ELSEVIER

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



What experimental experience affects dogs' comprehension of human communicative actions?

Marc D. Hauser^{a,b,*}, Jordan A. Comins^a, Lisa M. Pytka^a, Donal P. Cahill^a, Sofia Velez-Calderon^a

ARTICLE INFO

Article history: Received 21 June 2010 Received in revised form 29 July 2010 Accepted 29 July 2010

Keywords:
Action comprehension
Dogs
Spontaneous comprehension
Learned associations
Communicative gestures
Coding methods

ABSTRACT

Studies of dogs report that individuals reliably respond to the goal-directed communicative actions (e.g., pointing) of human experimenters. All of these studies use some version of a multi-trial approach, thereby allowing for the possibility of rapid learning within an experimental session. The experiments reported here ask whether dogs can respond correctly to a communicative action based on only a single presentation, thereby eliminating the possibility of learning within the experimental context. We tested 173 dogs. For each dog reaching our test criteria, we used a single presentation of six different goal-directed actions within a session, asking whether they correctly follow to a target goal (container with concealed food) a (1) distal hand point, (2) step toward one container, (3) hand point to one container followed by step toward the other, (4) step toward one container and point to the other, (5) distal foot point with the experimenter's hands free, and (6) distal foot point with the experimenter's hands occupied. Given only a single presentation, dogs selected the correct container when the experimenter hand pointed, foot pointed with hands occupied, or stepped closer to the target container, but failed on the other actions, despite using the same method. The fact that dogs correctly followed foot pointing with hands occupied, but not hands free, suggests that they are sensitive to environmental constraints, and use this information to infer rational, goal-directed action. We discuss these results in light of the role of experience in recognizing communicative gestures, as well as the significance of coding criteria for studies of canine competence.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

Many human gestures are not only communicative, but also designed to manipulate the attentional state of an audience toward a particular goal. When we point or look in a particular direction, we generate a signal that designates a particular goal – an object or event that is worthy of attention. Infants begin to point at approximately 9–12 months. At around 14 months of age, they understand both the referential nature of pointing and that the target object depends in part on shared experiences (i.e., as opposed to merely personal or egocentric experience) (Behne et al., 2005; Liebal et al., 2009). Thus, for example, if an infant has shared the experience of cleaning up with a person, she is more likely to engage in cleaning up when this person points to the clean-up area, than when a person has not shared this experience.

Though nonhuman animals lack the range of gestures that we have, they nonetheless have communicative signals that have evolved to manipulate the attentional states of perceivers, and in this sense, are at least functionally goal-directed (Bradbury and Vehrencamp, 1998; Hauser, 1996; Krebs and Dawkins, 1984; Owings and Morton, 1998). A different, but related issue, is the nature of signal perception and comprehension, and of direct relevance to the present work, the capacity to comprehend the communicative gestures of another species, especially gestures that they themselves are incapable of producing. This problem is relevant to at least four different theoretical concerns: (1) the evolved capacity to infer communicative intent (Tomasello et al., 2005), (2) the role of environmental context in action comprehension (Csibra, 2008; Gergely and Csibra, 2003), (3) the importance of prior experience producing an action in interpreting the action (Rizzolatti et al., 2001), and (4) the relative contribution of experience in sculpting particular capacities. These four issues arise, in part, from a rich comparative literature on the perception of pointing in domesticated dogs and silver foxes, wild wolves and silver foxes, and chimpanzees (Hare et al., 2002, 2005; Miklosi and Soproni, 2006; Virányi et al., 2008; Call et al., 2000). We turn next to a brief summary of some of the key issues before addressing the primary aims of our research and our empirical findings.

A considerable amount of research has been carried out to assess whether nonhuman animals can use the communicative actions

^a Department of Psychology, Harvard University, 33 Kirkland Street, Cambridge, MA 02138, United States

^b Department of Human Evolutionary Biology, Harvard University, Cambridge, MA 02138, United States

^{*} Corresponding author. Tel.: +1 617 496 7077; fax: +1 617 496 7077. E-mail address: mdh102559@gmail.com (M.D. Hauser).

of a human experimenter to locate hidden food. In the basic task, carried out with dogs and wolves (Gácsi et al., 2009b; Hare et al., 2002; Lakatos et al., 2009; Miklosi and Soproni, 2006; Range et al., 2009; Udell et al., 2008a; Virányi et al., 2008), an experimenter places two containers on the ground and then conceals them with an occluder. The experimenter then shows the subject a piece of food, lowers it behind the occluder, baits one container, removes the occluder, spreads the containers apart, points to the container with hidden food, and then gives the subject a choice. Numerous variations of the pointing gesture have been implemented, including a contrast between distal and proximal (i.e., the latter associated with finger-to-container contact), long-lasting versus momentary (the former allowing the subject to use visually guided search based on the continued presence of the gesture), and pointing to the same side versus cross-body with respect to the target container. Critical to the studies we present are comparative data on domesticated versus wild subjects, and canids versus chimpanzees. Whereas the apes, including chimpanzees, show some motoric capacity to point (Call and Tomasello, 1994; Leavens et al., 1998) and the canids do not, the canids generally outperform the chimpanzees in pointing comprehension tasks, particularly distal, momentary presentations. These data would appear to rule out the strong version of the direct-matching hypothesis (Rizzolatti et al., 2001) in which action comprehension requires matched-action production (i.e., animals such as dogs that lack the capacity to point nonetheless comprehend pointing).

The comparative data also raise the interesting hypothesis that domestication on its own has greatly enhanced the capacity of some animals to read the communicative gestures of humans (Hare et al., 2002, 2005). Thus, studies of domesticated dogs and silver foxes suggest that they surpass the wild types (wolves and nondomesticated silver foxes, respectively) in reading the communicative gestures of humans, especially when one considers the diversity of action types presented. Although it appears that hand-reared wolves respond with considerable accuracy to simple pointing gestures, domesticated dogs appear to outperform wolves when a greater variety of gestures are presented, and especially, novel ones (Gácsi et al., 2009a,b; Hare et al., 2002, 2010; Lakatos et al., 2009; Range et al., 2009; Udell et al., 2008a; Virányi et al., 2008).

A critical issue in the current debate about whether domestication, on its own, can contribute to the fundamental differences in social cognition observed in several studies of domesticated dogs and wolves is whether systematic exposure to human generated, goal-directed gestures can also transform the capacities of a wild animal, inducing the ability to read communicative intent. Though this issue has focused on the domestication hypothesis, it is equally relevant to the human capacity and the extent to which the infant's capacity requires a fairly long and extensive set of experiences with human pointing, or whether it appears sometime after the first year of life due to maturational factors. Here we directly explore the role of experimental experience in action comprehension by revisiting many of the human-generated gestures presented to dogs (and other species) with novel individuals. Further, and in parallel with studies of free-ranging rhesus monkeys (Hauser et al., 2007), we restricted our methods and analyses to first-trial data. In particular, we sought evidence relevant to five distinctive but related goals - the first four conceptual, the fifth methodological.

