



ELSEVIER

Contents lists available at ScienceDirect

## Applied Animal Behaviour Science

journal homepage: [www.elsevier.com/locate/applanim](http://www.elsevier.com/locate/applanim)



# Dogs are able to generalise directional acoustic signals to different contexts and tasks

Anna Gergely<sup>a,\*</sup>, József Topál<sup>b</sup>, Antal Dóka<sup>a</sup>, Ádám Miklósi<sup>a,c</sup>

<sup>a</sup> Department of Ethology, Eötvös Loránd University, Pázmány P. s. 1/c, 1117 Budapest, Hungary

<sup>b</sup> Institute of Cognitive Neuroscience and Psychology, Hung. Acad. Sci., Victor Hugo u. 18-22, 1132 Budapest, Hungary

<sup>c</sup> MTA-ELTE Comparative Ethology Research Group, Pázmány P. s. 1/c, 1117 Budapest, Hungary

### ARTICLE INFO

#### Article history:

Accepted 15 April 2014

Available online xxx

#### Keywords:

Dog

Generalisation

Spatial navigation

Dog training

### ABSTRACT

Previous studies suggested that dogs are able to use both egocentric and allocentric cues spontaneously in specified spatial tasks. They can also learn rapidly 'go-left/go-right' tasks based on stimulus location but relying on stimulus quality. At the same time, relatively little research has looked at the possibility of whether dogs are able to solve a spatial problem based on previously trained signals in novel situations. In the present study we have examined whether dogs are able to rely on quality differences in sound stimuli for directional behaviour and to generalise this rule in different field conditions. First, we trained 16 adult pet dogs in the lab to go left and right based upon qualitatively different sound signals. After having reached the criterion, subjects participated in five field test sessions that included several novel targets (balls/trees/humans) at different distances (7–18 m) and angular deviations (36°–87°). We wanted to see whether these aspects of the novel context affect the dogs' performance. After having reached the criterion, subjects participated in five field test sessions that included several novel targets at different distances and angular deviations. The test sessions were followed by a control session in the laboratory in order to exclude the Clever Hans effect. We found that dogs chose the target object that matched the sound signal significantly above the chance level in each test condition and also in the Clever Hans control. Their performance was not affected by different targets and distances, but decreased as a function of angular deviation. These results suggest that dogs are able to learn the 'go left/go right' task based on qualitatively different sounds and utilise this rule in novel situations. The angular deviation in choosing the correct target direction proved to be an important factor in the dogs' performance in a novel context.

© 2014 Elsevier B.V. All rights reserved.

\* Corresponding author at: Department of Ethology, Eötvös University, Pázmány P. s. 1/c, H-1117 Budapest, Hungary. Tel.: +36 1 381 2179; fax: +36 1 381 2180.

E-mail addresses: [anna.gergely66@gmail.com](mailto:anna.gergely66@gmail.com) (A. Gergely), [topaljozsef@gmail.com](mailto:topaljozsef@gmail.com) (J. Topál), [dokaantal@gmail.com](mailto:dokaantal@gmail.com) (A. Dóka), [amiklosi62@gmail.com](mailto:amiklosi62@gmail.com) (Á. Miklósi).

<http://dx.doi.org/10.1016/j.applanim.2014.04.005>  
0168-1591/© 2014 Elsevier B.V. All rights reserved.

## 1. Introduction

Dogs (*Canis familiaris*) are descendants of territorial predators, wolves (*Canis lupus*), and it is expected that they are able to learn and use the location of objects in space (Gallistel, 1990). Two different types of basic mechanisms are used for spatial navigation. The egocentric orientation relies on one's own body position in space, while in the case of allocentric orientation the animal uses the position of an external cue (beacon or landmark) as a reference (Pohl,

1973). Relying on either type of information has advantages as well as disadvantages. Allocentric cues provide high flexibility for the animal because they allow the utilisation of several different pathways to the same target. Egocentric spatial information provides relatively inflexible information for navigation, however it is useful to rely on if environmental conditions are permanent, no environmental cues are available or the goal is near the animal (Fiset et al., 2006).

Several studies have shown that dogs are able to use both egocentric and allocentric navigation spontaneously to solve different spatial tasks (e.g. Head et al., 1995; Milgram et al., 1999; Chan et al., 2001) and that their spatial encoding process is flexible and can be adjusted to the particularities of the situation. For example, Fiset et al. (2006) examined the geometric components used by domestic dogs in an object permanence task and reported that dogs preferred a linear egocentric frame of reference when they were searching for the location of a disappearing object regardless of the distance between their own spatial coordinates and those of the hiding position. Thus, dogs' performance in finding the hidden object did not differ when the object was moved from 100 cm to 142 cm from the starting point, that is, they did not simultaneously use the vector components of direction and of distance to locate the target object. At the same time, dogs seem to have difficulty using allocentric cues to locate a hidden object in some situations (Fiset and Malenfant, 2013), but they may be able to use allocentric spatial information when the linear egocentric information is not available. Fiset et al. (2006) also found that the angular deviation between adjacent hiding locations and the position of the dog had an effect on dogs' performance: the subjects performed more correctly if the angular deviation between the two hiding places was 15° rather than only 5°. Dogs tried to minimise angular deviation from the target in a detour task in which the shortest route to reach the desired goal was unavailable but the target was visible. Thus, they preferred the less divergent path over the shortest route. However, if the target was invisible they chose the shortest route regardless of the angular deviation (Chapuis et al., 1983).

