

Learning and owner–stranger effects on interspecific communication in domestic dogs (*Canis familiaris*)

Angel M. Elgier, Adriana Jakovcevic, Alba E. Mustaca, Mariana Bentosela*

Laboratorio de Psicología Experimental y Aplicada (PSEA) - Instituto de Investigaciones Médicas (IDIM-CONICET) - Universidad de Buenos Aires (UBA), Argentina

ARTICLE INFO

Article history:

Received 5 August 2008

Received in revised form 12 December 2008

Accepted 22 December 2008

Keywords:

Dogs
Pointing
Learning
Owner

ABSTRACT

Domestic dogs are very successful at following human cues like gazing or pointing to find hidden food in an object choice task. They solve this kind of situation at their first attempts and from early stages of their development and perform better than wolves. Most of the authors proposed that these abilities are a domestication product, and independent from learning processes. There are few systematic studies on the effects of learning on dogs' communicative skills. We aim to evaluate the effect of extinction and reversal learning procedures on the use of the pointing gesture in an object choice task. The results showed that dogs stopped following the pointing cue in the extinction and that they learned to choose the not pointed container in the reversal learning. Results suggest that instrumental learning plays an important role in interspecific communication mechanisms between humans and dogs. In both experiments for half of the subjects the pointer was the owner and for the rest was a stranger. A differential effect was found: extinction was slower but reversal learning was faster when the owner gave the cue. This data indicates that the relationship of the dog with the person who emits the cue influences performance.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

Diverse evidence shows that dogs are able to use social cues to solve problems like the object choice task (Miklósi et al., 2004; Hare and Tomasello, 2005). In this task, an experimenter hides a piece of food in an opaque container, and the animal that does not have visual access to the place where the food was hidden must choose between two containers. The dogs solve this task if the experimenter gives a communicative cue to them, like gazing or pointing. Non-social cues like odor were controlled (e.g., Hare and Tomasello, 1999; Soproni et al., 2001). Dogs may even solve this kind of task at their first attempt (e.g., Hare and Tomasello, 1999; Agnetta et al., 2000; Soproni et al., 2001) and from early stages of their development (Agnetta et al., 2000; Riedel et al., 2008). Furthermore, in these tasks dogs are more successful than wolves (Hare et al., 2002; Miklósi et al., 2003). The authors proposed that the interspecific communicative abilities of dogs were a product of domestication, and independent of the learning processes (e.g., Bräuer et al., 2006). However, it is yet undecided whether dogs' communicative skills are a genetic trait or develop during ontogeny (Schwab and Huber, 2006).

* Corresponding author at: Laboratorio de Psicología Experimental y Aplicada (PSEA) - Instituto de Investigaciones Médicas (IDIM-CONICET), Combatientes de Malvinas 3150 (1427), Buenos Aires, Argentina.

E-mail address: marianabentosela@gmail.com (M. Bentosela).

Virányi et al. (2008) showed that socialized wolves highly respond just as dogs to habitual signals such as pointing, but do not respond to more subtle gestures. Furthermore, socialized wolves, which daily received treats by the human hand, followed momentary distal pointing to find food with only 10 trials of testing and without previous explicit training just like dogs (Udell et al., 2008). Wynne et al. (2008), reanalyzing data of Riedel et al. (2008) with dog puppies, found a significant effect of age, showing that the oldest dog puppies had a better performance than the young ones. Besides, the youngest puppies improved their responses throughout the tests demonstrating a learning effect during training. All these results as a whole show the importance of the ontogeny in the interspecific communication.

Also, there is a controversy about the mechanisms involved in this type of interaction. The main question is whether this communicative ability should be regarded as an associative learning where the subject forms an association between the cue and the place of reward (Povinelli and Giambone, 1999; Shapiro et al., 2003) or whether this is a communicative situation where subjects might learn about the meaning of the cue, thus requiring higher cognitive skills (Miklósi et al., 1998; Soproni et al., 2002; Bräuer et al., 2006; Riedel et al., 2006).