Our first aim was to assess whether the capacity of dogs to respond correctly to an unknown human's goal-directed actions is mediated in part by experimental experience, and specifically, rapid learning within a session. Though no study has looked explicitly at first-trial performance in the context of action comprehension, Udell et al. (2008a,b) showed within-session changes, with some dogs improving from the first to second half, whereas Lakatos et al. (2009) showed no within-session changes in a split-block analysis. In the present study, therefore, we presented each dog

with only a single trial per action type, and tested a large number of dogs.

Our second aim was to explore whether, in the context of a single presentation, some cues are more important than others. In tests using repeated trials, domesticated dogs use point over proximity (Soproni et al., 2002), whereas dingoes do not (Smith and Litchfield, 2010). Here we test whether distal hand pointing or stepping toward a container provide stronger signals of hidden food location to dogs, based on single-trial presentations, and with order of cue presentation contrasted.

Third, we explored the question of rational action (Gergely and Csibra, 2003), and in particular, the extent to which dogs take into account environmental constraints on goal-directed action when interpreting an agent's behaviour. This topic has been elegantly explored by Range et al. (2007) in their study of dog imitation. We pick up on their findings here by testing dogs on a pair of single-trial conditions, both of which involve the same cue (a distal foot point), but only one of which involves an environmental constraint (i.e., experimenter's hands are occupied) to render the action rational. Thus, in contrast to the studies by Range et al., we present only one trial per condition, and instead of imitation, test for appropriate goal-directed action.

Our fourth aim was to explore whether individual variation in performance on warm-up trials accurately predicted performance on test trials. In all experimental studies of animals, there is individual variation in performance, and it is not always clear how such variation impacts upon findings of cognitive capacity. Here, we take advantage of our pre-testing, warm-up conditions to look, a posteriori, at performance on each of the critical test conditions.

The fifth aim was methodological. In particular, though many, but not all studies videotape and blind code the subject's response, we know of no study on dogs in which the experimenter and handler are also coded. We consider the latter to be critical for two reasons. First, though most of this work is aimed at the capacity of dogs to read human cues, in the absence of coding the experimenter, it is possible that cues other than those intended might also be provided. For example, in studies looking at pointing, the key is to show that only pointing, and no other cue (e.g., eye gaze, head orientation), is necessary. However, because pointing and looking are typically produced together, it is possible that experimenters will unintentionally look to where they point, thereby providing two potentially relevant cues. Similarly, because the handlers in these studies are typically owners, and thus, untrained, it is possible that they will also cue their dog or make mistakes in terms of how they release the dog. Thus, we consider coding of experimenter, handler, and dog to be critical aspects of this work, a methodological procedure that provides a stronger guarantee that there are no errors or unintentional cues during the experiments.

2. Material and methods

2.1. Subjects

We tested a total of 173 domestic pet dogs (*Canis familiaris*), 87 in Condition 1 and 86 in Condition 2, from May, 2009 to October, 2009, at the Canine Cognition Laboratory, Harvard University, Cambridge, MA. Dog owners voluntarily logged on to the Canine Cognition Lab Web site, and signed up for participation (URL: http://www.wjh.harvard.edu/~mnkylab/doglab.html). Subjects were all adults over 1 year of age. All individuals participating in the study were experimentally naïve. We included all breeds and individuals as long as they had good sight, hearing, and the capacity to move independently. Subjects were all pre-screened for aggressive behaviour using a scoring sheet prepared by Harvard's Animal Care and Use Committee (URL:



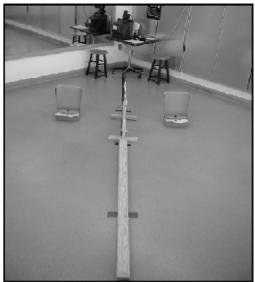


Fig. 1. The image on the left is a screenshot from the camera used to code the *handler's behaviour*. The handler sits in the chair, beneath one of the camera's, and holds the dog centred in the black square on the floor in front of the chair. The image on the right is a screenshot from the camera capturing both the *experimenter's performance* and the *subject's choice*. The wooden beam bisects the dog's path of motion towards the two containers.

http://www.wjh.harvard.edu/~mnkylab/BehavSheet.doc). Those dogs scoring 10 or higher on the prescreening test were not allowed to participate in this study.

2.2. Experimenters

Before testing subjects, all experimenters underwent several training sessions to minimize variation in experimental presentation and the possibility of unintentional cueing. Following a mandatory seminar that included both the observation of an actual testing session and the recital of the specifics of our study protocol. experimenters were required to videotape themselves performing the experiment. Highly trained experimenters (MDH, JAC, or LMP) subsequently reviewed this tape for quality before the new experimenter could begin to run dogs; if any undesired variation in the presentation was detected (e.g., inappropriate speed when presenting a point, incorrect alignment of containers, use of the wrong hand for baiting, looking at the container while pointing), the experimenter was asked to carry out additional practice sessions, and provide a new videotape for evaluation. Additionally, MDH, JAC, and LMP performed weekly, unannounced spot checks, to review experimenters' execution of the action types during testing.

Despite this high level of attention to experimenter presentation, subsequent video coding yielded evidence of experimenter error given the details of our protocol. Specifically, we excluded (blind-to-subject performance; see below) any trial in which one or more of the following occurred: (1) the experimenter failed to perform the action type exactly as designed (see below for description of actions); (2) containers were inadvertently baited instructively (e.g., both hands were not symmetrically lowered into each bucket to conceal food location); (3) containers were misaligned (i.e., we required that both containers were equidistant from the experimenter, aligned along an imaginary line perpendicular to the direct path between subject and experimenter, and facing forward with no tilt); or (4) the experimenter forgot to step back following the target action and then put his or her head down to eliminate inadvertent eye gaze cueing. By eliminating such trials, we ensured that our results accurately reflected subjects' decisions rather than mere variation in experimenter performance, including unintentional cueing.

2.3. Dog handlers

During testing, we elected to have owners serve as the dog handlers to reduce subject stress or anxiety. We provided dog handlers with three instructions to follow throughout the course of testing. Handlers were required to: (1) centre their dogs within the designated black square in front of their chair (see Fig. 1, *Testing room*) before each trial; (2) release the dog only after the experimenter's head was lowered; and (3) avoid any unintentional cueing in the form of hand or body movements or verbal reinforcement. Handler performance was later coded blind-to-condition and subject performance by offline coders to ensure complicity with these criteria.