In a landmark discrimination task Milgram et al. (2002) trained dogs to choose the food-container closest to a small landmark (yellow wooden peg) in a two way choice task. Next, dogs were exposed to a similar task with a novel landmark (pink heart-shaped object), and finally, this novel landmark was moved to novel positions. Dogs' performance remained stable throughout these novel conditions. The authors concluded that dogs generalised both to the shape and relative position of the landmark, thus they were using a general concept of the landmark to solve this two-way choice task.

Dogs are also able to learn go/no-go tasks based on differences in stimulus quality and go-left/go-right tasks based on differences in stimulus location, whereas the opposite stimulus-action pairings are more difficult to learn (Lawicka, 1964; Dobrzecka et al., 1966; Dobrzecka and Konorski, 1967; Konorski, 1967; Dobrzecka and Konorski, 1968; Lawicka, 1969). These results raise the Quality-Location Hypothesis suggesting that the quality of a stimulus best serves as a cue for the quality of a response,

whereas the location of a stimulus facilitates the orientation of the action. Although several researchers assumed that this hypothesis is fundamental to understanding possible constraints of learning (e.g. Müller and Bowe, 1982), others argued that the quality-location distinction effect in these studies stems from the experimental design and is highly affected by the inclusion or exclusion of naturalistic features (e.g. Harrison, 1984; Neill and Harrison, 1987). The finding that herding dogs can be directed by voice commands (or whistles) of different tone and pitch of the human shepherd during cooperative herding (McConnell and Baylis, 1985) also casts some doubt on the Quality-Location Hypothesis.

The main goal of the present study, therefore, was to find out whether dogs trained to perform oriented movement (go left/right) in response to different acoustic signals are able to generalise this experience to novel contexts. In this latter phase of the training we also investigated whether or not salient objects placed in the target area improve dogs' learning efficiency in the go left/right task. We assumed that dogs trained to approach a conspicuous target (small object on the ground) upon hearing the signal would show a better performance than those who had to approach a specific spatial location (left/right corner) in the room. The less specific nature of the latter task (i.e. the absence of a specific target object which could be approached) predicts a slower learning rate (c.f. Fiset et al., 2006). In the second part of the study, dogs were exposed to novel situations where they had to rely on the same acoustic signals to solve a series of new spatial tests. We applied several novel targets in these test situations at different distances and angular deviations in relation to the dogs' starting position. We measured the dogs' performance which was calculated on the basis of the number of correct choices after receiving the sound signal. We assume that dogs' performance would not drop in the novel context independent of their distance to the target, partly because they are able to generalise learnt behaviour to novel contexts (Lindsay, 2000); for example, Braem and Mills (2010) reported that dogs are able to generalise a novel acoustic signal (verbal cue)-action association learnt in Room A to Room B.

## 2. Materials and methods

### 2.1. Subjects

Sixteen adult pet dogs (mean age  $\pm$  SE: 5.5  $\pm$  2.5 years) were recruited for this study. The participants were 5 male and 11 female dogs from different breeds (3 Border collies, 2 Mudis, Hungarian Vizsla, Labrador, Golden Retriever, Groenendale, Beauceron, Nova Scotia Duck Tolling Retriever, Croatian Sheepdog, Boxer, 3 mongrels). All dogs were clicker trained (by the means of the shaping procedure) and trained for fetching and going ahead. Regarding the training of the "going ahead" command, dogs were trained for two different tasks as a part of the obedience training: (1) based on the combination of owners' verbal and hand signals, owners used clicker-training to positively reinforce moving away from the owner in a straight line (0% deviation) in a given direction without a visible target, (2) dogs were also trained with clicker to go



Fig. 1. The Click & Treat Collar.

ahead and lie down next to special visible targets (yellow cones) based on the direction of the owners' hand signal. Dogs and their owners were recruited through the website of Department of Ethology (<http://kutyaetologia.elte.hu/>).

