 s, the overall latency was $2 \times 45 \text{ s} + 25 \text{ s} = 115 \text{ s}$). We coded for all trials whether a dog actively tried to manipulate the apparatus (e.g. by scratching, pushing) or not, which part of the body (paw vs. muzzle) the dog used for the manipulation and at which part of the apparatus the action was directed (towel or opening vs. somewhere else) (see below).

To test for inter-observer reliability, a second person blind to the hypothesis coded 19.4% of the material. Concordance between observers was excellent: latency of 1st successful trial: intraclass correlation coefficient for single measures (ICC) = 0.954 and latency of 2nd successful trial: ICC = 0.981, (Landis & Koch 1977); 1st manipulative contact in 1st active trial: Cohen's $\kappa = 0.833$; position of first manipulative contact in first active trial: Cohen's $\kappa = 0.842$; (Cicchetti & Sparrow 1981).

For statistical analyses, we followed the same principles as mentioned in the Detour Test. In addition, to compare all three demonstration groups against the control condition, we pooled the demonstration groups into one experimental group if they did not differ significantly from one another. To compare two unrelated samples if the assumptions of parametric testing were not fulfilled, we used *U*-tests, and for related samples, Wilcoxon matched-pairs signed-ranks tests. To compare frequency distributions of two or more independent samples, we used the Chi-square test for homogeneity.

Results

Only 40% of the dogs managed to get the food at least once. From these 25 dogs, two to four dogs per condition were already successful in their first trial (Md: 3 from 7; Pd: 4 from 9; Hd: 2 from 4; C: 3 from 7). Neither the number of successful dogs nor the number of successful trials per dog differed between the four conditions (success or no: exact Chi-square test: $\chi_3^2 = 2.596$, p = 0.50; overall success: Kruskal–Wallis test: $H_3 = 1.805$, N = 62, p = 0.614; Fig. 4a). The latency until the food was obtained did not differ between conditions (Kruskal–Wallis tests: latency



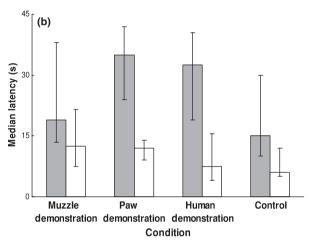


Fig. 4: Results of towel test A: (a) Overall success (median \pm quartiles) reflecting the number of trials out of four in which the dogs obtained the food by pulling out the towel in the four experimental conditions. (b) Latencies (median \pm quartiles) to obtain the food in the four conditions (grey bars: first successful trials; white bars: second successful trials). Neither overall success nor latencies differed between conditions.

in the first successful trial: $H_3 = 5.458$, N = 25, p = 0.141; latency in the second successful trial: $H_3 = 1.622$, N = 22, p = 0.654; Fig. 4b; overall latency: $H_3 = 0.543$, N = 25, p = 0.909). Dogs were faster in their second than in their first successful trials, all conditions pooled (median, 25–75% quartiles: 1st successful trial = 24s, 10.5–36s; 2nd successful trial = 11s, 5.75–14.25s; Wilcoxon test: T = 27, N = 22, p = 0.001).

No significant differences were found when comparing the four experimental groups for the place of first manipulative contact (towel or opening vs. somewhere else at the basket) and the part of the body used (paw vs. muzzle; exact Chi-square tests; place: C: 3/7; Md: 7/3; Pd: 6/8; Hd 2/8: $\chi_3^2 = 5.824$,

p = 0.137; part of the body: C: 6/4; Md 5/5; Pd 8/6; Hd 4/6, χ_3^2 = 0.9969, p = 0.908). However, when successfully pulling the towel out, almost all dogs used their paw. In only two of 73 successful trials, the towel was pulled out by the mouth, but in both cases, this was performed by dogs that had not witnessed a muzzle demonstration.

Female dogs solved significantly more trials than male dogs (overall success: median, 25–75% quartiles: females = 1, 0–3, 25; males = 0, 0–0.75; U-test: U = 333.0, $N_{\rm F}$ = 34, $N_{\rm M}$ = 28, p = 0.022). However, they were neither faster than male dogs (U-tests: latency of first successful trial: U = 57.5, $N_{\rm F}$ = 18, $N_{\rm M}$ = 7, p = 0.739; overall latency: U = 62.5, $N_{\rm F}$ = 18, $N_{\rm M}$ = 7, p = 0.976) nor did they differ significantly regarding whether they tried to manipulate the apparatus or not (exact χ^2_1 = 2.406, p = 0.151).