2.4. Testing room

Before testing, the experimenter setup two digital cameras, one focused on the dog's handler and the pre-release behaviour of the dog and a second focused on the experimenter and the post-release behaviour of the dog (see Fig. 1 for screenshots from these cameras). The cameras were synched for coding by means of an audiovisual cue presented at the start of every session. Within the testing room $(5.5~{\rm m}\times5.25~{\rm m}),$ we placed a chair in one corner for the handler. At the handler's feet was a black, tape-outlined box $(80~{\rm cm}\times40~{\rm cm});$ the handler centred the dog within this box before each trial. A 2 m wooden beam was laid on the ground so as to symmetrically bisect the approach path from the dog's vantage point; though dogs could cross over the beam, and often did, it made the choice between containers more explicit.

2.5. Procedure

2.5.1. Pre-testing

Prior to testing, the experimenter conducted a series of trials designed to familiarize the subject with the choice apparatus. The experimenter first presented a piece of food on the floor approximately 1 m from the dog, then stepped back and lowered his or her head to cue the release. On the next trial, the experimenter placed a custom-built, lidded container on the floor with the lid open, placed the food reward inside the container, and then stepped back. This allowed the dog to retrieve the food from the container, but with-







Fig. 2. The far left frame shows our olfactory control. Five pieces of food are located on the bottom of the container on the right; the container on the left, with the white hinged lid, is placed into the left container, concealing the five pieces of food. The centre frame shows the container with the hinged lid in position, covering the concealed food. Once the dog lifts the lid, it affixes to the back wall of the container by means of a magnet. The right frame shows the white hinged-lid raised, revealing a single food reward inside

out having to lift the lid. The next trial was the same, except that the experimenter closed the lid before stepping back. Each dog had to lift the lid covering the food with its snout, and then remove the food on its own (see Fig. 2). As reported below, most dogs flipped the lid immediately, whereas other dogs required more experience and in some cases, additional help from the experimenter who would open and close the lid, thereby facilitating access to the food.

Once dogs readily opened the lid of the container, they were presented with two containers, spread 1.5 m apart, and with the lids in the open position. The experimenter then stood midway between the containers, showed one food treat, lowered it into one container, lowered both lids simultaneously, stood up, took one step back, and then lowered his or her head, cueing the handler to release the dog. To proceed to the test trials, each dog had to retrieve the food from the correct container on two consecutive trials. A single-alternation pattern was used to determine food location on each pre-test trial; this criterion ensured that dogs successfully visited both containers before being tested. This procedure was implemented so that we could alternate the location of the hidden food item and ensure dogs had been reinforced at each container. Dogs were given a maximum of 10 such trials. Failure to retrieve food from the baited container on two consecutive trials, within the 10 allotted trials, resulted in elimination from the study. Only 11.56% of all dogs tested failed to reach criterion, thus confirming that the task was not overly difficult for our subjects.

2.5.2. Testing

We tested each dog on one trial of each action type, totalling six trials per dog. There were two condition orders. In Condition 1, the first trial was always distal hand point. We started with this gesture because it replicates across many studies, and thus, allowed us to start with a presumably simple task. Distal hand point was followed by a randomized block of foot-point-hands-free and foot-point-hands-occupied; foot pointing with hands free (but not hands occupied) has been tested before, but with a repeated trial design (Lakatos et al., 2009; Udell et al., 2008b). Condition 1 ended with a further randomized block of step, step-then-point and point-then-step.

The second block of Condition 1 focused on the relatively uncommon action of foot pointing (Lakatos et al., 2009; Udell et al., 2008b), and on the possibility that certain environmental constraints might modify subjects' interpretation of this action. Thus, from a human perspective, foot pointing appears rational if the person's hands are occupied (holding something heavy with both

hands), but less so if their hands are free and could be used to indicate a target goal. The second block of Condition 1 explored the role of proximity (step toward one container), and more importantly, the relative strength of two different, competing cues (step versus point).

Because of the particular order in which we tested dogs in Condition 1, and the possibility that particular within-session experience might affect subsequent performance, we tested a new sample of dogs on Condition 2, using the same action types but with a different order of presentation, and three distinct blocks within the test session. In particular, block 1 consisted of a randomized presentation of distal hand point and step. We ran these first in order to assess the robustness of each action tested alone; if dogs consistently use these cues on their own, then putting both cues in competition within the same event is of theoretical interest, especially given the single-trial exposure. Block 2 consisted of a randomized presentation of step-then-point and point-then-step; thus, both cues were presented, but the order of presentation varied. In block 3, we randomized the presentation of foot-point-hands-free and foot-point-hands-occupied.

Our methods were, in many ways, similar to previous twoalternative forced choice tasks with domestic dogs (Hare et al., 2002; Lakatos et al., 2009; Udell et al., 2008a; Virányi et al., 2008). With the subject positioned 3 m away, the experimenter simultaneously placed two food containers $(18 \text{ cm} \times 30 \text{ cm} \times 38 \text{ cm})$ on the ground in front of them. Next, a free-standing foam core occluder (75 cm \times 50 cm) was placed between the subject and the containers, blocking the dog's visual access to the containers. The experimenter then showed the subject a single dog treat for 1 s, approximately 0.5 m above the top edge of the occluder, before slowly lowering it behind the occluder. The experimenter then brought their second hand to join the first behind the occluder, transferring the food if necessary, and proceeded as if baiting both containers simultaneously, though in reality only baiting one. Thus, we provided subjects with information that food had been hidden, but not about the location of the food with respect to the containers. After baiting, the containers were spread 1.5 m apart, exactly aligned and facing forward with no asymmetries. Next, the foam core occluder was rotated 90° so as to run continuously with the wooden beam, symmetrically partitioning the room from the dog's perspective. The experimenter then performed one of the action types toward the target container/s (see Description of action types). The lateral designation of the target container/s was determined in a counterbalanced fashion prior to the experimental session. After performing the action, the experimenter took one

large step back from the containers and lowered his or her head. As previously noted, lowering the head eliminated any unintentional eye gaze or head orienting cues, and also signalled to the dog's handler to release the subject. The subject was then allowed to approach and choose a container. If the handler cued the dog in any way, this was noted at the end of the experiment; offline coding was then used to check on cueing by the handler (see *Coding*).

