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Title: Dogs are able to generalize directional acoustic signals to different contexts and tasks

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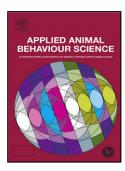
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- 1 Highlights
- We examine dogs' ability to learn to perform oriented movements.
- We also examine dogs' command generalization ability in novel contexts and tasks.
- Dogs easily learn directional response based on different sound signals.
- Dogs are able to generalize this rule to novel environments and tasks.
- Dogs' performance decreases as a function of angular deviation.

7	Dogs are able to generalize directional acoustic signals to different contexts and tasks
8	
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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 generalize 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 to 18
m) and angular deviations (36° to 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 utilize 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.

Keywords: dog, generalization, spatial navigation, dog training

1. Introduction

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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, 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 generalized 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. Miller 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 generalize 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

2.2. Equipment and Signals

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 generalize learnt
behaviour to novel contexts (Lindsay, 2000); for example, Braem and Mills (2010) reported that dogs
are able to generalize 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 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/).

146	The Click & Treat (C&T) Collar was developed by Tamás Ferenczy (see Fig. 1). It consists of two
147	parts: the collar and the remote control unit. The collar is a cylindrical collar-mounted device in which
148	the double-barreled treat storage, the dispenser, the control electronics, the loudspeaker, the radio
149	modules, and the batteries are located. The storage can be baited with 16 pieces of dry dog food
150	(Kennel Kost premium dog food), by placing 8-8 pieces into each barrel. Four different signals can be
151	emitted directly from the collar by pressing different buttons on the remote control: (1) click sound
152	(0.3 s long; 1700 Hz); (2) click sound + food; (3) high pitched (HP) sound (0.3 s long, 2150 Hz
153	"beeping" repeated 3 times, 0.1 s pauses in between trials); (4) low pitched (LP) sound (0.3 s long,
154	1150 Hz "beeping" repeated three times 0.1 s pauses in between trials). The radio connection has a
155	working radius of maximally 400 m.
156	
157	Insert Figure 1
158	
159	2.3. Procedure
160	Familiarization, Basic training, Advanced training, and warm-up session before testing took place
161	in a 4.5 m x 3.5 m test room at the Department of Ethology, Eötvös Loránd University Budapest.
162	Testing was carried out on a plain green area on the University Campus.
163	
164	2.3.1. Familiarization
165	The aim of the familiarization was to introduce the C&T Collar to the dogs, and to train them to go
166	to one of the potential targets in the room. After arriving at the department with their owner, the dog
167	took part in the following procedure (Steps 1 to 6):
168	
169	1. The experimenter filled up the collar with dry food then gave it to the owner. The owner heldthe
170	collar in his/her hand, called the dog, then pushed the 'click+ food' button on the controller. The dog
171	was allowed to eat the reward (one piece of dry dog food) which dropped from the collar to the floor.
172	We repeated this procedure 10 times. Then, the experimenter asked the owner to push the 'Click'
173	button but no food was given. If the dog looked down to the floor after the click sound, we moved to