Experiment 2B: Towel Test with Owner as Demonstrator

It might be that the motivation of test dogs to copy the demonstrated action in the towel test was affected by the fact that the human demonstrator was unknown to the test animals. We therefore conducted a follow-up experiment in which we used the same method but with the dogs' owner as demonstrator. To further increase the likelihood that dogs may learn from the demonstrator, we increased the number of demonstrations. In addition, we only used female dogs as subjects, as they were more successful in the task.

Materials and Methods

Subjects

We tested 30 female dogs of various breeds (Appendix Table S1) together with their owners from Oct. until Dec. 2002. Dog acquisition was the same as before. Subjects were randomly assigned to one of two experimental conditions.

Procedure

Before testing, we conducted motivation trials to ensure that dogs were motivated to perform the task and understood that the basket contained food. Each dog received three trials in which E placed the reward in front of the basket in full view of the subject. To prevent them from accidentally pulling the towel, the entire towel was placed inside the basket.

Then the owner encouraged the dog to take the food using the same command he/she would later use in the test phase. The apparatus, testing area and the general procedure were otherwise similar to the previous test (test 2A). Subjects observed one of two possible demonstrations corresponding to two experimental conditions.

Owner demonstration (Od. N = 15)

After E placed the food into the basket, the dog owner pulled the towel out, demonstrating a scratching-like movement of the hand, and subsequently took the food.

Control (C, N = 15)

After E placed the food directly in front of the basket, the owner tapped on the towel twice (stimulus enhancement) and then took the food.

E blocked the subject's view with a cardboard barrier to prepare the towel for the second demonstration (of the same condition) or for the following test phase. To provide similar odour stimuli on the towel in both conditions, E manipulated the towel similarly in both conditions (i.e. while preparing, she touched the towel in both conditions: in addition, in the owner demonstration condition, she rubbed the food on the towel directly in front of the basket). After the second demonstration, the test followed. The test was exactly the same for both conditions. For the test, the owner led the dog to the basket, inserted the food into the basket and encouraged the dog to get the food. The trial ended as soon as the dog obtained the food or after 45 s had passed. Owners were instructed to ignore their dog during the trial and to visually focus on a specific spot. Each dog was tested in four successive trials of the same condition, which were completed within one session. Each trial consisted of two demonstrations and a test phase.

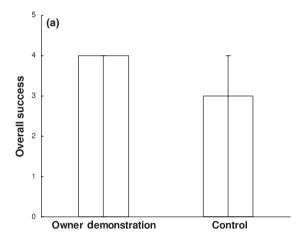
Data Collection and Analysis

Data collection and analysis were identical to experiment 2A. For the motivational trials, we coded for each trial whether dogs took the food without hesitation (and needed no further encouragement by their owner to take the food). Dogs thus could receive a motivational score between 0 and 3, and those with a score of 1 or 0 were excluded from the test. To test observer reliability, a second person blind to the hypothesis recoded 20% of the material. Concordance between observers was excellent:

latency of 1st successful trial: ICC for single measures = 0.983 (Landis & Koch 1977); 1st active contact in 1st active trial (paw, muzzle, not active): Cohen's $\kappa = 1.0$; position of first active contact in first active trial towel/opening vs. somewhere else: Cohen's $\kappa = 1.0$; (Cicchetti & Sparrow 1981).

Results

There were no significant differences in overall success between conditions (U-test: U = 103.0, $N_C = 15$, $N_{Od} = 15$, p = 0.336, one-tailed; Fig. 5a). In each condition, ten of 15 dogs were successful. There were no significant differences between conditions in the latency to solve the task (unpaired t-test: $t_{18} = 0.730$, p = 0.48; Fig. 5b). Dogs, which were more motivated (pre-test score of 3 vs. 2), tended to



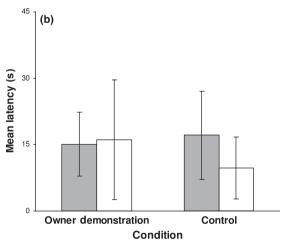


Fig. 5: Results in towel test B. (a) Overall success (median \pm quartiles) reflecting the number of trials out of four in which the dogs obtained the food by pulling out the towel. (b) Latencies (median \pm quartiles) to obtain the food. Overall success and latencies did not differ significantly between conditions.

solve more trials (*U*-test: U = 39.0, $N_3 = 24$, $N_2 = 6$, p = 0.065), but they were not faster in their first successful trial (*t*-test: latency in first successful trial: $t_{18} = -0.086$, p = 0.933).