Both our choice measure and apparatus differed from previous studies (Gácsi et al., 2009a; Hare et al., 2010; Range et al., 2009; Soproni et al., 2001; Udell et al., 2008a; Virányi et al., 2008). Previous studies have defined choice as an approach to within a designated distance, as touching the container, or as an actual retrieval of the concealed food from an open container or inverted cup. In contrast, as noted above, we required each dog to lift the lid of the chosen container within 20 s of being released in order to be considered as having made a choice. If a dog sniffed one container, but

did not lift the lid, this was not considered a choice; dogs infrequently sniffed one container and then lifted the lid of the other container. Though lid lifting was an unambiguous choice measure, we also coded the dog's choice offline, blind-to-food location. Once the dog made its choice, the experimenter took the dog by its leash and returned it to the handler.

Our apparatus included a false bottom containing five food treats (see above, and Fig. 2). The false bottom was designed to control for the possibility that olfactory cues might mediate dog choice. Though some studies have explicitly tested for and ruled out olfactory cueing (Szetei et al., 2003), we felt that it was important to include an olfactory control in all of our tests, and then to statistically test for an effect. To use olfaction as a cue to food location in our experiments, dogs would have to distinguish between the odour of five treats and that of six treats (five in the false bottom plus the one target treat). This, we assumed, was

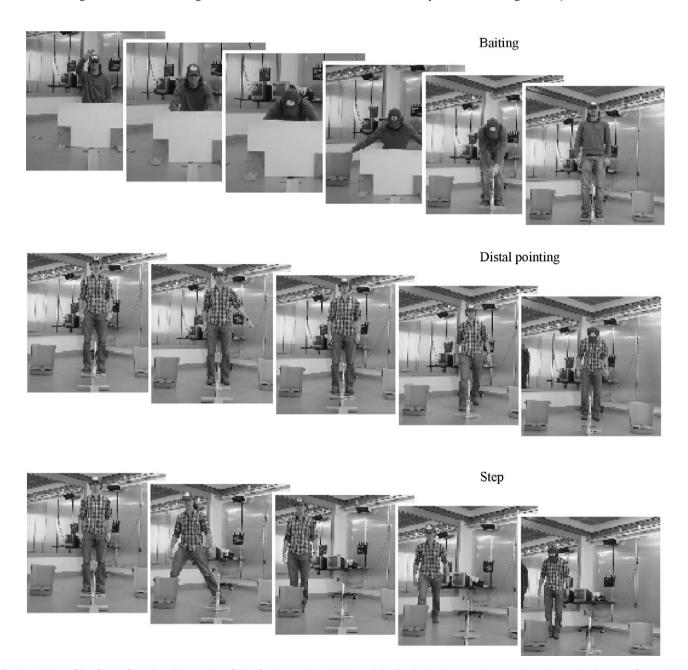
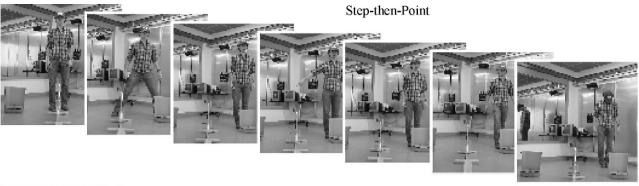
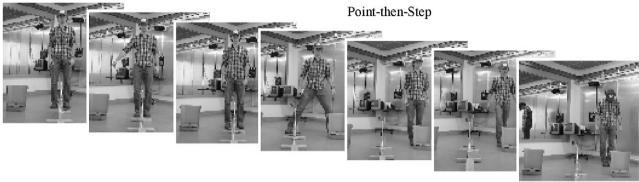
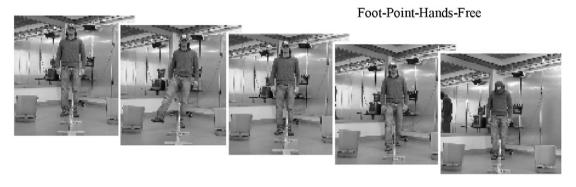


Fig. 3. Depiction of key frames from the subject's point of view for the container baiting and the distal pointing, stepping, step-then-point, point-then-step, foot-pointing-hands-free and foot-pointing-hands-occupied conditions. Baiting (top) occurred prior to all action types shown below. All action types ended when the experimenter stepped away from the containers, and then lowered his head (the cue given to the owners to release the dog).







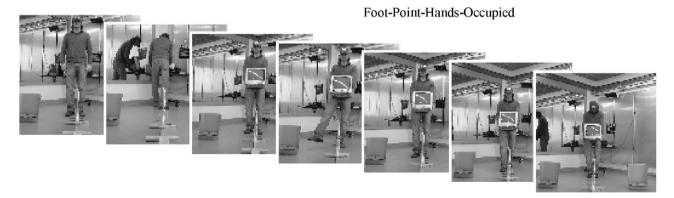


Fig. 3. (Continued).

most likely beyond their olfactory abilities. In the Section 3 below, however, we test this assumption by looking at the performance of dogs in a single olfactory control trial in which we baited the containers as per usual, but presented them with no accompanying action. Furthermore, we analysed the possible relationship between those dogs that succeeded in locating the baited piece of food on this single control and their overall success on the action conditions. If some dogs successfully used olfactory cues to locate

the hidden food, then we would expect their performance on the 6-trial action session to exceed that of dogs that failed to use such olfactory cues.

2.6. Description and motivation for action type

Fig. 3 provides a frame-by-frame illustration of an experimenter presenting each of the action types. A session consisted of six dis-

tinctive actions followed by the single olfactory control trial, for a total of seven unique test trials per dog.

2.6.1. Distal hand point

This action was used because numerous studies have demonstrated dogs' robust comprehension of this gesture, at least when presented with multiple trials. The experimenter pointed with his arm fully extended and index finger raised in the direction of the target container. The experimenter always used the arm closest to the target to point, while keeping the other arm flush with the side of his body. The experimenter held this position for 1 s, with the index finger 40–50 cm from the container. Following the presentation, the experimenter lowered his arm, took one step back, and lowered his or her head.

2.6.2. Step

This action was used both because several studies reveal that dogs use proximity cues to locate hidden food, and because even if proximity is not the central cue, we would expect dogs to approach the experimenter. The experimenter took one step laterally to position him or herself 10 cm behind the target container. Once located behind the container, the experimenter waited for 1 s, then took one step back, and lowered his or her head.

2.6.3. Step-then-point

We assumed that even with a single-trial presentation, that dogs would successfully find the hidden food following either (distal hand) point or step. Here we put these two cues into competition in order to assess whether one cue dominates the other within a single presentation. Our hypothesis was that point would trump step because of the more specifically communicative quality of this action. Consequently, we baited the container associated with point, leaving the container associated with step empty. Since we only presented one trial of this condition per dog, we expected reinforcement to have little to no effect on subsequent performance. We test for such effects in the Section 3.