Despite this controversy, few systematic studies on the effects of learning on the communicative capacities of domestic dogs have so far been performed. Recently, Bentosela et al. (2008) showed that the gazing response of the dog towards an unknown human face can increase as a consequence of reinforcement and diminish by omission, extinction and downshift of the reward in a succes-

sive negative contrast procedure (Bentosela et al., in press). These data suggest that instrumental learning has an important role on interspecific communication.

Most of dogs' interactions take place primarily with humans, from where they obtain most of the resources (Udell and Wynne, 2008). In particular, the relation that dogs maintain with their owners with whom they coexist takes relevancy. There is evidence that the influence of the owner affects problem solving abilities. For example, dogs with a dependent attachment style towards their owner perform worse than less dependent dogs in a learning task (Topál et al., 1997). In the same sense, in an object choice task dogs have shown abilities to discriminate between different amounts of food. Nevertheless, after observing their owner expressing a preference for the small food quantity, they chose the large quantity of food significantly less than in the independent choice situation (Prato-Previde et al., 2008). Most of the works compare the presence or the absence of the owner, or different styles of attachment. There are few works comparing the effects of the presence of the owner versus a stranger in a task. Recently, Tóth et al. (2008) did not find differences in the playing styles of dogs with respect to the owner or to a stranger.

In the first place, we aim to evaluate the effects of learning upon the human point-following behaviour of the dogs. With this aim, we evaluated the effect of extinction (Experiment 1) and reversal learning procedures (Experiment 2) on the use of the proximal pointing gesture in an object choice task. There are few studies on extinction and reversal learning effects in dogs, outside of the laboratory context (Smith and Davis, 2008). These experiments will give information about which are the mechanisms involved in the use of human communicative signals, specifically, the contribution of reinforcement history. If the responses of the animals can be modified during the extinction and the reversal learning, the instrumental learning processes could be playing a role.

Secondly, we evaluate whether the familiarity of the dog with the person who emits the pointing cue influences performance during the extinction and the reversal learning. In both experiments, a group that received cues from the owner, Owner Group (OG), was compared with another group which received cues from an unknown person, Stranger Group (SG). The differences in these groups would show the importance of the previous experiences of the animals upon the performance of a communicative task.

2. Experiment 1

The aim of this experiment is to study the effect of the extinction on point-following behaviour. Extinction is a procedure in which a behaviour that has been reinforced ceases to be so, thereby producing a gradual decrease in the response (Thorndike, 1911; Skinner, 1953). If the behaviour of the animal changes during this phase, that is to say, if the dog stops approaching the pointed container, then instrumental learning can be suggested as one of the responsible mechanisms for this type of communicative interaction. Regarding to the effect of the familiarity of the person who points, since in both cases the information that the animal receives is the same, the possible differences between these two groups could be explained by the animals' previous experience.

2.1. Materials and method

2.1.1. Subjects

Thirteen adult dogs, 6 males and 7 females (*Canis familiaris*; mean age = 59 months; range 12–96 months) that lived with human families since they were puppies were used. Prior approval to par-

Table 1

Characteristics of the dogs used in Experiments 1 and 2: breed, gender (M: male; F: female), age in years, training level, experimental condition and group (owner or stranger).

Breed	Gender	Age	Training level	Condition	Group
German Shepherd	M	7	Advanced	Extinction	Owner
Labrador	M	5	Basic	Extinction	Owner
Mixed breed	F	8	None	Extinction	Owner
Mixed breed	F	6	None	Extinction	Owner
Mixed breed	F	6	None	Extinction	Owner
Labrador	F	1	None	Extinction	Owner
Rottweiler	F	5	None	Extinction	Stranger
Labrador	M	3	Basic	Extinction	Stranger
Labrador	M	6	None	Extinction	Stranger
Labrador	M	4	None	Extinction	Stranger
Mixed breed	F	6	None	Extinction	Stranger
Mixed breed	F	6	None	Extinction	Stranger
Mixed breed	M	1	None	Extinction	Stranger
Poodle	M	2	None	Reversal	Owner
German Shepherd	M	2	None	Reversal	Owner
Mixed breed	M	6	Basic	Reversal	Owner
Mixed breed	M	5	Basic	Reversal	Owner
Mixed breed	M	2	None	Reversal	Owner
Mixed breed	F	8	None	Reversal	Owner
German Shepherd	M	2	None	Reversal	Stranger
Bracco	F	3	None	Reversal	Stranger
Labrador	F	9	None	Reversal	Stranger
Shih Tzu	M	4	None	Reversal	Stranger
Mixed breed	F	6	None	Reversal	Stranger