Discussion

The results of these two experiments clearly show that dogs did not use social learning mechanisms other than local or stimulus enhancement. The lack of demonstration effects on the behaviour of the subjects was not because of a lack of motivation. If dogs had used any additional information provided by the skilful demonstrators, their ability to solve the task should have increased in the demonstration conditions. However, dogs performed similarly, regardless of whether they had witnessed a skilful conspecific demonstrator or a conspecific just eating in the vicinity of the basket, or a human demonstrator manipulating the towel, respectively. Dogs did not appear to learn anything about how the demonstrator's action altered the environment [e.g. emulation, object movement re-enactment (Custance et al. 1999)], which would have resulted in a higher number of dogs manipulating the towel or the opening first in the tests of the demonstration conditions. Nor did they appear to learn about the specific action itself (mimicry, imitation), as they did not use the same part of the body as the demonstrator when first manipulating the apparatus and when pulling out the towel. Furthermore, as the performance of the dogs in the demonstration conditions did not differ from the performance in the control condition, the dogs did not appear to utilize other potential learning mechanisms (e.g. observational conditioning, response facilitation). As stated earlier, dogs saw a demonstrator acting in front of the basket and close to the towel in the control conditions as well as in the demonstration conditions, which provided similar possibilities to all of them for social facilitation and for local and stimulus enhancement.

Dogs clearly preferred the paw over the muzzle to pull the towel out. This might be the reason why we did not find differences in the dogs' behaviour according to which demonstration they had witnessed. However, it is striking that the dogs did not use any of the extra information provided by the paw, muzzle or human hand demonstrations in comparison with the control condition, which would have helped them to solve the problem. The results of the current study are in accordance with previous findings by Kubinyi et al. (2003). In their study, dogs utilized stimulus enhancement to

solve a manipulation task. However, these dogs did not seem to benefit from observing the outcome of an action compared with seeing the action without an outcome (Kubinyi et al. 2003).

An unexpected finding from the towel test was that female dogs performed better than male dogs. Male dogs might be less skilled than female dogs in individual and/or social learning (stimulus enhancement and social facilitation). As yet there is no published evidence for gender differences in dogs' general cognitive abilities (e.g. individual learning). However, gender may affect dogs' behaviour in social learning settings as was recently suggested (Heberlein & Turner 2009), which may then cause different performance. For example, male dogs might have been less food-motivated or less active than female dogs. However, the sexes did not differ in their general activity (i.e. attempting to manipulate the apparatus at least once). Alternatively, the sex of the demonstrator dog (male) might have influenced the behaviour of observers or their 'social acquisition of information' (Choleris & Kavaliers 1999). However, the male dogs' success was similar between all conditions, regardless if they had witnessed a male conspecific or a woman as demonstrator. We therefore think it might be most likely that some male dogs were more distracted by the smell of previous dogs in the test room and therefore less focused on the task than were female dogs (cf. Heberlein & Turner 2009).

Regardless of what might have caused the poorer performance of male dogs in our study, if successful, they solved the task as quickly as the female dogs did. This indicates that among successful dogs, males and females were equally skilled in the task. The results of the towel tests with an unfamiliar demonstrator vs. the owner as demonstrator are not directly compared here. In the owner demonstration experiment, our aim was to enhance the likelihood of social learning. Therefore, we had not only introduced the owner as the demonstrator but also made other improvements (e.g. motivational trials prior to testing, more demonstrations, better angle of view during demonstration). This is why a comparison between experiments would tell us little about the cause of a potential improvement in performance. Instead, we focused on the within-test comparison to check whether dogs used any of the provided social information beyond local enhancement.