The experimenter first took one step laterally to place him or herself behind one of the two containers. Next, using the arm closest to the actual location of the food item, the experimenter pointed (as in action type [i]) with his or her arm fully extended and index finger raised in the direction of the target container. After maintaining the point for 1 s, the experimenter lowered his or her arm, took one step backward, and lowered his or her head.

2.6.4. Point-then-step

Point-then-step was the complement to action type (iii) and motivated by similar theoretical issues. First, the experimenter pointed toward the target location as described in action type (i), and then stepped laterally behind the container that did not contain the hidden food item. Then, the experimenter took one step back, and lowered his or her head.

2.6.5. Foot-point-hands-free

Most dogs have either infrequently or never been exposed to someone pointing with his or her foot. Recent experiments (Lakatos et al., 2009; Udell et al., 2008b), which classify foot pointing as "unfamiliar," nonetheless suggest that dogs correctly follow foot pointing in a repeated-trial design. Here, we explore the question of whether, on the first experimental trial, dogs correctly recognize foot pointing as a goal-directed action. In previous work, foot pointing was carried out with hands free. Humans are most likely to point with their feet when their hands are occupied because they cannot point with their hands. We test here for a possible difference in response to foot pointing with hands free and with hands occupied. This pair of trials represents a test of the rational-action hypothesis noted earlier.

The experimenter pointed with an extended foot in the direction of the container (5–15 cm away) with the hidden food item, maintaining the same ballistic movement of the leg as in the case of our distal hand point (action [i]). In all cases, the leg closer to the target was used. After sustaining the foot point for 1 s, the experimenter brought his or her leg back to resting position, took one step back, and lowered his or her head.

2.6.6. Foot-point-hands-occupied

As a contrast with action (v), and to test for the role of environmental constraints in the perception of rational action, here we test foot-point-hands-occupied. Though it is possible that dogs correctly respond to foot-point-hands-free by tapping into a more general capacity to respond to any limb that protrudes from the torso toward a target goal (Lakatos et al., 2009; Udell et al., 2008b), it is also possible that this capacity only emerges following repeated trials. Further, performance may be ameliorated when foot pointing is used because of environmental constraints on alternative actions.

The experimenter walked over to a small table opposite from the subject, lifted and held a television set with both arms, returned to his or her starting position, and then performed action type (v). Thus, the only difference between action (v) and (vi) was that the latter was carried out with hands occupied.

2.7. Splicing

Once a session was completed, both video files (one file recording the experimenter, the other recording the handler with the dog) were spliced using video editing software (Final Cut Express) to create three new video tracks per subject. The first track was the subject's choice. This track allowed an offline coder to observe the experimenter and dog from the conclusion of a given action type's presentation and lasting up until the dog selected a container (if any selection was made). This method of splicing ensured coders were blind to the location of the hidden food as well as the experimenter's action. The second spliced track was the experimenter's performance. Here, an offline coder observed an experimenter performing both the container baiting and a given action type. As such, this track allowed coders to score the experimenter's presentation blind to the dog's performance or the handler's behaviour. The final track was the handler's behaviour. This track allowed an offline coder to score the handler's behaviour without knowing the dog's choice or the quality of the experimenter's presentation. Coders remained vigilant for any handler behaviour that might have influenced dog choice. For example, the handler track enabled clear observation of failures to centre the dog on each trial, as well as explicit cueing in the form of pointing or verbal praise. Video samples of spliced files can be viewed on the Canine Cognition Lab Web site (URL: http://www.wjh.harvard.edu/~mnkylab/dogMedia.html).

2.8. Coding

Though each trial was coded online by the experimenter, all trials were subsequently coded by at least two individuals offline. In no instance did an individual code both the *subject's choice* and *experimenter's performance* tracks, so as to keep both parties blind as to either the food's location or the dog's selection. To ensure a high level of inter-observer reliability, four offline coders independently scored 40 randomly selected trials from the *subject's choice*, *experimenter's performance*, and *handler's behaviour* tracks. To quantify inter-observer reliability, we employed Fleiss' kappa analyses as given by the equation:

$$\kappa = \frac{(\bar{P} - \bar{P}_e)}{(1 - \bar{P}_e)},$$

Table 1Results of Fleiss' kappa of four offline coders individually scoring 40 trials each of the *subject's choice*, *experimenter's performance*, and *handler's behaviour* video tracks.

Video track	Number of trials with 100% agreement	Fleiss' kappa
Subject's choice	38 out of 40	0.96
Experimenter's performance	36 out of 40	0.87
Handler's behaviour	35 out of 40	0.72

Table 2Cohen's kappa results for two of the original four offline coders following the coding of all data in this study. Coders rated 20 trials each of the *subject's choice*, *experimenter's performance*, and *handler's behaviour* video tracks.

Video track	Number of trials with 100% agreement	Cohen's kappa
Subject's choice	20 out of 20	1.00
Experimenter's performance	19 out of 20	0.77
Handler's behaviour	20 out of 20	1.00

where $1-\bar{P}_e$ represents the level of agreement above chance and $\bar{P}-\bar{P}_e$ relays the actual measure of agreement above chance. Results from the Fleiss' kappa tests of inter-observer reliability are summarized in Table 1. In 38 out of the 40 trials, there was 100% agreement between all four coders (Fleiss' κ = 0.96) on *subject's choice*. The two instances of discrepancy between the coders did not involve *which* container the dog chose, but rather, if the subject's choice was affected by an experimenter error. In 36 out of the 40 trials, there was 100% agreement between all four coders regarding *experimenter's performance* (Fleiss' κ = 0.87). Finally, for the *handler's behaviour*, there was 100% agreement between all four coders on 35 out of 40 trials (Fleiss' κ = 0.72).

Additionally, subsequent to the coding of all trials, two of the coders, JAC and DPC, blind coded and compared scores for 20 trials in each of *subject's choice*, *experimenter's performance*, and *handler's behaviour*. Here, we used Cohen's kappa analyses as provided by the following equation:

$$\kappa = \frac{(Pr(a) - Pr(e))}{(1 - Pr(e))}$$

where Pr(e) is the probability of chance agreement between raters and Pr(a) is the actual observed agreement between raters. The results of these analyses are shown in Table 2. For both the subject's choice and handler's behaviour tracks, there was 100% agreement between both coders for 20 out of 20 trials (subject's choice — Cohen's $\kappa = 1.0$; handler's behaviour — Cohen's $\kappa = 1.0$). Regarding experimenter's performance, the two coders reached 100% agreement for 19 out of 20 trials (Cohen's $\kappa = 0.77$).