174	the next step. If the dog did not look down, then the dog was given another set of 10 trials of 'click and
175	food' until the dog looked down after the click sound in the absence of food rewards.
176	2. The owner gave verbal commands (for example Sit!, Down!, Lay! etc.) to the dog. All commands
177	referred to actions known by the dog prior to this study. If the dog acted in line with the command,
178	then she pushed the 'click + food' button and the dog received a piece of reward. Each dog
179	participated in 14 trials.
180	3. The owner put the collar on the dog and Step 2 was repeated 14 times.
181	4. The owner and the dog sat down. The experimenter brought a small black cardboard rectangle
182	(18x24 cm) to the room and put it on the floor. She placed it in front of the dog at a distance of 1.5m.
183	She called the dog and acted as if she placed one piece of food under the rectangle and then stepped
184	back. The owner encouraged the dog to approach the rectangle verbally (Let's go!). If the dog
185	approached the rectangle (within 10 cm), the experimenter pushed the 'click + food' button and the
186	dog was allowed to eat the treat. We repeated this two times.
187	5. We repeated Step 4, except that the rectangle was now at a distance of 3 m from the dog.
188	6. The experimenter brought a second rectangle (which was identical to the first one) to the room. She
189	placed the rectangles into the two corners of the room 3 m from the dog. She stepped next to one of
190	the rectangles and repeated the previous training four times (sequences: LRLR or RLRL; L=left,
191	R=right).
192	
193	2.3.2. Training phase
194	
195	2.3.2.1. Basic training
196	The aim of the Basic training was to develop associations between sounds and spatially oriented
197	motor responses (going left or right). This phase consisted of series of training trials.
198	Two target objects (cardboard rectangles) were placed at two corners of the lab. The owner and the
199	dog (with the mounted collar) were sitting in front of the rectangles (see Fig. 2). Upon hearing one of
200	the two sounds (HP or LP) emitted from the collar, the owner encouraged the dog to approach one of
201	the rectangles (using only neutral verbal utterances like "Let's go!"). Owners did not display any

202	gestures e.g. pointing. If the dog approached the object located in the designated corner (i.e. which
203	matched with the emitted sound) in 10 seconds within 20 cm ('approaching zone'), the dog received
204	the reward from the collar.
205	In the first series, we played one sound 10 times (left or right) and then the other sound also 10 times.
206	This was followed by a second series in which sound signals were alternated in LRLRRLRLLR (trials
207	1-10) and RLRLLRLRRL (trials 11-20) order.
208	These blocks of ten trials were then repeated until they reached learning criterion. Criterion for
209	learning the basic training task was set as 10 consecutive correct trials.
210	If the dog approached the 'incorrect' object (within 20 cm), the owner called the dog back and the trial
211	was repeated with the same sound signal. If the dog failed to show the correct response two times in a
212	row, then the owner was allowed to point at the correct rectangle during the subsequent trial. We
213	considered the trial also as incorrect and the dog did not get the reward if it passed along the midline in
214	between the objects without approaching either of them.
215	For half of the subjects (N=8) the HP sound was the 'go left' signal and the LP sound was the 'go
216	right' signal. For the other half (N=8) of the subjects we reversed the reference (left/right) of the
217	signals.
218	Dogs participated in 10-30 Basic training trials per session (mean±SE: 16±4) and each training session
219	was terminated when the owner indicated that the dog was getting tired and inattentive. Owners and
220	their dogs visited the department once or twice weekly.
221	
222	Insert Figure 2
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224	2.3.2.2. Advanced training
225	The aim of the advanced training was to investigate whether changes in the training situation
226	influence dogs' performance and generalization capability. Subjects were divided into two groups:
227	Rotation training: For half of the dogs (N=8) we rotated the position of the rectangles and the
228	orientation of the dog and the owner by 90°. Then subjects participated in 10-trial training sessions as
229	described above until reaching the criterion (10 consecutive correct trials)