ticipate in the experiments was given by the owners of all subjects. Dogs were deprived of food between 3 and 8 h before beginning the experiment. See Table 1 for a list of subjects showing their breeds, sexes and ages, and the experiment in which they took part.

2.1.2. Materials

The observations were made in a room familiar for the dog. For hiding the food, two opaque containers were used, of 30 cm in diameter and 8 cm in height. These containers were placed on two chairs. The height of the chairs varied based on the size of the subjects, in a way that they did not have visual access to the content of the containers. The containers were separated by 1 m from each other. The human pointer was placed 50 cm from each one. The starting point of the dog was 2 m in a straight line from the position of the human pointer. The dog was always next to a handler, who carried it to the starting point with a leash of 1 m. During the training phase, the person who pointed, the handler, the cameraman and the dog were present. As reinforcer, small pieces of dry liver of 3 g were used. In order to control the odor, both containers were greased with abundant liver before the experience.

2.1.3. Procedure

Responses to gestures are usually tested in an object-choice task. In this test, a reward (in this case, liver) is hidden in one of two containers. The subject enters the test area, and a gesture (in this case, pointing) is given to indicate the location of the food. In our study, for half of the dogs the cue was given by the owner (OG) and for the rest of the animals the pointing was made by an unknown person in absence of the owner (SG).

2.1.3.1. Pre-training. The objective of the pre-training was to show to the dogs that the containers had food. The handler took the dog towards each container, showed the food and allowed the dog to eat. Immediately following baiting, the animal was located in the starting point and the human pointer called it by its name, showing a piece of food in the hand. While the dog was looking, the food was placed in one of the containers. Later, the handler took the dog to the container to eat the liver pellet. This action was repeated twice in each side, in a random order.

Table 2
Performance of each subject in Experiments 1 and 2.

Subject	Experiment	Group	No. of correct trials in acquisition	No. of trials to criterion in extinction/reversal
Tango	Extinction	Owner	30	27
Jaco	Extinction	Owner	25	23
Betty	Extinction	Owner	30	37
Suri	Extinction	Owner	28	8
Clarita	Extinction	Owner	29	26
Batata	Extinction	Owner	27	51
Rod	Extinction	Stranger	30	25
Frodo	Extinction	Stranger	29	8
Marito	Extinction	Stranger	28	28
Chocolate	Extinction	Stranger	28	6
Juanita	Extinction	Stranger	28	6
Luz	Extinction	Stranger	29	7
Teo	Extinction	Stranger	29	6
Goofy	Reversal	Owner	4	9
Gringo	Reversal	Owner	4	9
Koko	Reversal	Owner	4	20
Neurón	Reversal	Owner	4	24
Surfero	Reversal	Owner	4	13
Sole	Reversal	Owner	4	23
Olaf	Reversal	Stranger	4	60
Ruany	Reversal	Stranger	4	62
Shiva	Reversal	Stranger	4	61
Teo	Reversal	Stranger	4	40
Cushi	Reversal	Stranger	4	7

Note: The number of correct responses during acquisition trials in Experiment 1 were over a total of 30 trials, meanwhile in Experiment 2 over a total of 4 consecutive trials.