3. Results

3.1. Trials eliminated from the analyses

We eliminated 197 of 1038 (18.97%) trials from the analyses due to experimenter or handler error, as defined in the Section 2. We also eliminated from the analyses 76 of 1038 (7.32%) trials where a dog failed to make a choice. A further 209 (20.13%) trials were eliminated for various reasons detailed in Table 3. This left 556 trials available for the analyses (53.56% of the total trials run). Though this highly restrictive coding and selection procedure resulted in significant data loss, it also enabled us to guarantee that all trials included in our analyses were carried out in the same way, with no experimenter or handler biases or errors, and no ambiguity in our coding of responses. Table 3 presents the exact breakdown of the number of eliminated trials per condition.

3.2. Condition 1

Results per condition and action type are detailed in Table 4. Results from Condition 1 showed a significant effect for both the distal hand point (P<0.01, one-tailed binomial test) and step (P=0.033, one-tailed binomial test) conditions, indicating that on the first experimental trial, dogs respond appropriately to both hand pointing and proximity as cues to food location. Furthermore, when step and point were put into competition as cues, dogs selectively used step in the step-then-point condition (P<0.01, two-tailed binomial test), but not in the point-then-step condition. Dogs failed to selectively approach the container associated with foot-point-hands-free or foot-point-hands-occupied.

3.3. Condition 2

Results from Condition 2 were similar to those obtained in Condition 1. Again, both distal hand point (P=0.019, one-tailed binomial test) and step (P<0.001, one-tailed binomial test) were statistically significant. However, neither step-then-point nor point-then-step were statistically significant (see Table 4). Though dogs failed to approach the container associated with the foot-point-hands-free condition (P=0.432, one-tailed binomial test), they selectively approached the container associated with the foot-point-hands-occupied condition (P=0.019, one-tailed binomial test).

3.4. Effects of condition and order

In order to test for possible effects of condition, *Z*-tests of proportionality were applied to the results of each action type over both Conditions 1 and 2. The results are detailed in Table 5. No significant differences were found between Conditions for any of the action types. Given the randomization of action order within

Table 3Breakdown of number of trials discounted for analysis per action type. Included are the number of trials discounted for reasons pertaining to experimenter/handler error, and for the failure of the dog to make a choice in accordance with the criteria outlined in the Section 2.

Reason for discounting	Distal hand point	Step	Step-then-point	Point-then-step	Foot-point- hands-free	Foot-point-hands- occupied	Total
Failure to choose	7	12	15	8	15	19	76
Experimenter error	20	18	20	24	38	22	142
Handler error	8	5	8	6	5	7	39
Both experimenter and handler errors	2	2	4	2	2	4	16
Failure to pass warm-ups	3	3	3	3	3	3	18
Bucket aversion	8	8	8	8	8	8	48
Video errors	3	3	3	3	3	3	18
General aborts	18	18	20	19	25	25	125
Total	69	69	81	73	99	91	482

Table 4Breakdown of results per Condition per action type.

		Condition 1	Condition 1		Condition 2			Pooled		
Action type	n-tailed test	Correct	Total	p-value	Correct	Total	p-value	Correct	Total	p-value
Distal hand point	1	35	52	<0.01	34	52	0.019	69	104	<0.001
Step	1	32	50	0.033	41	54	< 0.001	73	104	< 0.001
Step-then-point	2	34 (step)	48	< 0.01	26 (step)	44	0.289	60 (step)	92	< 0.01
Point-then-step	2	29 (step)	50	0.322	24 (step)	50	0.889	53 (step)	100	0.617
Foot-point-hands-free	1	25	40	0.078	18	34	0.432	43	74	0.1
Foot-point-hands-occupied	1	23	42	0.323	27	40	0.019	50	82	0.03

Condition and the lack of difference between Conditions in which different orders were used, these results suggest that neither order nor prior experience within a session impacted subsequent performance. In order to be certain of this, we also submitted each action type to a one-way analysis of variance with order within the experimental session as the between-groups factor. As detailed in Table 5, no effect of order was found. Based on these results, we pooled the data for Conditions 1 and 2 to carry out additional analyses, detailed below.

3.5. Results pooled across conditions

As expected, dogs were more likely to choose the baited container for distal hand point (P < 0.001, one-tailed binomial test) and step (P < 0.001, one-tailed binomial test). In the step-then-point condition, dogs were more likely to approach the container associated with experimenter location (step) than the container associated with point ($P_{\text{step}} < 0.01$, two-tailed binomial test). This pattern was not observed for the complementary point-then-step condition where dog choice was at chance ($P_{\text{step}} = 0.617$, two-tailed binomial test).

Dogs were more likely to choose the baited container in the foot-point-hands-occupied condition (P=0.03, one-tailed binomial test), but not in the foot-point-hands-free condition (P=0.1, one-tailed binomial test). Though this difference between actions suggests that dogs are sensitive to environmental constraints when assessing human goal-directed behaviour, a Z-Test of proportions failed to reach statistical significance (Z=0.364, P=0.358, one-tailed).

3.6. Olfactory control

Dogs were no more likely to choose the baited container over the non-baited container in our Olfactory Control task (56 out of 98 trials, P = 0.189, two-tailed binomial test), suggesting that in general, dogs were unable to use smell as a guide to food location (Szetei et al., 2003). However, the possibility remained that the successful dogs on this control were using olfaction as a cue. If so, then their performance in particular would be driving the pattern of results obtained. To test this possibility, we compared the performance of the successful dogs on the olfactory control trial (150 out of 251

trials) to the performance of the unsuccessful dogs (114 out of 187 trials), across all action types. The comparison (Z=0.254, P=0.4, one-tailed Z-Test of proportions) showed no effect of success on the olfaction control, allowing us to rule out olfaction as a potential factor in our results.

3.7. Pre-test trial success

Dogs had to choose the baited container twice in succession on pre-test trials before being permitted to proceed to the experimental trials. The majority of dogs(N=67) achieved this criterion on the first two trials ("fast learners"), whereas others (N=37) required additional trials ("slow learners"). Here we contrast the performance of fast versus slow learners (Table 6).

In contrast to fast learners, slow learners failed on every action type except step and step-then-point. In contrast, fast learners succeeded on every action type except step-then-point and point-then-step. The critical difference between slow and fast learners appears, therefore, to be driven by the distinction between proximity (step) on the one hand and all pointing actions (hand and foot) on the other, with fast learners showing significantly greater performance than slow learners on all pointing actions combined (Z=2.39, P=0.017).

3.8. Analyses by dog size and breed

A breakdown of performance per dog breed is shown in Figs. 4–6. The generally small number of dogs tested per breed, however, prohibited analysis over specific breed. As an alternative, dog breeds were classified as small, medium, or large in accordance with the Animal Hospitals USA Web site (see URL: http://www.animalhospitals-usa.com/dogs/dog-breed-characteristics.html), and performance was analysed within these categories. The results are detailed in Table 7. The pattern of performance across action types was broadly consistent across breed size, and no significant difference was found between any of the breed sizes when results were pooled across action types. This might, however, reflect important differences in the single-trial approach given recent reports of physically larger dog breeds outperforming smaller ones in a multi-trial pointing task (Helton and Helton, 2010).