230	No target training: For the other half of dogs (N=8) we repeated the Basic training without target
231	objects until they reached the criterion (10 consecutive correct trials). Dogs received the reward if they
232	approached the former location of the rectangle within 20 cm.
233	Owners and their dogs visited the department once or twice weekly, and they participated 10-20
234	Advanced training trials per visit (mean±SE: 14±2).
235	
236	2.3.3. Testing phase
237	Test trials were staged outdoors on the campus of the Eötvös Loránd University in a 40 m x 40 m
238	grassy area with some peripheral woods. We could not use a fenced area, thus some students and dog
239	walkers were usually walking nearby during the test and were asked verbally to avoid the test area
240	during the testing. Each session started with a short 6-trial warm-up training performed in the
241	experimental room (in these trials we used the same procedure as in the Advanced training). Each
242	testing session consisted of 5 different types of trials ('condition'). Three different targets and 5
243	different distances with different angular deviations from the position of the dog were utilized: Close
244	ball, Distant ball, Close tree, Distant tree and Human (see Fig. 3). We decided to use the unbaited
245	C&T collar during the testing in order to exclude accidental falls of the reward during fast running and
246	the possible loss of the reward in high grass or snow in winter. Reward was provided by the owner
247	after the dogs' return.
248	In each condition the owner and the dog were standing in front of two targets (trees, balls or two
249	female humans). Dogs were wearing the empty C&T collar. After the sound was emitted from the
250	collar, the dog was allowed to set off. The owner was not allowed to say anything to the dog except
251	"GO!" or "Go ahead!" without any additional verbal or gestural signals. If the dog approached the
252	correct target within 1 m, then it received verbal praise from the owner during first two trials. In the
253	remaining 8 trials they received food or a ball as a reward from the owner except in the Human
254	condition in which the female humans provided the reward in order to maintain dogs' motivation.
255	Approach toward the incorrect target was considered a failed trial: the owner was instructed to call the
256	dog back and then the trial was repeated with the same sound.

257	Order of the test conditions was counterbalanced among dogs. Exact places, angles, targets and
258	their relative positions were constant. Dogs were provided with 10 trials in each condition using a
259	LRLRRLRLR or RLRLLRLRRL orders.
260	Dogs took part in only one test condition per day, thus the test session contained 5 occasions with
261	intervals of no more than one week.
262	
263	Insert Figure 3
264	
265	2.3.4. 'Clever Hans' control trials
266	The aim of these trials was to control for owners' and experimenter's influence on dogs'
267	performance. After finishing the testing sessions, dogs participated in 10 additional Advanced training
268	trials in the laboratory setting, but in this case owners were wearing opaque sunglasses and they were
269	listening to loud music during the test. This prevented them from hearing the played sound and from
270	seeing in which direction the dog was moving. The experimenter, who controlled the C&T collar, was
271	facing the wall when she pushed the sound button on the controller, thus she did not see the dog either.
272	The experimenter turned back to the scene only after the sound was emitted and informed the owner
273	what had happened (if the dog went to the proper side the owner had to praise the dog, if the dog went
274	to the wrong side the owner had to call the dog back). We predicted that, if no Clever Hans effect was
275	involved in the Basic and Advanced training, then the changed appearance and behaviour of the owner
276	and experimenter would not affect the dogs' performance.
277	
278	2.4. Variables and Data analysis
279	The experimenter coded the performance of the dog in situ during the basic and advanced training,
280	test conditions and also during Clever Hans control (she marked each trial as correct or incorrect). Test
281	conditions were videotaped and analysed later with Solomon coder 12.06.06 (András Péter
282	http://solomoncoder.com). Trials of training sessions were also supervised by coding recorded videos.
283	
284	Measured variables:

285	Target: The dog approached one of the targets within 20 cm during training trials (rectangle), or within
286	1 m during test trials (tree/ball/human).
287	First movement: The direction of dog's first three steps from the start point (left/right/straight from the
288	middle line) in test trials.
289	We scored correct trials with 1, and incorrect trials with 0. We considered a trial as correct if (1) the
290	dog went to the specific target (rectangle/tree/ball/human) on the side indicated by the specific sound
291	(left/right) (Target variable), (2) the dog made the first three steps toward the target
292	(rectangle/tree/ball/human) indicated by the specific sound signal (left/right) First movement variable).
293	If the dog moved towards the middle area we considered it as an incorrect trial.
294	Sometimes it happened that dogs stopped before reaching one of the targets and did not go further
295	in 10 sec. In this case, the owner was instructed by the experimenter to call the dog back, and we
296	played the same sound again. In this case, the First movement score was based on the direction of the
297	first start and Target score was determined by the performance on the subsequent trial. It also
298	happened that the dog changed its direction during the approach (for example, the dog started to go
299	toward the target on the left but after several meters changed its direction and went to the target on the
300	right). For the statistical analysis, the test conditions were split into two groups based on their angular
301	deviations. Test conditions in which the angular deviation was sharper or wider than the training angle
302	(53°) were grouped together, thus Close tree and Distant ball conditions formed the 'Angle $< 53^{\circ}$ '
303	group, and <i>Close ball</i> , <i>Distant tree</i> and <i>Human</i> conditions formed the 'Angle > 53°' group.
304	For statistical analysis we used IBM SPSS Statistics 21.
305	
306	3. Results
307	Dogs reached the criterion in 72 ± 36 (mean $\pm SD$) correct trials on average in the Basic training,
308	and in 34 \pm 12 (mean \pm SD) additional trials in the Advanced training. We excluded one dog because it
309	failed to reach the training criterion in 180 trials in the Basic training. Another dog's owner quit the
310	study after completing the first test condition; therefore the data of this dog are included only in the
311	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 generalized 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±3 and 15±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 seconds in the <i>Distant tree</i> condition,
and one of them failed also in the <i>Close tree</i> 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).
Insert Figure 4
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