2.1.3.2. Acquisition. This phase consisted of three sessions of 10 trials each, with an interval between trials of 30 s. The interval between sessions was 10 min. Once the animal was taken by the handler to the starting point, the human called it by name, trying to make eye contact with the dog. If the dog did not look at the human pointer, he called once again. A maximum of two calls per trial were made. Immediately after, the human pointer pointed to the baited container. After the pointing cue was emitted, the handler allowed the dog to choose one of the containers. It was considered that the animal made a selection when it touched the container with its muzzle, or approached less than 10 cm to the container. If the dog chose the baited container, it was allowed to eat the reinforcer. If it chose the non-pointed place, the handler corrected it saying to the dog “no”. Immediately after, the human pointer showed the dog that the chosen container was empty and that the other one was full, without allowing to accede to the reinforcer. The food was placed in random order to the right or to the left of the experimenter, without repeating the same position in more than two consecutive trials. On all occasions, the human that pointed continued to look at the dog throughout the test, without looking at the containers. Once the trial finished, the dog was hidden behind some furniture or a door so that it did not have visual access to the container during the baiting.

2.1.3.3. Extinction. The interval between the acquisition and the extinction phases was 10 min. In extinction phase, sessions of 10 trials were made, each one with an interval between trials of 30 s. The interval between sessions was 10 min. The procedure was identical to the acquisition phase, but none of the containers had food. The extinction response was considered to be performed when the dog did not make any choice (not choosing any container) during 15 s after the pointing cue. The animal could remain in the starting point, or go to any other place, without approaching any of the containers. The extinction phase was extended until the animal acquired the established criterion of extinction, which consisted of four consecutive trials of no choice response.

2.1.4. Data analysis

An average of the accumulated correct responses during the phase of acquisition in all the subjects was calculated. The num-

ber of trials necessary to reach the criterion of extinction in each group was measured, and independent samples *t*-test was used to evaluate the effect of the person who pointed. The alpha level was of 0.05.

2.2. Results

The average of correct responses during the phase of 30 trials of acquisition taking all the subjects ($n = 13$) was 28.46 trials, S.E.M. ± 1.39 . In order to evaluate the Owner–Stranger effect, the performance of each group during acquisition was compared with an independent sample *t*-test, not showing significant differences, $t(11) = 0.692$, $p = 0.503$. In the extinction phase, both groups fulfilled the criterion of 4 consecutive trials without choosing. For a binomial distribution, the probability of giving four consecutive extinction (or reversal) responses by chance is 0.0625. These results suggest that animals extinguished their point-following behaviour, when that response no longer allowed them to obtain the reinforcer. Table 2 shows individual subject performance.

Fig. 1 shows the average of the number of trials until reaching the criterion of extinction for each group. An independent samples *t*-

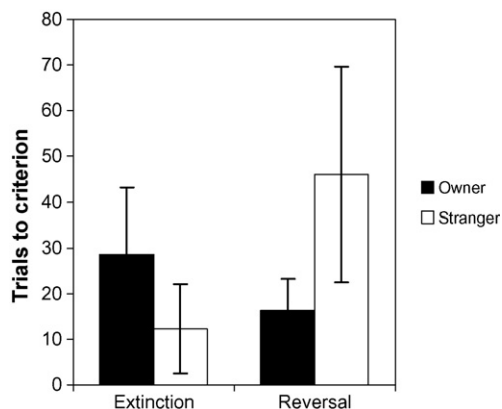


Fig. 1. Mean and standard error of trials to criterion of extinction (Experiment 1, $n = 13$) and reversal learning (Experiment 2, $n = 12$); $p < 0.05$.

test showed a group effect, finding significant differences between OG and SG, $t(11) = 2.433$, $p = 0.033$. This result indicates that when the pointer was the owner, the dogs significantly needed more trials to extinguish their response, in comparison with the dogs pointed by a stranger.