General Discussion

Overall, our results suggest that in our experimental paradigms, dogs benefited from observing a demon-

strator. However, in both cases, the underlying mechanism was most likely stimulus (and local) enhancement. First, in the detour test, dogs managed to detour a fence to reach a piece of food with equal success, regardless of whether they had witnessed a live demonstrator or an object bypassing the end of the fence. While both - live demonstrator and object - drew the observer's attention to the end of the fence, the live demonstrator offered additional social learning opportunities. However, it appears that dogs did not use any additional learning mechanisms (e.g. response facilitation, imitation), suggesting that the driving mechanism of the dogs' improvement in performance was stimulus enhancement. Second, in the towel test, dogs were equally successful in reaching the target after they had seen a dog or a human solving the problem (successfully pulling the towel to reach the food) or after they had simply seen a dog eating near the towel or a demonstrator taking the food without manipulating the towel. As in the detour test, dogs did not use any other learning mechanisms (e.g. emulation, object movement re-enactment, response facilitation). This again suggests that amongst other potential forms of social influence, simply enhancing the towel alone helped the dogs to solve the problem, which includes both stimulus and local enhancement as potential mechanisms. However, as there was no control conditions without enhancing the towel and thus without local and stimulus enhancement offered, an experimental proof is still lacking. Finally, there was no evidence that subjects copied any of the actions of the demonstrator. This is true for both, the detour test, in which test dogs did not preferentially use the end of the fence that the demonstrators had used, and the towel test, in which dogs did not preferentially use their mouth or paw to pull the towel in dependence of the demonstration.

One could argue that stimulus enhancement sufficed that the dogs could solve the tasks individually, and observing others more closely was therefore not necessary. While this could be true in the detour test, this cannot account for the results in the towel test A, as only 40% of dogs solved the experimental task successfully. Therefore, the majority of dogs would have benefited from using more of the provided information.

It might be argued that the failure to find any group differences in the towel test may result from a general failure of the manipulation. Even if this possibility cannot be completely ruled out for the towel test A, it is very unlikely to apply to the towel test B, in which two-thirds of the dogs

managed to manipulate the apparatus successfully. Again, there were no differences between the conditions found, indicating that dogs did not use extra information given by the skilful demonstration as opposed to the sham demonstration in the control.

As mentioned earlier, differences between our results and those of Pongrácz et al. (2001, 2003a, 2004) are likely due to seemingly little, but in fact important differences in the set-up (e.g. straight vs. V-shaped fence, inexperienced test dogs vs. subjects that were already experienced to detour around the fence prior to experimental demonstration, owner absent during the test vs. owner present). Different test-paradigms have different confounding variables and may thus cause diverging results. In addition, in the detour task, we added a 'control' condition (the object demonstration), which had not been used so far but provided valuable insight into the underlying mechanisms.

Our results may seem to contradict recent findings suggesting that dogs have the potential to copy the action of others (Topál et al. 2006; Range et al. 2007, 2011; but see Tennie et al. 2009). However, for some of those studies, a different mechanism may explain the results (but see Miller et al. 2009).

Topál et al. (2006) found that a dog succeeded to refer to human movements with matching movements, after being trained in the 'Do as I Do' paradigm. However, the tested dog was an assistance dog and thus highly trained to do things that are usually performed by humans (e.g. open cupboards, doors and drawers, switch the light on and off). Even if this ability was shown in other dogs that had not undergone training in 'human-like' behaviour before, it is unclear whether these dogs would use this ability spontaneously when confronted with a problem-solving task like the towel test (see Tennie et al. 2006). Range et al. (2007) proposed that dogs imitate other dogs selectively. Their claim was that dogs attend to the means of others' actions and copy those means only when they are the rational solution to a problem, but not if they are irrational. The female demonstrator dog pulled down a rod using her paw to release a piece of food. She sometimes did that with her mouth being occupied by a ball and sometimes with her mouth being free. When allowed to act on the apparatus, the observer dogs performed the paw action (less preferred by naïve dogs) when the demonstrator dog's mouth had been free during the demonstration, but they used their mouth when the demonstrator dog's mouth had been occupied. Range et al.'s (2007) explanation for

this was that the observers attended to the context in which a certain action is performed, e.g. whether or not an object (a ball) constrains the demonstrator's behaviour.