340	the Advanced training type ($F_{1,809}$ =0.004, p=0.947) and interaction between Advanced training type
341	and Test condition was also not significant ($F_{1,809}$ =0.68, p=0.630).
342	We also compared dogs' performance between two test condition groups, the $Angle < 53^{\circ}$ and the
343	$Angle > 53^{\circ}$ group, with GLMM for Binomial distribution. Results showed that dogs' performance
344	was lower if the angular deviation in the test condition was sharper than the training angle ($F_{1,661}$ =5.33,
345	p=0.021) (Fig. 5).
346	
347	Insert Figure 5
348	
349	4. Discussion
350	
351	The objective of the present study was to investigate whether dogs are capable of learning to go
352	left/right after training using two qualitatively different sound signals and whether they can generalize
353	this experience to novel contexts. Contrary to previous findings suggesting that dogs failed to rely on
354	tone frequency cues in a go left/go right task (e.g. Lawicka, 1969), our results showed that dogs had no
355	difficulty in learning directional responses based on qualitatively different sound signals after a
356	relatively short training.
357	Methodological differences may explain this discrepancy: (1) Dogs in our study were clicker
358	trained family dogs from different breeds with well described training history, while Lawicka tested 8
359	laboratory mongrels with unknown training background. Dogs in the present study were previously
360	trained with clicker to follow the direction of the owners' verbal and hand signals toward distant
361	locations as a part of the obedience training, thus these dogs already had experience in directional
362	response tasks. While owners were prevented from using these well known signals during the training
363	and test phases, we assume that it had no effect on dogs' performance in the present role. (2) In our
364	study, signals were emitted and dogs were rewarded directly from the C&T collar, while in Lawicka's
365	experiment sound sources were loudspeakers situated at 2 m from the starting platform and the target
366	objects contained the reward. This latter difference might have drawn dogs' attention more toward the
367	target object than the sound signals from the C & T collar and caused the prolonged learning time. Our