## 2.2. Equipment and signals

The Click & Treat (C&T) Collar was developed by Tamás Ferenczy (see Fig. 1). It consists of two parts: the collar and the remote control unit. The collar is a cylindrical collar-mounted device in which the double-barreled treat storage, the dispenser, the control electronics, the loudspeaker, the radio modules, and the batteries are located. The storage can be baited with 16 pieces of dry dog food (Kennel Kost premium dog food), by placing 8–8 pieces into each barrel. Four different signals can be emitted directly from the collar by pressing different buttons on the remote control: (1) click sound (0.3 s long; 1700 Hz); (2) click sound + food; (3) high pitched (HP) sound (0.3 s long, 2150 Hz “beeping” repeated 3 times, 0.1 s pauses in between trials); (4) low pitched (LP) sound (0.3 s long, 1150 Hz “beeping” repeated three times 0.1 s pauses in between trials). The radio connection has a working radius of maximally 400 m.

## 2.3. Procedure

Familiarisation, Basic training, Advanced training, and warm-up session before testing took place in a 4.5 m × 3.5 m test room at the Department of Ethology, Eötvös Loránd University Budapest. Testing was carried out on a plain green area on the University Campus.

### 2.3.1. Familiarisation

The aim of the familiarisation was to introduce the C&T Collar to the dogs, and to train them to go to one of the potential targets in the room. After arriving at the

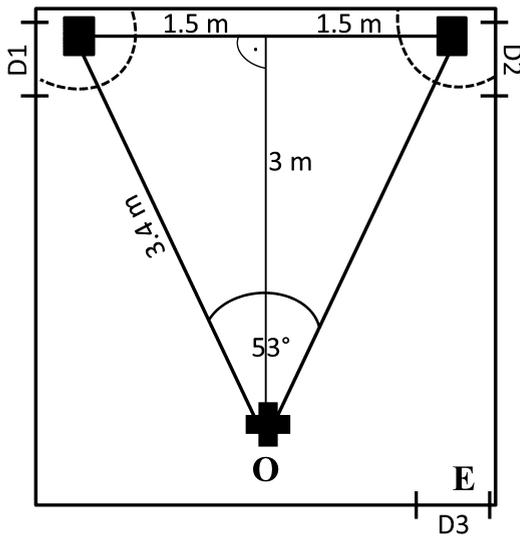
department with their owner, the dog took part in the following procedure (Steps 1–6):

1. The experimenter filled up the collar with dry food then gave it to the owner. The owner held the collar in his/her hand, called the dog, then pushed the ‘click + food’ button on the controller. The dog was allowed to eat the reward (one piece of dry dog food) which dropped from the collar to the floor. We repeated this procedure 10 times. Then, the experimenter asked the owner to push the ‘Click’ button but no food was given. If the dog looked down to the floor after the click sound, we moved to the next step. If the dog did not look down, then the dog was given another set of 10 trials of ‘click and food’ until the dog looked down after the click sound in the absence of food rewards.
2. The owner gave verbal commands (for example Sit!, Down!, Lay! etc.) to the dog. All commands referred to actions known by the dog prior to this study. If the dog acted in line with the command, then she pushed the ‘click + food’ button and the dog received a piece of reward. Each dog participated in 14 trials.
3. The owner put the collar on the dog and Step 2 was repeated 14 times.
4. The owner and the dog sat down. The experimenter brought a small black cardboard rectangle (18 cm × 24 cm) to the room and put it on the floor. She placed it in front of the dog at a distance of 1.5 m. She called the dog and acted as if she placed one piece of food under the rectangle and then stepped back. The owner encouraged the dog to approach the rectangle verbally (Let's go!). If the dog approached the rectangle (within 10 cm), the experimenter pushed the ‘click + food’ button and the dog was allowed to eat the treat. We repeated this two times.
5. We repeated Step 4, except that the rectangle was now at a distance of 3 m from the dog.
6. The experimenter brought a second rectangle (which was identical to the first one) to the room. She placed the rectangles into the two corners of the room 3 m from the dog. She stepped next to one of the rectangles and repeated the previous training four times (sequences: LRLR or RLRL; L = left, R = right).

### 2.3.2. Training phase

2.3.2.1. *Basic training.* The aim of the Basic training was to develop associations between sounds and spatially oriented motor responses (going left or right). This phase consisted of series of training trials.

Two target objects (cardboard rectangles) were placed at two corners of the lab. The owner and the dog (with the mounted collar) were sitting in front of the rectangles (see Fig. 2). Upon hearing one of the two sounds (HP or LP) emitted from the collar, the owner encouraged the dog to approach one of the rectangles (using only neutral verbal utterances like “Let's go!”). Owners did not display any gestures e.g. pointing. If the dog approached the object located in the designated corner (i.e. which matched with the emitted sound) in 10 s within 20 cm (‘approaching zone’), the dog received the reward from the collar.



**Fig. 2.** Experimental layout for the Basic training phase. The black cross indicates the dogs' starting position, the O indicates the owner's and the E the experimenter's position. The black rectangles indicate the location of two identical target objects, the interrupted lines indicate the 20 cm 'approaching zone'. D1, D2 and D3 indicate the locations of the three doors (0.6 m width) in the lab.