3. Experiment 2

The aim of this experiment was to evaluate the effect of a reversal learning procedure on the point-following behaviour of the dogs. That is to say, to study the choice behaviour of the dog when the reinforcer is in the not pointed container. If a behaviour does not produce appetitive consequences and other responses receive positive outcomes, the first behaviour probability decreases. This phenomenon is known as “omission”. The omission procedure involved in this reversal learning allows us to evaluate if a response fundamentally depends on its instrumental consequences, that is to say, on the reinforcement processes (Mackintosh, 1983).

On the other hand, as in the previous experiment we evaluated whether there are differences in the performance of the subjects when the pointing cue is given by the owner (OG) or by a stranger (SG).

3.1. Materials and method

3.1.1. Subjects and materials

The subjects were 11 dogs, 7 males and 4 females (*C. familiaris*; age in months mean = 53; range = 24–108 months). See Table 1 for details. The materials were similar to the previous experiment. All dogs were tested indoors.

3.1.2. Procedure

3.1.2.1. Pre-training and acquisition. The procedure of the pre-training and acquisition phases was identical to Experiment 1, except in the acquisition phase extension. This phase was extended until the animal reached the learning criterion, that is, until each dog chose the pointed place during four consecutive trials.

3.1.2.2. Reversal learning. The interval between acquisition and reversal phases was 10 min. This second phase was divided in two parts; the first one was called Instigation, in which the dog does not make a choice. It is gently taken by the handler to the not pointed bowl. The aim is that the dog learns that the reinforcer is in the not pointed bowl. The second part consisted of the reversal training.

3.1.2.3. Instigation. This phase consisted of three sessions of 10 trials, with an interval between trials of 30 s. The interval between sessions was 10 min. The trial began with the animal in the starting point, the pointer called the dog by its name, making eye contact with it. Once visual contact was made, the experimenter pointed to the container which did not contain the reinforcer, and the handler took the dog towards the not pointed container, where the reinforcer was. The pointer remained with the arm extended, pointing to the empty container, and looking at the dog until it ate the liver. The reinforcer was placed in one of both containers, in random order to the right or left, without repeating the same position in more than two consecutive trials. During this phase, responses of the dogs were not registered.

3.1.2.4. Reversal training. The interval between the Instigation phase and the Reversal training phase was 10 min. The test began with the animal in the starting point, the pointer called it by its name making visual contact with the dog. Immediately after making visual contact, the pointer gave the cue pointing towards the empty container. The handler eased the leash and left the dog to choose the container. If the dog chose the non-pointed container,

it could eat the pellet inside the container, and this response was registered as “correct”. When the animal chose the pointed container, without food, a correction was made. The handler took the leash again. The correction consisted of a slight pull of the leash, and simultaneously the handler said “no”. If the dog corrected its response, going to the non-pointed place, it was allowed to consume the reinforcer and that trial was computed as “correct with correction”. If the animal persisted in the non-correct response after the correction, the handler say “no” again and the human pointer showed the dog the unbaited and the baited containers, so the trial finished without giving access to the reinforcer. In this case the response was registered as “incorrect”, and this trial was repeated until the dog made a correct response. The reinforcer was placed randomly in both containers. The same position could not be repeated in more than two consecutive trials. This reversal training was repeated until reaching the learning criterion, which consisted of making four consecutive correct responses without correction.

If the animal did not learn the task after 30 trials, the session finalized and the training continued on the following day. In the case of one subject the training continued 1 week later.

If the animal did not learn the task after 65 trials of the Reversal training phase, corrections with the leash were interrupted but the handler continued saying “no” when the dogs chose the incorrect container. Also, the human pointer showed the empty and the full containers, and the dog was not allowed access to the reinforcer.

3.1.3. Data analysis

An average of the accumulated correct responses during the acquisition phase in all the subjects was calculated. The number of trials to reach the criterion of four consecutive correct reversal responses in each group (OG and SG) was measured. The number of required trials to reach the criterion in acquisition and reversal phases and the effect of the person who pointed were compared with an independent samples *t*-test. The demanded alpha level was 0.05.

3.2. Results

In the acquisition phase, all the subjects chose the pointed place during four consecutive trials, successfully reaching the trials to criterion. Since all the subjects obtained the criterion of acquisition with the highest effectiveness, there were no differences between the groups.