368	results support the presumption that the Quality-Location effect is not a general constraint of learning,
369	but more likely it emerges under particular experimental designs and conditions (Harrison, 1984; Neill
370	and Harrison, 1987).
371	In order to examine context dependency of learning, we changed the training situation after the
372	Basic training by either removing the target objects (No target training) or rotating the position of the
373	targets and the dog (Rotation training). We found that dogs' performance decreased equally in both
374	conditions. Braem and Mills (2010) reported also that dogs show a decline in performing a newly
375	learned command in a novel environment. In contrast to our prediction, dogs that participated in the
376	No target training showed as rapid recovery as dogs in the Rotating training. We presume that during
377	the Basic training, dogs learnt to "go left/right" instead of "approaching the target on the left/right",
378	thus the absence of the target objects in the Advanced training (in the No target training condition) did
379	not affect their performance. The lack of such difference could also be explained by the fact that the
380	reward was not hidden into/behind the target object (c.f. Lawicka, 1969; Fiset et al., 2006) but it came
381	directly from the C&T collar worn by the dog.
382	In the testing phase, dogs were exposed to a novel area (outdoor field), novel targets
383	(balls/trees/humans), and extended distances (9.5 to 19.5 m) and angular deviations (36 $^{\circ}$ to 87 $^{\circ}$) in
384	order to reveal whether they are able to generalize the "go left/right" task (see Fig. 3). Dogs'
385	performance was significantly above chance level in all test conditions, thus they approached the
386	correct target matching with the sound command significantly more often than expected. Target types
387	and their relative distance from the dog had no influence on dogs' performance, similarly to previous
388	findings in search for disappearing objects in dogs (Fiset et al., 2006). However dogs' performance in
389	this task decreased as a function of angular deviation between two adjacent hiding locations and the
390	relative position of the dog (Fiset et al., 2006). If the target is visible, then the angular deviation is the
391	most relevant factor for dogs in a detour task, and they show a preference for using the less divergent
392	route (Chapuis, 1983). A similar result was also reported for chimpanzees. The spatial separation of
393	two adjacent hiding locations together with the varying angular deviation influenced animals'
394	accuracy in a spatial delayed response object choice task (Harrison and Nissen, 1941). Our results also
395	showed that dogs' performance was lower if, in the test condition, the angular deviation between the