In the first series, we played one sound 10 times (left or right) and then the other sound also 10 times. This was followed by a second series in which sound signals were alternated in LRLRLRLR (trials 1–10) and RLRLRLRL (trials 11–20) order.

These blocks of 10 trials were then repeated until they reached learning criterion. Criterion for learning the basic training task was set as 10 consecutive correct trials.

If the dog approached the 'incorrect' object (within 20 cm), the owner called the dog back and the trial was repeated with the same sound signal. If the dog failed to show the correct response two times in a row, then the owner was allowed to point at the correct rectangle during the subsequent trial. We considered the trial also as incorrect and the dog did not get the reward if it passed along the midline in between the objects without approaching either of them.

For half of the subjects ( $N=8$ ) the HP sound was the 'go left' signal and the LP sound was the 'go right' signal. For the other half ( $N=8$ ) of the subjects we reversed the reference (left/right) of the signals.

Dogs participated in 10–30 Basic training trials per session (mean  $\pm$  SE:  $16 \pm 4$ ) and each training session was terminated when the owner indicated that the dog was getting tired and inattentive. Owners and their dogs visited the department once or twice weekly.

**2.3.2.2. Advanced training.** The aim of the advanced training was to investigate whether changes in the training situation influence dogs' performance and generalisation capability. Subjects were divided into two groups:

**Rotation training:** For half of the dogs ( $N=8$ ) we rotated the position of the rectangles and the orientation of the dog and the owner by  $90^\circ$ . Then subjects participated in

10-trial training sessions as described above until reaching the criterion (10 consecutive correct trials).

**No target training:** For the other half of dogs ( $N=8$ ) we repeated the Basic training without target objects until they reached the criterion (10 consecutive correct trials). Dogs received the reward if they approached the former location of the rectangle within 20 cm.

Owners and their dogs visited the department once or twice weekly, and they participated 10–20 Advanced training trials per visit (mean  $\pm$  SE:  $14 \pm 2$ ).

**2.3.3. Testing phase**

Test trials were staged outdoors on the campus of the Eötvös Loránd University in a  $40\text{ m} \times 40\text{ m}$  grassy area with some peripheral woods. We could not use a fenced area, thus some students and dog walkers were usually walking nearby during the test and were asked verbally to avoid the test area during the testing. Each session started with a short 6-trial warm-up training performed in the experimental room (in these trials we used the same procedure as in the Advanced training). Each testing session consisted of 5 different types of trials ('condition'). Three different targets and 5 different distances with different angular deviations from the position of the dog were utilised: *Close ball*, *Distant ball*, *Close tree*, *Distant tree* and *Human* (see Fig. 3). We decided to use the unbaited C&T collar during the testing in order to exclude accidental falls of the reward during fast running and the possible loss of the reward in high grass or snow in winter. Reward was provided by the owner after the dogs' return.

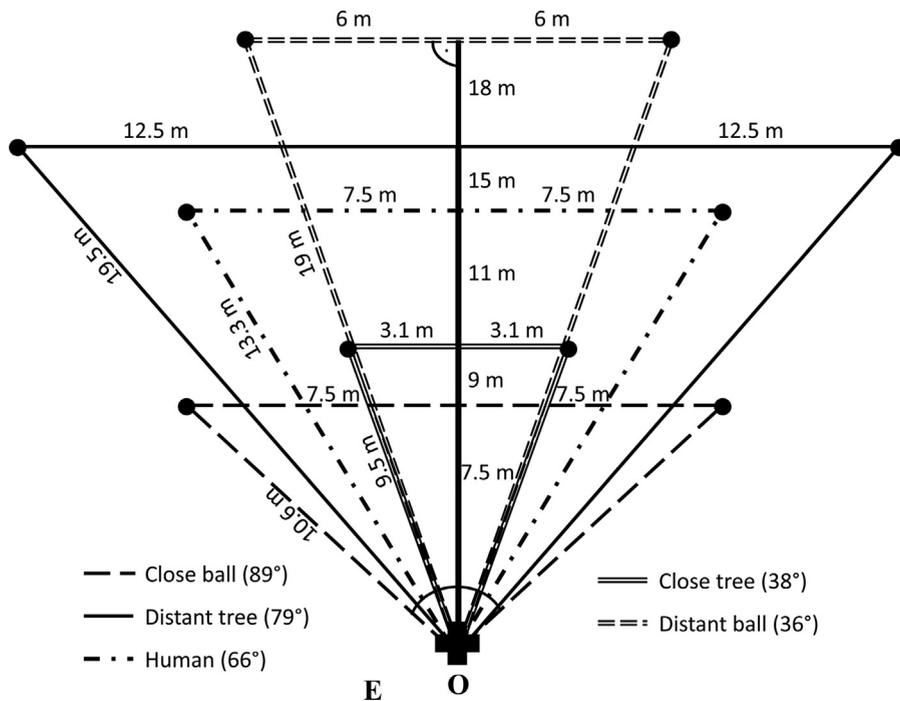
In each condition the owner and the dog were standing in front of two targets (trees, balls or two female humans). Dogs were wearing the empty C&T collar. After the sound was emitted from the collar, the dog was allowed to set off. The owner was not allowed to say anything to the dog except "GO!" or "Go ahead!" without any additional verbal or gestural signals. If the dog approached the correct target within 1 m, then it received verbal praise from the owner during first two trials. In the remaining 8 trials they received food or a ball as a reward from the owner except in the *Human* condition in which the female humans provided the reward in order to maintain dogs' motivation. Approach towards the incorrect target was considered a failed trial: the owner was instructed to call the dog back and then the trial was repeated with the same sound.