However, Range et al. (2007) did not perform a key control condition in which the demonstrator's mouth is free but a ball is still present. Indeed the inclusion of this control in a recent attempt to replicate Range et al.'s (2007) findings showed that the sheer presence of a ball may trigger a mouth response. This suggests that dogs in the previous study may have been distracted in the 'irrational' condition rather than selectively attending to the irrational nature of the action (Kaminski et al. 2011).

Our study adds to the evidence that task solving in social learning situations may often be explained by relatively simple mechanisms. From an evolutionary perspective, there is probably no need for dogs (or wolves) to have evolved 'higher' social learning mechanisms. It seems more likely that imitative skills evolve in species using complex, difficult-tolearn food searching and handling techniques (Caldwell & Whiten 2002). Accordingly, some primates have been shown to use higher forms of social learning like emulation (Call et al. 2005; Tennie et al. 2006) and possibly even imitation (see Tomasello 1996; Call & Carpenter 2002 for review). This, however, may not apply for dogs, wolves or canids in general, who are not known to use complex food searching techniques similar to those used by some primates. It has been hypothesized that wolves may outperform dogs in social learning situations (see Frank 1980; Frank & Frank 1987), but the mechanisms involved in wolves' social learning are yet unexplored. Future studies will determine whether and to what extent simple forms of social learning in dogs and wolves might be complemented by more complex mechanisms like, e.g., imitation. It could be, for instance, that with extensive training in the course of development, imitative skills in dogs can be 'shaped' (Range et al. 2011).

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Literature Cited

- Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C. & Matsuzawa, T. 2003: Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. Anim. Cogn. **6**, 213—223
- Bräuer, J., Kaminski, J., Riedel, J., Call, J. & Tomasello, M. 2006: Making inferences about the location of hidden food: social dog causal ape. J. Comp. Psychol. **120**, 38—47.
- Brodgen, W. J. 1942: Imitation and social facilitation in the social conditioning of forelimb-flexion in dogs. Am. J. Psychol. **55**, 77—83.
- Byrne, R. W. & Russon, A. E. 1998: Learning by imitation: a hierarchical approach. Behav. Brain Sci. **21**, 667—721.
- Caldwell, C. A. & Whiten, A. 2002: Evolutionary perspectives on imitation: is a comparative psychology of social learning possible? Anim. Cogn. **5**, 193—208.
- Call, J. & Carpenter, M. 2002: Three sources of information in social learning. In: Imitation in Animals and Artifacts (Dautenhahn, K. & Nehaniv, C. L., eds). MIT Press, Cambridge, MA, pp. 211—228.
- Call, J., Carpenter, M. & Tomasello, M. 2005: Copying results and copying actions in the process of social learning: chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). Anim. Cogn. **8**, 151—163.
- Catchpole, C. K. & Slater, P. J. B. 1995: Bird Song: Biological Themes and Variations. Cambridge Univ. Press, New York.
- Choleris, E. & Kavaliers, M. 1999: Social learning in animals: sex differences and neurobiological analysis. Pharmacol. Biochem. Behav. **64**, 767—776.
- Christiansen, F. O., Bakken, M. & Braastad, B. O. 2001: Social facilitaion of predatory, sheep-chasing behaviour in Norwegian elkhounds, grey. Appl. Anim. Behav. Sci. **72**, 105—114.
- Cicchetti, D. V. & Sparrow, S. A. 1981: Developing criteria for establishing interrater reliability of specific items: applications to assessment of adaptive behavior. Am. J. Ment. Defic. **86**, 127—137.
- Curio, E. 1988: Cultural transmission of enemy recognition by birds. In: Social Learning: Psychological and Biological Perspectives (Zentall, T. R. & Galef, B. G. J., eds). Erlbaum, Hillsdale, pp. 75—97.
- Custance, D., Whiten, A. & Fredman, T. 1999: Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*). J. Comp. Psychol. **113**, 13—23.
- Dawson, B. V. & Foss, B. M. 1965: Observational learning in budgerigars. Anim. Behav. 13, 470—474.
- Dugatkin, L. A. 1996: Copying and mate choice. In: Social Learning in Animals: The Roots of Culture (Heyes, C. M. & Galef, B. G. J., eds). Academic Press, Inc., San Diego, CA, pp. 85—105.