Table 5Tests for effects of condition and order within experimental session (all two-tailed).

cool to check of containing and office manufacture and the check of th									
	Effect across condi	Effect across conditions Effect of position in experimental session							
Action	Condition 1	Condition 2	Z-score	<i>p</i> -value	F-value	<i>p</i> -value			
Distal hand point	35/52	34/52	0.208	0.835	$F_{(1,102)} = 0.18$	0.6723			
Step	32/50	41/54	-1.328	0.184	$F_{(4.99)} = 0.76$	0.5547			
Step-then-point	34/48	26/44	1.181	0.238	$F_{(3.88)} = 1.44$	0.2366			
Point-then-step	29/50	24/50	1.002	0.317	$F_{(3,96)} = 0.73$	0.5366			
Foot-point-hands-free	25/40	18/34	0.813	0.406	$F_{(3,69)} = 0.36$	0.7798			
Foot-point-hands-occupied	23/42	27/40	-1.182	0.237	$F_{(3,78)} = 1.34$	0.2667			

 Table 6

 Breakdown of results dependent upon pretrial performance, contrasting subjects who correctly accessed the food on the first two trials ("fast learners") with those who required multiple trials ("slow learners").

Action type	Fast learners	Binomial te	est	Slow learners	Binomial test		Z-test of proportions	
		n-tailed	p-value		n-tailed	p-value	Z-score	<i>p</i> -value
Distal hand point	50 out of 67	1	<0.001	19 out of 37	1	0.5	2.405	0.016
Step	46 out of 67	1	< 0.01	27 out of 37	1	< 0.01	-0.461	0.645
Step-then-point	36(step) out of 58	2	0.087	24 (step) out of 34	2	0.024	-0.828	0.408
Point-then-step	35(step) out of 68	2	0.904	18 (step) out of 32	2	0.597	-0.447	0.655
Foot-point-hands-free	32 out of 51	1	0.046	11 out of 23	1	0.5	1.204	0.229
Foot-point-hands-occupied	36 out of 53	1	<0.01	14 out of 29	1	0.5	1.744	0.081
Total	235 out of 364	2	<0.001	113 out of 192	2	0.017	1.322	0.186

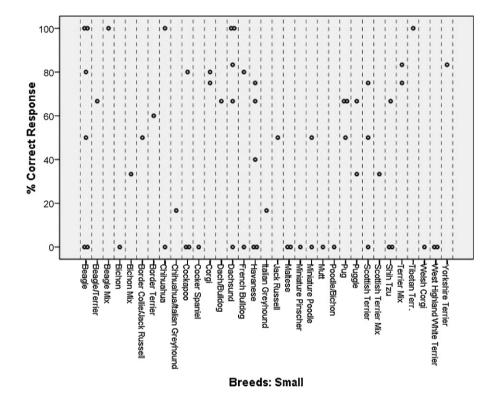


Fig. 4. Scatterplot depicting the performance of each subject classified by breed. Small breeds are illustrated here.

Table 7Performance of dogs classified by breed size. *p*-values are the result of binomial tests.

	n-tailed	Breed size								
		Small			Medium			Large		
		Correct	Of	p-value	Correct	Of	p-value	Correct	Of	<i>p</i> -value
Distal hand point	1	25	36	0.014	17	25	0.054	27	43	0.063
Step	1	25	35	0.008	19	25	0.007	30	44	0.011
Step-then-point	2	22 (step)	32	0.05	12 (step)	20	0.503	26 (step)	40	0.08
Point-then-step	2	19 (step)	35	0.608	11 (step)	22	1	24 (step)	43	0.542
Foot-point-hands-free	1	20	29	0.03	6	16	0.773	18	29	0.132
Foot-point-hands-occupied	1	18	31	0.237	8	17	0.5	24	34	0.012
Pooled	2	114	198	0.039	69	125	0.283	132	233	0.049
Proportion correct			0.576			0.552			0.567	
Chi-squared			0.18			<i>p</i> -value			0.914	

4. Discussion

The primary aim of this work was to explore the kind of experimental experience dogs require to comprehend human social cues (Gácsi et al., 2009a,b; Hare et al., 2002; Lakatos et al., 2009; Miklosi, 2008; Pongracz et al., 2003; Udell et al., 2008a,b). More specifically, and in contrast to previously published work in which subjects

received multiple trials per action type, we sought to explore the nature of action comprehension in dogs following a single experimental presentation. Thus, even though some studies suggest that there is no within-session learning, whereas others suggest some evidence of learning, we were interested in the possibility of successful comprehension of communicative actions based on only a single presentation. A second goal was to explore the dog's capac-

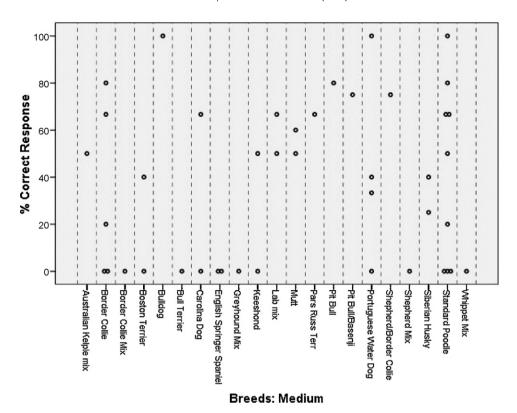


Fig. 5. Scatterplot depicting the performance of each subject classified by breed. Mid-sized breeds are illustrated here.

ity to interpret uncommon or unfamiliar actions, and whether such comprehension is influenced by environmental constraints on action production. In particular, for actions that appear irrational, can changes in the environment transform irrational into rational actions (Gergely and Csibra, 2003; Range et al., 2007)? A third goal was to examine whether dogs perceive some actions as more important than others, based on only a single exposure. Lastly, our aim was to implement a series of coding procedures that we

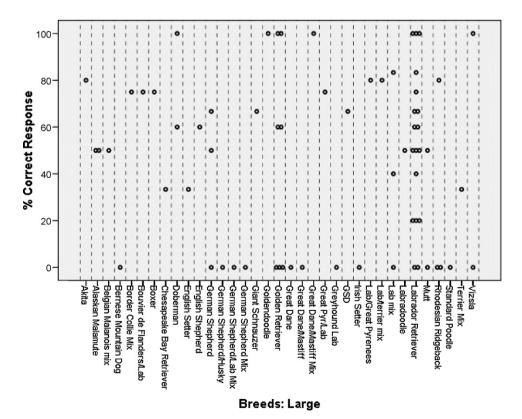


Fig. 6. Scatterplot depicting the performance of each subject classified by breed. Large breeds are illustrated here.

believe are critical with respect to eliminating experimental errors and biases. We discuss these points in turn.