Fig. 1 shows the average in each group, of the number of trials to criterion necessary to accomplish the omission. In this phase all the animals acquired the response to go to the non-pointed place. For a binomial distribution, the probability of giving four consecutive extinction (or reversal) responses by chance is 0.0625. The OG reached the criterion in 16.33 trials, S.E.M. \pm 6.86, whereas SG did so with an average of 46 trials, S.E.M. \pm 23.63. The independent samples *t*-test revealed a significant group effect $t(9) = 2.958$, $p = 0.016$. This result suggests that dogs learned the omission more quickly when the owner pointed, compared with the animals that received the cue from a stranger. Table 2 shows individual subject performance.

4. Discussion

Diverse evidence showed that dogs are able to solve different tasks to obtain food, based on human communicative cues. In this work we showed that dogs do not follow human cues when these do not lead to the reinforcer. Specifically, in an object choice task, the dogs learn to inhibit their response to go to the pointed container during the extinction phase (non reinforced). Furthermore, the dogs can make a reversal learning of this response and choose the non-pointed container during the reversal training. The obtained

results are similar to those reported by Bentosela et al. (2008) on the emission of a communicative response and suggest that learning processes could also be playing a role in the point-following behaviour, and that these responses show a high degree of flexibility. Cognitive flexibility is the ability to adapt ongoing behaviour to environmental changes. Several functions underlie this ability like response selection, inhibition and extinction, as well as encoding of reward-related information and reversal learning (Van der Plasse and Feenstra, 2008). It involves the adaptation of behaviour according to changes in stimulus-reward contingencies, a capacity relevant to socio-emotional behaviour (e.g., Rolls, 2000; Van der Plasse and Feenstra, 2008).

Nevertheless, these data differ from the works that consider the interspecific communicative responses to be independent of the learning processes (Miklósi et al., 1998; Virányi et al., 2004) and of the individual history of the subjects (Riedel et al., 2008). Furthermore, at least in the situation here evaluated, this communicative responses would depend at least in part on associative processes. Dogs do not seem to require other cognitive skills such as the capacity to understand the communicative intention of the human. However, our data is not enough to completely exclude “high level” explanations; further research in this area is required.

On the other hand, these results revealed that the familiarity of the person who emits the cue influences the extinction and reversal learning. The dogs that received the cue from their owners needed significantly more trials to extinguish their response of going to the pointed place, whereas they learned the reversal response faster. These results are the first showing the effect of the interaction between the dog and its owner in a communicative task. These differences emphasize the importance of the ontogeny upon the learning of new communicative patterns.

Besides, there are few studies regarding extinction and reversal learning in dogs, specially in natural settings, so this work is a valuable contribution to the learning literature (Head et al., 1998; Tapp et al., 2003; Smith and Davis, 2008).

Several different hypothesis could explain the effect of the owner presence in this communicative task. At first place, possibly the dogs showed more obedience towards the owner compared with the stranger. Therefore, during the extinction they continued to choose the pointed container during a greater number of trials. Nevertheless, if the dogs acted by obedience, they would need more trials to learn the reversal task. However, the dogs learned the reversal faster when the owner pointed. Also, according to this obedience hypotheses, one would expect differences in the acquisition phase of the two experimental groups, but they did not differ may be the task was too easy and masked possible differences in learning.

Secondly, dogs are submitted to a partial reinforcement schedule during ontogeny. The cues that the owners emit frequently allow them to obtain different rewards but, sometimes, those signals are not reinforced. This type of schedule usually produces a slower extinction (e.g., Amsel, 1992). So, this could explain why the Owner Group needed more trials to extinguish. Moreover, although scarce, evidence would indicate that partial reinforcement also deteriorates the reversal learning (e.g., Erlebacher, 1963; Elam and Tyler, 1958). Because of this, the partial reinforcement hypothesis would not be suitable to explain the results obtained in the reversal experiment.