- Dumas, C. & Pagé, D. D. 2006: Strategy planning in dogs (*Canis familiaris*) in a progressive elimination task. Behav. Process. **73**, 22—28.
- Frank, H. 1980: Evolution of canine information processing under conditions of natural and artificial selection. Z. Tierpsychol. **53**, 389—399.
- Frank, H. & Frank, M. G. 1987: The University of Michigan canine information-processing project (1979–1981). In: Man and Wolf: Advances, Issues, and Problems in Captive Wolf Research, Vol. 4 (Frank, H., ed.). Dr. W. Junk Publishers, Dordrecht, The Netherlands, pp. 143—167.
- Gácsi, M., McGreevy, P., Kara, P. & Miklósi, Á. 2009: Effects of selection for cooperation and attention in dogs. Behav. Brain Funct. **5**, 31.
- Galef, B. G. 1996: Social enhancement of food preferences in Norway rats: a brief review. In: Social Learning in Animals: The Roots of Culture (Heyes, C. M. & Galef, B. G. J., eds). Academic Press Inc., San Diego, CA, pp. 49—64.
- Galef, B. G. 2001: Social influences in food choices of Norway rats and mate choices of Japanese quail. Int. J. Comp. Psychol. **14**, 1—24.
- Hare, B., Brown, M., Williamson, C. & Tomasello, M. 2002: The domestication of social cognition in dogs. Science **298**, 1634—1636.
- Heberlein, M. & Turner, D. C. 2009: Dogs, *Canis familiaris*, find hidden food by observing and interacting with a conspecific. Anim. Behav. **78**, 385—391.
- Hile, A. G. & Striedter, G. F. 2001: Call convergence within groups of female budgerigars (*Melopsittacus undulatus*). Ethology **106**, 1105—1114.
- Hoppitt, W. & Laland, K. N. 2008: Social processes influencing learning in animals: a review of the evidence. Adv. Study Behav. **38**, 105—165.
- Itani, J. & Nishimura, A. 1973: The study of infra-human culture in Japan. In: Precultural Primate Behavior (Menzel, E., ed.). Karger, Basel, pp. 26—50.
- Kaminski, J., Nitzschner, M., Wobber, V., Tennie, C., Bräuer, J., Call, J. & Tomasello, M. 2011: Do dogs distinguish rational from irrational acts? Anim. Behav. **81**, 195—203.
- Köhler, W. 1926: The Mentality of Apes. Harcourt, Brace & Company, Inc., New York.
- Kubinyi, E., Topál, J., Miklósi, Á. & Csányi, V. 2003: Dogs (*Canis familiaris*) learn from their owners via observation in a manipulation task. J. Comp. Psychol. **117**, 156—165.
- Landis, J. & Koch, G. 1977: The measurement of observer agreement for categorical data. Biometrics **33**, 159—174.
- McKinley, S. & Young, R. J. 2003: The efficacy of the model-rival method when compared with operant conditioning for training domestic dogs to perform a