Order of the test conditions was counterbalanced among dogs. Exact places, angles, targets and their relative positions were constant. Dogs were provided with 10 trials in each condition using a LRLRLRLR or RLRLRLRL orders.

Dogs took part in only one test condition per day, thus the test session contained 5 occasions with intervals of no more than one week.

**2.3.4. 'Clever Hans' control trials**

The aim of these trials was to control for owners' and experimenter's influence on dogs' performance. After finishing the testing sessions, dogs participated in 10 additional Advanced training trials in the laboratory setting, but in this case owners were wearing opaque sunglasses and they were listening to loud music during the test. This



**Fig. 3.** Experimental design of testing conditions. The black cross indicates the dogs' starting position, the O indicates the owner's and the E the experimenter's position. The black circles indicate the location of two target objects (balls/trees/humans) in the different testing conditions.

prevented them from hearing the played sound and from seeing in which direction the dog was moving. The experimenter, who controlled the C&T collar, was facing the wall when she pushed the sound button on the controller, thus she did not see the dog either. The experimenter turned back to the scene only after the sound was emitted and informed the owner what had happened (if the dog went to the proper side the owner had to praise the dog, if the dog went to the wrong side the owner had to call the dog back). We predicted that, if no Clever Hans effect was involved in the Basic and Advanced training, then the changed appearance and behaviour of the owner and experimenter would not affect the dogs' performance.

#### 2.4. Variables and data analysis

The experimenter coded the performance of the dog in situ during the basic and advanced training, test conditions and also during Clever Hans control (she marked each trial as correct or incorrect). Test conditions were videotaped and analysed later with Solomon coder 12.06.06 (András Péter <http://solomoncoder.com>). Trials of training sessions were also supervised by coding recorded videos.

##### 2.4.1. Measured variables

**2.4.1.1. Target.** The dog approached one of the targets within 20 cm during training trials (rectangle), or within 1 m during test trials (tree/ball/human).

**2.4.1.2. First movement.** The direction of dog's first three steps from the start point (left/right/straight from the middle line) in test trials.

We scored correct trials with 1, and incorrect trials with 0. We considered a trial as correct if (1) the dog went to the specific target (rectangle/tree/ball/human) on the side indicated by the specific sound (left/right) (Target variable), (2) the dog made the first three steps towards the target (rectangle/tree/ball/human) indicated by the specific sound signal (left/right) (First movement variable). If the dog moved towards the middle area we considered it as an incorrect trial.

Sometimes it happened that dogs stopped before reaching one of the targets and did not go further in 10 s. In this case, the owner was instructed by the experimenter to call the dog back, and we played the same sound again. In this case, the First movement score was based on the direction of the first start and Target score was determined by the performance on the subsequent trial. It also happened that the dog changed its direction during the approach (for example, the dog started to go towards the target on the left but after several metres changed its direction and went to the target on the right). For the statistical analysis, the test conditions were split into two groups based on their angular deviations. Test conditions in which the angular deviation was sharper or wider than the training angle ( $53^\circ$ ) were grouped together, thus *Close tree* and *Distant ball* conditions formed the '*Angle < 53°*' group, and *Close ball*, *Distant tree* and *Human* conditions formed the '*Angle > 53°*' group.

For statistical analysis we used IBM SPSS Statistics 21.

### 3. Results

Dogs reached the criterion in  $72 \pm 36$  (mean  $\pm$  SD) correct trials on average in the Basic training, and in  $34 \pm 12$

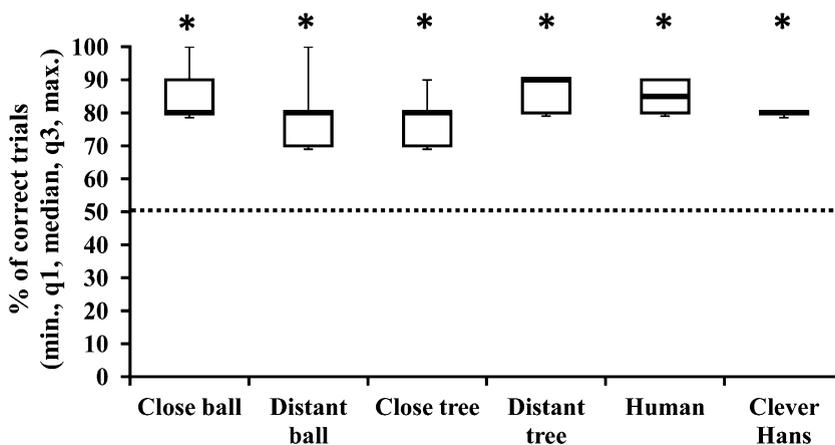


Fig. 4. Percent (%) of correct trials in each Test conditions (Close ball, Distant ball, Close tree, Distant tree, Human) and in the Clever Hans control. \*  $p < 0.001$ .