Finally, it would be possible to interpret that the presence of the owner facilitates the learning of the task in an indirect way, due to a positive emotional state. Diverse evidence indicates that the separation of a dog from its owner produces stress since the dogs maintain an attachment bond with their owners (e.g., Topál et al., 1998). However, it is difficult to explain that stress improves learning in one task and deteriorates performance in the other.

The data reported here does not allow us to discriminate which of the different hypotheses explain the observed dif-

ferences according to who pointed. Further studies will be necessary.

Briefly, dogs learn to do not follow the human pointing when this cue is no longer associated with a reinforcer. The results show that dogs stop choosing in the extinction procedure, and that they learn to choose the non-pointed container in the reversal training. In both cases, they are capable of inhibiting the previous response (point-following behaviour).

This work showed the learning processes relevancy during ontogeny on the dog's point-following behaviour and the flexibility of this skill, although genetics must not be discarded. On the other hand, a differential effect was observed when the owner was giving the pointing cue. This result showed that a dog's previous experience has an influence on the learning of new communicative situations with persons.

Acknowledgements

The present research was supported by CONICET and AGENCIA (PICT 2005, number 38020). We would like to give our special gratitude to Nadia Justel and Clive Wynne for reading the manuscript and for their valuable comments. Furthermore we would like to thank Gabriela Barrera, Canine School GB and its director Gustavo Bianco for his collaboration. We are grateful for the help of all the owners who participated in these studies.

References

- Agnetta, B., Hare, B., Tomasello, M., 2000. Cues to food locations that domestic dogs (*Canis familiaris*) of different ages do and do not use. *Anim. Cogn.* 3, 107–112.
- Amsel, A., 1992. *Frustration Theory: An Analysis of Dispositional Learning and Memory*. Cambridge University Press, Cambridge.
- Bentosela, M., Barrera, G., Jakovcevic, A., Elgier, A.M., Mustaca, A.E., 2008. Effect of reinforcement, reinforcer omission and extinction on a communicative response in domestic dogs (*Canis familiaris*). *Behav. Process* 78, 464–469.
- Bentosela, M., Jakovcevic, A., Elgier, A., Mustaca, A., Papini, M., in press. Incentive contrast in domestic dogs (*Canis familiaris*). *J. Comp. Psychol.*
- 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.
- Elam, C.B., Tyler, D.W., 1958. Reversal-learning following partial reinforcement. *Am. J. Psychol.* 71, 583–586.
- Erlebacher, A., 1963. Reversal learning in rats as a function of percentage of reinforcement and degree of learning. *J. Exp. Psychol.* 66, 84–90.
- Hare, B., Brown, M., Williamson, C., Tomasello, M., 2002. The domestication of social cognition in dogs. *Science* 298, 1634–1636.
- Hare, B., Tomasello, M., 2005. Human-like social skills in dogs? *Trends Cogn. Sci.* 9, 439–444.
- Hare, B., Tomasello, M., 1999. Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *J. Comp. Psychol.* 113, 173–177.
- Head, E., Callahan, H., Muggenburg, B.A., Cotman, C.W., Milgram, N.W., 1998. Visual-discrimination learning ability and b-amyloid accumulation in the dog. *Neurobiol. Aging* 19, 415–425.
- Mackintosh, N.J., 1983. *Conditioning and Associative Learning*. Oxford University Press, New York.
- Miklósi, A., Kubinyi, E., Topál, J., Gácsi, M., Virányi, 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.
- Miklósi, A., Polgárdi, R., Topál, J., Csányi, V., 1998. Use of experimenter given cues in dogs. *Anim. Cogn.* 1, 113–121.
- Miklósi, A., Topál, J., Csányi, V., 2004. Comparative social cognition: what can dogs teach us? *Anim. Behav.* 67, 995–1004.
- Povinelli, D.J., Giambone, S., 1999. Inferring other minds: failure of the argument by analogy. *Philos. Top.* 27, 167–201.
- Prato-Previde, E., Marshall-Pescini, S., Valsecchi, P., 2008. Is your choice my choice? The owners' effect on pet dogs' (*Canis lupus familiaris*) performance in a food choice task. *Anim. Cogn.* 11, 167–174.
- Riedel, J., Buttelmann, D., Call, J., Tomasello, M., 2006. Domestic dogs (*Canis familiaris*) use a physical marker to locate hidden food. *Anim. Cogn.* 9, 27–35.
- Riedel, J., Schumann, K., Kaminski, J., Call, J., Tomasello, M., 2008. The early ontogeny of human–dog communication. *Anim. Behav.* 5, 1003–1014.
- Rolls, E.T., 2000. The orbitofrontal cortex. *Cereb. Cortex* 10, 284–294.
- Schwab, C., Huber, L., 2006. Obey or not obey? Dogs (*Canis familiaris*) behave differently in response to attentional states of their owners. *J. Comp. Psychol.* 120, 169–175.
- Shapiro, A.D., Janik, V.M., Slater, P.J.B., 2003. A gray seal's (*Halichoerus grypus*) responses to experimental-given pointing and directional cues. *J. Comp. Psychol.* 117, 355–362.