- retrieval-selection task. Appl. Anim. Behav. Sci. **81**, 357—365.
- Miklósi, Á., Kubinyi, E., Topál, J., Gacsi, M., Viranyi, Z. & Csányi, V. 2003: A simple reason for a big difference: wolves do not look back at humans, but dogs do. Curr. Biol. **13**, 763—766.
- Miller, H. C., Rayburn-Reeves, R. & Zentall, T. R. 2009: Imitation and emulation by dogs using a bidirectional control procedure. Behav. Process. **80**, 109—114.
- Mineka, S. & Cook, M. 1988: Social learning and the acquisition of snake fear in monkeys. In: Social Learning: Psychological and Biological Perspectives (Zentall, T. R. & Galef, B. G. J., eds). Erlbaum, Hillsdale, NJ, pp. 51—73.
- Mundry, R. & Fischer, J. 1998: Use of statistical programs for nonparametric tests of small samples often leads to incorrect p values examples from Animal Behaviour. Anim. Behav. **56**, 256—259.
- Pongrácz, P., Miklósi, Á., Kubinyi, E., Gurobi, K., Topál, J. & Csányi, V. 2001: Social learning in dogs: the effect of a human demonstrator on the performance of dogs in a detour task. Anim. Behav. **62**, 1109—1117.
- Pongrácz, P., Miklósi, Á., Kubinyi, E., Topál, J. & Csányi, V. 2003a: Interaction between individual experience and social learning in dogs. Anim. Behav. **65**, 595—603.
- Pongrácz, P., Miklósi, Á., Timár-Geng, K. & Csányi, V. 2003b: Preference for copying unambiguous demonstrations in dogs (*Canis familiaris*). J. Comp. Psychol. **117**, 337—343.
- Pongrácz, P., Miklósi, Á., Timár-Geng, K. & Csányi, V. 2004: Verbal attention getting as a key factor in social learning between dog (*Canis familiaris*) and human. J. Comp. Psychol. **118**, 375—383.
- Pongrácz, P., Miklósi, Á., Vida, V. & Csányi, V. 2005: The pet dogs ability for learning from a human demonstrator in a detour task is independent from the breed and age. Appl. Anim. Behav. Sci. **90**, 309—323.
- Pongrácz, P., Vida, V., Banhagyi, P. & Miklósi, Á. 2008: How does dominace rank status affect individual and social learning performance in the dog (*Canis familiaris*)? Anim. Cogn. **11**, 75—82.
- Range, F., Viranyi, Z. & Huber, L. 2007: Selective imitation in domestic dogs. Curr. Biol. 17, 1—5.
- Range, F., Huber, L. & Heyes, C. 2011: Automatic imitation in dogs. Proc. R. Soc. Lond. B Biol. Sci. **278**, 211—217.
- Scott, J. P. & Fuller, J. L. 1965: Genetics and the Social Behavior of the Dog. Univ. of Chicago Press, Chicago, IL. Shaffer, J. P. 1995: Multiple hypothesis testing. Annu.
- Rev. Psychol. **46**, 561—584.
- Slabbert, J. & Rasa, O. 1997: Observational learning of an acquired maternal behaviour pattern by working dog pups: an alternative training method? Appl. Anim. Behav. Sci. **53**, 309—316.

- Spence, K. 1937: Experimental studies of learning and higher mental processes in infra-human primates. Psychol. Bull. 34, 806—850.
- Tennie, C., Call, J. & Tomasello, M. 2006: Push or pull: imitation vs. emulation in great apes and human children. Ethology **112**, 1159—1169.
- Tennie, C., Glabsch, E., Sebastian, T., Bräuer, J., Kaminski, J. & Call, J. 2009: Dogs, *Canis familiaris*, fail to copy intransitive actions in third-party contextual imitation tasks. Anim. Behav. **77**, 1491—1499.
- Terkel, J. 1996: Cultural transmission of feeding behavior in the Black Rat (*Rattus rattus*). In: Social Learning in Animals: The Roots of Culture (Heyes, C. M. & Galef, B. G. J., eds). Academic Press Inc., San Diego, CA, pp. 17—47.
- Tomasello, M. 1990: Cultural transmission in the tool use and communicatory signaling of chimpanzees? In: "Language" and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives (Parker, S. T. & Gibson, K. R., eds). Cambridge Univ. Press, New York, pp. 274—311.
- Tomasello, M. 1996: Do apes ape? In: Social Learning in Animals: The Roots of Culture (Heyes, C. M. & Galef, B. G. Jr, eds). Academic Press Inc., San Diego, CA, pp. 319—364.
- Tomasello, M. 1999: The Cultural Origins of Human Cognition. Harvard Univ. Press, Cambridge, MA.
- Topál, J., Byrne, R. W., Miklósi, Á. & Csányi, V. 2006: Reproducing human actions and human action sequences: "Do as I Do!" in a dog. Anim. Cogn. **9**, 355—367.

- Voelkl, B. & Huber, L. 2000: True imitation in marmosets. Anim. Behav. **60**, 195—202.
- West, M. J., King, A. P. & Freeberg, T. M. 1996: Social malleability in cowbirds: new measures reveal new evidence of plasticity in the Eastern subspecies (*Molothrus ater ater*). J. Comp. Psychol. **110**, 15—26.
- Whiten, A. & Ham, R. 1992: On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. Adv. Study Behav. **21**, 239—283.
- Zajonc, R. B. 1965: Social facilitation. Science **149**, 269—274.
- Zentall, T. 1996: An analysis of imitative learning in animals. In: Social Learning in Animals: The Roots of Culture (Heyes, C. M. & Galef, B. G. Jr, eds). Academic Press Inc., San Diego, CA, pp. 221—243.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix Table S1. Dog breeds participating in the three experiments

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