(mean  $\pm$  SD) additional trials in the Advanced training. We excluded one dog because it failed to reach the training criterion in 180 trials in the Basic training. Another dog's owner quit the study after completing the first test condition; therefore the data of this dog are included only in the analysis of the Basic training, Advanced training and *Distant tree* test condition.

Due to the criterion, dogs' accuracy was 100% in the last 10 trials of the Basic training, thus we decided to use the last 15 trials in the Basic training and the first 15 trials in the Advanced training in order to compare dogs' performance between the two training types. We found that dogs' performance decreased significantly (Wilcoxon matched-pairs signed rank test,  $N = 15$ ,  $Z = -3.306$ ,  $p = 0.001$ ), which indicates that dogs in neither group generalised automatically from the Basic training to the Advanced training in which the objects were either rotated or removed. The performance did not differ between the Rotation and the No target group (Mann–Whitney test,  $N = 15$ ,  $U = 36$ ,  $p = 0.397$ ). However, dogs in both groups showed a rapid recovery, because they needed  $16 \pm 3$  and  $15 \pm 1$  trials respectively to reach the criterion which did not differ between the two groups (Mann–Whitney test,  $U = 28$ ,  $p = 0.95$ ).

In the test conditions, only two dogs failed to reach targets in 60 s in the *Distant tree* condition, and one of them failed also in the *Close tree* condition.

According to test conditions, first we compared mean scores for the Target and First movement variables. We found that these two variables did not differ (matched samples McNemar test,  $N = 15$ ,  $df = 1$ ,  $p = 1.00$ ), thus we decided to use Target variable for further analysis. Subjects performed better than chance in each test condition (one-sample Wilcoxon signed-rank test, *Close ball*  $N = 14$ ,  $T(+)=105$ ,  $p < 0.001$ ; *Distant ball*  $N = 14$ ,  $T(+)=105$ ,  $p < 0.001$ ; *Close tree*  $N = 13$ ,  $T(+)=91$ ,  $p < 0.001$ ; *Distant tree*  $N = 13$ ,  $T(+)=91$ ,  $p < 0.001$ ; *Human*  $N = 14$ ,  $T(+)=105$ ,  $p < 0.001$ ). This shows that the dogs went to the correct target (ball/tree/human) more frequently than to the target on the incorrect side (see Fig. 4). Dogs performed also above chance level in the Clever Hans control condition (one-sample Wilcoxon signed-rank test,  $N = 14$ ,  $T(+)=105$ ,  $p < 0.001$ ). The order of test conditions did not have any

effect on dogs' performance (Friedman test,  $N = 15$ ,  $df = 4$ ,  $p = 0.92$ ).

We also compared 0/1 data between test conditions and Clever Hans control and also the effect of trials within each test condition and Clever Hans control with GLMM for Binomial Distribution. Results showed no significant variability among test conditions ( $F_{5,761} = 1.11$ ,  $p = 0.35$ ), and repeated trials had also no effect ( $F_{9,761} = 1.3$ ,  $p = 0.230$ ). Dogs' accuracy in Test conditions was independent from the Advanced training type ( $F_{1,809} = 0.004$ ,  $p = 0.947$ ) and interaction between Advanced training type and Test condition was also not significant ( $F_{1,809} = 0.68$ ,  $p = 0.630$ ).

We also compared dogs' performance between two test condition groups, the  $Angle < 53^\circ$  and the  $Angle > 53^\circ$  group, with GLMM for Binomial distribution. Results showed that dogs' performance was lower if the angular deviation in the test condition was sharper than the training angle ( $F_{1,661} = 5.33$ ,  $p = 0.021$ ) (Fig. 5).