- Skinner, B.F., 1953. *Science and Human Behavior*. MacMillan, New York.
- Smith, S.M., Davis, E.S., 2008. Clicker increases resistance to extinction but does not decrease training time of a simple operant task in domestic dogs (*Canis familiaris*). *Appl. Anim. Behav. Sci.* 110, 318–329.
- Soproni, K., Miklósi, A., Topál, J., Csányi, V., 2001. Comprehension of human communicative signs in pet dogs (*Canis familiaris*). *J. Comp. Psychol.* 115, 122–126.
- Soproni, K., Miklósi, A., Topál, J., Csányi, V., 2002. Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. *J. Comp. Psychol.* 116, 27–34.
- Tapp, P.D., Siwak, C.T., Estrada, J., Head, E., Muggenburg, B.A., Cotman, C.W., Milgram, N.W., 2003. Size and reversal learning in the Beagle dog as a measure of executive function and inhibitory control in aging. *Learn. Mem.* 10, 64–73.
- Thorndike, E.L., 1911. Animal intelligence. *Am. Psychol.* 53, 1125–1127.
- Topál, J., Miklósi, A., Csányi, V., 1997. Dog–human relationship affects problem solving behavior in the dog. *Anthrozoös* 10, 214–224.
- Topál, J., Miklósi, A., Doka, A., Csányi, V., 1998. Attachment behavior in dogs (*Canis familiaris*): a new application of Ainsworth's (1969) strange situation test. *J. Comp. Psychol.* 112, 219–229.
- Tóth, L., Gácsi, M., Topál, J., Miklósi, A., 2008. Playing styles and possible causative factors in dogs' behaviour when playing with humans. *Appl. Anim. Behav. Sci.* 114, 473–484.
- Udell, M.A.R., Dorey, N.R., Wynne, C.D.L., 2008. Wolves outperform dogs in following human social cues. *Anim. Behav.* 76, 1767–1773.
- Udell, M.A.R., Wynne, C.D.L., 2008. A review of domestic dogs (*Canis familiaris*) human like behaviors: or why behavior analysts should stop worrying and love their dogs. *J. Exp. Anal. Behav.* 89, 247–261.
- Van der Plasse, G., Feenstra, M.G.P., 2008. Serial reversal learning and acute tryptophan depletion. *Behav. Brain Res.* 186, 23–31.
- Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D., Miklósi, A., 2008. Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Anim. Cogn.* 11, 373–387.
- Virányi, Z., Topál, J., Gácsi, M., Miklósi, A., Csányi, V., 2004. Dogs respond appropriately to cues of humans' attentional focus. *Behav. Process* 66, 161–172.
- Wynne, C.D.L., Udell, M.A.R., Lord, K., 2008. Ontogeny's impacts on human–dog communication. *Anim. Behav.* 76, e1–e4.