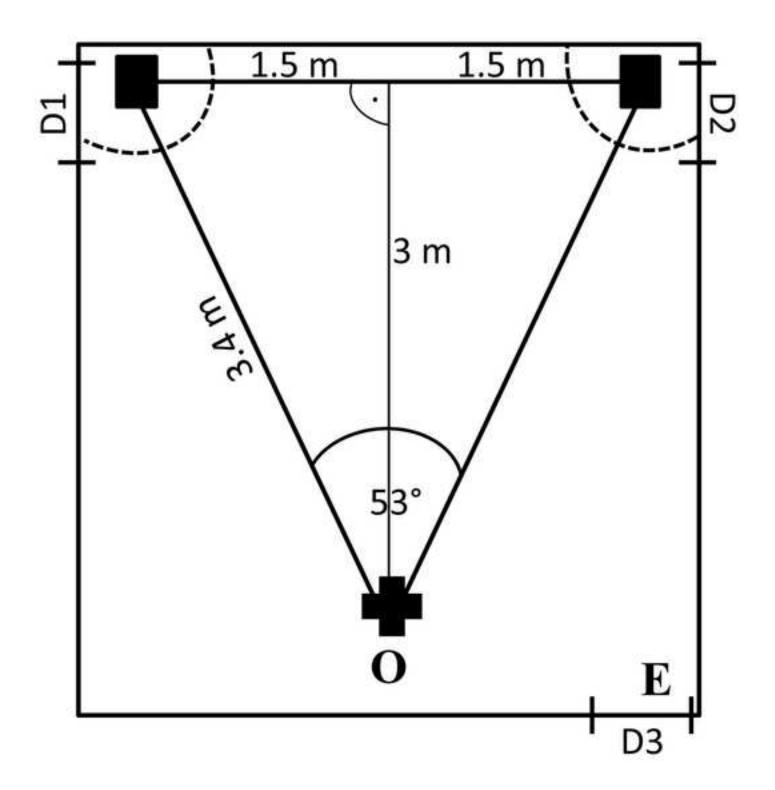
396	adjacent targets and the dogs' position was sharper than the angle experienced in the training angle.
397	This is the first evidence that angular deviation influences dogs' ability to generalize learned
398	directional commands from the training context to a novel context.
399	Dogs' similar accuracy in all test conditions after different Advanced training suggests that dogs
400	learnt the general rule of 'go left/right', and that they were able to utilize this rule in unfamiliar
401	environments. Dogs showed similar generalization ability in a landmark discrimination task by
402	efficiently using novel landmarks in novel positions for locating target objects. This was also
403	interpreted as learning the general concept of the landmark (Milgram et al., 2002). The control testing
404	aimed to exclude human influence (i.e. Clever Hans effect) also supported our findings that the dogs'
405	performance was based on their attention to the signals.
406	In summary, these results clearly show that dogs can internalise a simple behaviour rule for taking
407	directional action upon hearing qualitatively different signals. This capacity of dogs has long been
408	used in traditional settings (e.g. shepherds have long known how to train herding dogs by whistle
409	sound), but our elaborated method offers the possibility to train dogs explicitly if needed for specific
410	employments (e.g. search and rescue, Ferworn et al., 2006).
411	
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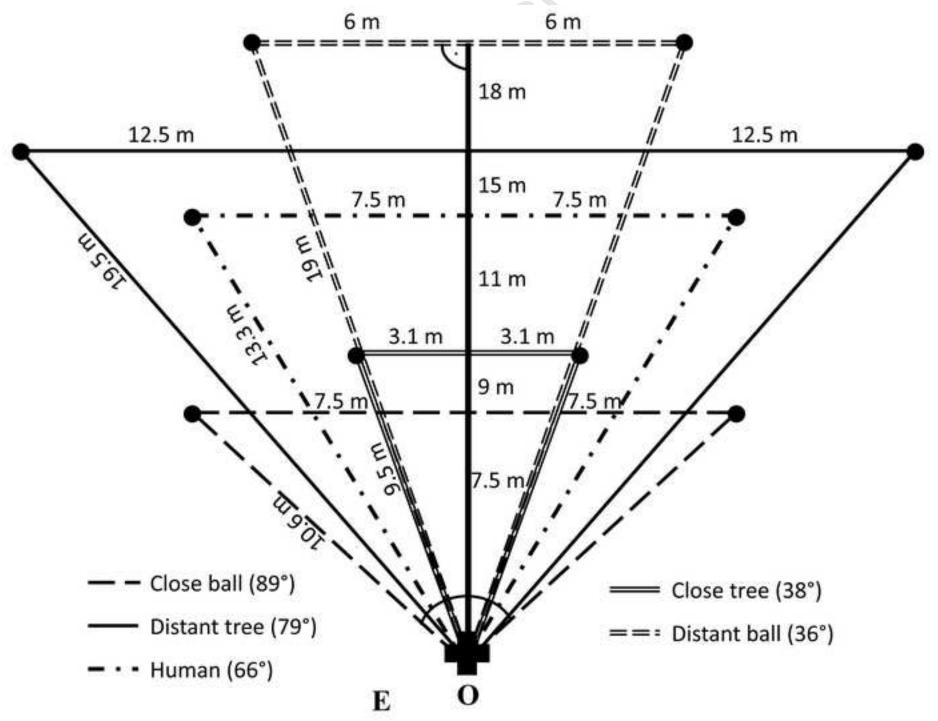
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479	Figure caption
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481	Fig. 1. The Click & Treat Collar
482	
483	Fig. 2. Experimental layout for the Basic training phase. The black cross indicates the dogs' starting
484	position, the O indicates the owner's and the E the experimenter's position. The black rectangles
485	indicate the location of two identical target objects, the interrupted lines indicate the 20 cm
486	'approaching zone'. D1, D2 and D3 indicate the locations of the three doors (0.6 m width) in the lab.
487	
488	Fig. 3. Experimental design of testing conditions. The black cross indicates the dogs' starting position,
489	the O indicates the owner's and the E the experimenter's position. The black circles indicate the
490	location of two target objects (balls/trees/humans) in the different testing conditions.
491	
492	Fig. 4. Percent (%) of correct trials in each Test conditions (Close ball, Distant ball, Close tree, Distant
493	tree, Human) and in the Clever Hans control. * p<0.001
494	
495	Fig. 5. Means of the correct trials in the two experimental groups which differ with regard to the visual
496	angle (Angle<53°: Distant ball, Close tree; Angle > 53°: Close ball, Distant tree, Human). * p<0.05
497	







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