#### 4. Discussion

The objective of the present study was to investigate whether dogs are capable of learning to go left/right after

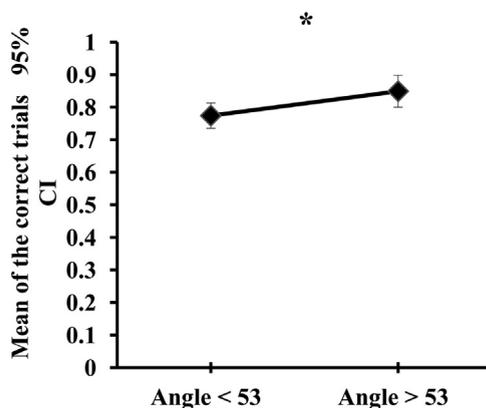


Fig. 5. Means of the correct trials in the two experimental groups which differ with regard to the visual angle ( $Angle < 53^\circ$ : Distant ball, Close tree;  $Angle > 53^\circ$ : Close ball, Distant tree, Human). \*  $p < 0.05$ .

training using two qualitatively different sound signals and whether they can generalise this experience to novel contexts. Contrary to previous findings suggesting that dogs failed to rely on tone frequency cues in a go left/go right task (e.g. Lawicka, 1969), our results showed that dogs had no difficulty in learning directional responses based on qualitatively different sound signals after a relatively short training.

Methodological differences may explain this discrepancy: (1) Dogs in our study were clicker trained family dogs from different breeds with well described training history, while Lawicka tested 8 laboratory mongrels with unknown training background. Dogs in the present study were previously trained with clicker to follow the direction of the owners' verbal and hand signals towards distant locations as a part of the obedience training, thus these dogs already had experience in directional response tasks. While owners were prevented from using these well known signals during the training and test phases, we assume that it had no effect on dogs' performance in the present role. (2) In our study, signals were emitted and dogs were rewarded directly from the C&T collar, while in Lawicka's experiment sound sources were loudspeakers situated at 2 m from the starting platform and the target objects contained the reward. This latter difference might have drawn dogs' attention more towards the target object than the sound signals from the C & T collar and caused the prolonged learning time. Our results support the presumption that the Quality-Location effect is not a general constraint of learning, but more likely it emerges under particular experimental designs and conditions (Harrison, 1984; Neill and Harrison, 1987).

In order to examine context dependency of learning, we changed the training situation after the Basic training by either removing the target objects (No target training) or rotating the position of the targets and the dog (Rotation training). We found that dogs' performance decreased equally in both conditions. Braem and Mills (2010) reported also that dogs show a decline in performing a newly learned command in a novel environment. In contrast to our prediction, dogs that participated in the No target training showed as rapid recovery as dogs in the Rotating training. We presume that during the Basic training, dogs learnt to "go left/right" instead of "approaching the target on the left/right", thus the absence of the target objects in the Advanced training (in the No target training condition) did not affect their performance. The lack of such difference could also be explained by the fact that the reward was not hidden into/behind the target object (c.f. Lawicka, 1969; Fiset et al., 2006) but it came directly from the C&T collar worn by the dog.

In the testing phase, dogs were exposed to a novel area (outdoor field), novel targets (balls/trees/humans), and extended distances (9.5–19.5 m) and angular deviations (36° to 87°) in order to reveal whether they are able to generalise the "go left/right" task (see Fig. 3). Dogs' performance was significantly above chance level in all test conditions, thus they approached the correct target matching with the sound command significantly more often than expected. Target types and their relative distance from the dog had no influence on dogs' performance, similarly to

previous findings in search for disappearing objects in dogs (Fiset et al., 2006). However dogs' performance in this task decreased as a function of angular deviation between two adjacent hiding locations and the relative position of the dog (Fiset et al., 2006). If the target is visible, then the angular deviation is the most relevant factor for dogs in a detour task, and they show a preference for using the less divergent route (Chapuis et al., 1983). A similar result was also reported for chimpanzees. The spatial separation of two adjacent hiding locations together with the varying angular deviation influenced animals' accuracy in a spatial delayed response object choice task (Harrison and Nissen, 1941). Our results also showed that dogs' performance was lower if, in the test condition, the angular deviation between the adjacent targets and the dogs' position was sharper than the angle experienced in the training angle. This is the first evidence that angular deviation influences dogs' ability to generalise learned directional commands from the training context to a novel context.

Dogs' similar accuracy in all test conditions after different Advanced training suggests that dogs learnt the general rule of 'go left/right', and that they were able to utilise this rule in unfamiliar environments. Dogs showed similar generalisation ability in a landmark discrimination task by efficiently using novel landmarks in novel positions for locating target objects. This was also interpreted as learning the general concept of the landmark (Milgram et al., 2002). The control testing aimed to exclude human influence (i.e. Clever Hans effect) also supported our findings that the dogs' performance was based on their attention to the signals.

In summary, these results clearly show that dogs can internalise a simple behaviour rule for taking directional action upon hearing qualitatively different signals. This capacity of dogs has long been used in traditional settings (e.g. shepherds have long known how to train herding dogs by whistle sound), but our elaborated method offers the possibility to train dogs explicitly if needed for specific employments (e.g. search and rescue, Ferworn et al., 2006).

## Acknowledgements

This project was supported by the Swiss National Science Foundation (SNSF) Sinergia project SWARMIX (project number CRSI22 133059) and the Hungarian Science Foundation (OTKA grant K-100695). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. The authors are grateful to Tamás Ferenczy for developing the Click & Treat Collar, to András Kosztolányi for his assistance in statistical analysis and to all owners and their dogs for their enthusiastic and constant work.

## References

- Braem, M.D., Mills, D., 2010. Factors affecting response of dogs to obedience instruction: a field and experimental study. *Appl. Anim. Behav. Sci.* 125, 47–55.
- Chan, A.D.F., Nippak, P.M.D., Murphey, H., Ikeda-Douglas, C.J., Muggenburg, B., Head, E., Cotman, C.W., Milgram, N.W., 2001. *Visuospatial*

- impairments in aged canines (*Canis familiaris*): the role of cognitive-behavioral flexibility. *Behav. Neurosci.* 116, 443–454.
- Chapuis, N., Thinus-Blanc, C., Poucet, B., 1983. Dissociation of mechanisms involved in dogs' oriented displacements. *Q. J. Exp. Psychol.* 35B, 213–219.
- Dobrzecka, C., Szwejkowska, G., Konorski, J., 1966. Qualitative versus directional cues in two forms of differentiation. *Science* 153, 87–89.
- Dobrzecka, C., Konorski, J., 1967. Qualitative versus directional cues in differential conditioning. I. Left leg-right leg differentiation to cues of a mixed character. *Acta Biol. Exp.* 27, 163–168.
- Dobrzecka, C., Konorski, J., 1968. Qualitative versus directional cues in differential conditioning. IV. Left leg-right leg differentiation to non-directional cues. *Acta Biol. Exp.* 28, 61–69.
- Ferworn, A., Sadeghian, A., Barnum, K., Rahnama, H., Pham, H., Erickson, C., Ostrom, D., Dell'Agnesse, L., 2006. Urban search and rescue with canine augmentation technology. In: *System of Systems Engineering IEEE/SMC International Conference on*, 24–26.
- Fiset, S., Landry, F., Ouellette, M., 2006. Egocentric search for disappearing objects in domestic dogs: evidence for a geometric hypothesis of direction. *Anim. Cogn.* 9, 1–12.
- Fiset, S., Malenfant, N., 2013. Encoding of local and global cues in domestic dogs' spatial working memory. *Open J. Anim. Sci.* 3, 1–11.
- Gallistel, C.R., 1990. *The Organization of Learning*. MIT Press, Cambridge, MA.
- Harrison, R., Nissen, H.W., 1941. Spatial separation in the delayed response performance of chimpanzees. *J. Comp. Psychol.* 31, 427–435.
- Harrison, J.M., 1984. The functional analysis of auditory discrimination. *J. Acoust. Soc. Am.* 75, 1848–1854.
- Head, E., Mehta, R., Hartley, J., Kameka, M., Cummings, B.J., Cotman, C.W., Ruehl, W.W., Milgram, N.W., 1995. Spatial learning and memory as a function of age in the dog. *Behav. Neurosci.* 109, 851–858.
- Konorski, J., 1967. *Integrative Activity of the Brain*. University of Chicago Press, Chicago, 438 pp.
- Lawicka, W., 1964. The role of stimulus modality in successive discrimination and differentiation learning. *Bull. Acad. Pol. Sci.* 12, 35–38.
- Lawicka, W., 1969. Differing effectiveness of auditory quality and location cues in two forms of differentiation learning. *Acta Biol. Exp.* 29, 83–92.
- Lindsay, S.R., 2000. *Handbook of Applied Dog Behavior and Training, Adaptation and Learning*. Blackwell Publishing, Iowa.
- McConnell, B., Baylis, R., 1985. Interspecific communication in cooperative herding: acoustic and visual signals from human shepherds and herding dogs. *Z. Tierpsychol.* 67, 302–328.
- Milgram, N.W., Adams, B., Callahan, H., Head, E., Mackay, B., Thirlwell, C., Cotman, C.W., 1999. Landmark discrimination learning in the dog. *Learn. Mem.* 6, 54–61.
- Milgram, N.W., Head, E., Muggenburg, B., Holowachuk, D., Murphey, H., Estrada, J., Ikeda-Douglas, C.J., Zicker, S.C., Cotman, C.W., 2002. Landmark discrimination learning in the dog: effects of age, an antioxidant fortified food, and cognitive strategy. *Neurosci. Biobehav. Rev.* 26, 679–695.
- Miller, J.D., Bowe, C.A., 1982. Roles of the qualities and locations of stimuli and responses in simple associative learning. *Pavlov. J. Biol. Sci.* 17, 129–139.
- Neill, J.C., Harrison, J.M., 1987. Auditory discrimination: The Konorski quality-location effect. *J. Exp. Anal. Behav.* 48, 81–95.
- Pohl, W., 1973. Dissociations of spatial discrimination deficits following frontal and parietal lesions in monkeys. *J. Comp. Physiol. Psychol.* 82, 227–239.