Numerous studies have demonstrated that dogs and wolves successfully locate hidden food following the presentation of a pointing gesture with arm and hand (see Introduction for references). Because subjects in these studies have, to some extent, prior experience with such pointing in the rearing environment, the question of interest is whether they can generalize to unfamiliar people, in unfamiliar environments, and under highly controlled circumstances. In all of the published work on this problem to date, success in following pointing is based on the proportion of successful trials out of some 10-20 opportunities. Though some studies have explored differences in performance across a session (contrasting the first to the second half), with mixed results concerning within-session learning, no study has explored first-trial effects, presumably because the available sample sizes are relatively small for this type of analysis, often less than 20. In Conditions 1 and 2, both individually and combined, dogs successfully approached the container associated with the experimenter's ephemeral, distal hand-pointing gesture. The majority of dogs, regardless of size and breed, performed in this way, although fast learners tended to outperform slow learners on not only distal hand point, but on foot point as well. Why this difference emerged is presently unclear, but it is discussed further below.

Our single-trial method also generated statistically significant effects for step, a proximity-based cue. This pattern was observed in both Conditions 1 and 2, and for the conditions combined; and it also was consistent across dog size and pre-trial performance. As such, proximity appears to be a highly robust and significant factor in dogs' comprehension of human actions.

To explore the potential relationship between cues and the possibility that some are more important than others, we presented subjects with step and point within a trial, manipulating the order in which each was presented. Though there was some indication in Condition 1 that step was more important than point, this effect was not replicated in Condition 2, and was unrelated to the slow-fast learner distinction, dog size, or breed. However, when we pooled across conditions, we found an asymmetry in the relative importance of these two cues. In particular, when step was presented first within a trial, so that the distal-pointing gesture was made from behind one of the containers, dogs chose in accordance with the step cue. However, when point was presented first within a trial, so that the pointing gesture was made from the midline, prior to the experimenter's step towards a container, dogs showed no preference for either cue. These results suggest both that temporal order plays a role in dogs' action perception, and furthermore, that the perception of distal hand point as a communicative cue is sensitive to the distance from the target object. These results are, to some extent, different from studies suggesting that dogs preferentially attend to point when an experimenter stands in front of one container and then points to the other (Soproni et al., 2002). In these experiments, the step is not considered an action, and there has been no attempt to manipulate the order of step and point. Further, dogs' success on this condition comes from multiple trials where the response to the point cue is reinforced. Thus, the pattern presented here differs from previous work. We hypothesize that the primary mediating factor is the difference between single- and multiple-trial presentations.

The final set of action types focused on current debates about the nature of action comprehension in humans and nonhuman animals. In one view, action comprehension requires the capacity to produce the target action (Rizzolatti et al., 2001). If this perspective is correct, then organisms lacking the capacity to produce a particular action should not be able to comprehend it when performed by an agent that can. Several studies raise problems for this perspective, including experiments with animals that lack the capacity

to reproduce a human action (e.g., foot pointing, throwing), but nonetheless show evidence of action comprehension (Lakatos et al., 2009; Wood et al., 2007; Udell et al., 2008b), as well as experiments with human infants who comprehend the actions (and goals) of inanimate geometric shapes on a computer monitor (Csibra, 2008; Csibra et al., 1999). These results invite a second perspective in which action comprehension operates by means of a teleological stance (Gergely and Csibra, 2003) that infers goals based on environmental constraints and details of object motion (e.g., the capacity for self-propelled movement).

Results from the present experiments suggest that, overall, dogs do not spontaneously recognize an ephemeral, distal foot point as goal-directed, at least when the experimenter's hands are free. These results stand in contrast with those presented by both Udell et al. (2008b) as well as Lakatos et al. (2009), and raise the possibility that understanding this gesture requires learning over repeated presentations. That is, despite the fact that at least some dogs may have had some experience seeing their owner's foot point in their home environment, this level or frequency of experience was insufficient to enable generalization to our experimental conditions. Of interest, however, is the observation that a significant number of dogs recognized foot point with hands occupied as goal-directed. Thus, environmental constraints appear to transform dogs' comprehension of foot point into a goal-directed action without previous experimental reinforcement of this trial type.

There is a potential behaviorist interpretation of these results: because we lack information on the history of reinforcement of dogs in all such studies, perhaps dogs typically experience foot pointing with hands occupied, and this is why they were more successful in this condition. We believe there are three reasons to reject this account. First, and as noted above, two prior studies showed evidence of following foot pointing with hands-free. Thus, if anything dogs seem to respond appropriately to foot pointing in the less commonly reinforced condition, if this is in fact what occurs most commonly at home; this performance was, however, in the context of repeated trials. Second, we contrasted dogs' performance on foot pointing with hands free versus hands occupied based on a singletrial design, and with order counter-balanced. Not only did we find success on hands occupied and not on hands free, but there was no order effect. One might have expected based on an association account that having succeeded first on foot pointing-hands occupied, that dogs' performance would improve on the subsequent trial with hands free. They did not. Third, we showed a significant effect of pre-test trial success, that is, fast learners were largely responsible for the significant performance on foot-pointing with hands occupied. Though we can't rule out the possibility that the fast learners, in contrast to the slow learners, were the ones who experienced foot pointing with hands occupied at home, this seems

We conclude, therefore, that based on a single, unfamiliar or uncommon action, our results converge with those presented by Range et al. (2007) using a repeated trial, imitation task. Specifically, dogs appear to use environmental constraints to infer a human actor's goals, and thus, to distinguish between rational and irrational actions, in line with the theoretical perspective developed by Gergely and Csibra (2003). It is, nonetheless, important to pursue this line of research – exploring a broader range of actions and environmental constraints – in tasks requiring imitation as well as non-imitative goal-directed action.

Summarizing, a single experimental presentation was sufficient to motivate correct, goal-directed behaviour following three communicative actions: hand point, step, and foot point with hands occupied. Despite identical presentation methods, a single trial was insufficient to motivate correct, goal-directed approach for step-then-point, point-then-step, and foot point with hands free. As demonstrated in other studies, we presume that the multiple-

trial presentation method would yield correct approach behaviour for these actions as well. But that, of course, is our point: some actions are readily recognized as goal-directed, communicative actions following a single presentation, whereas others are not; the single-trial approach distinguishes between actions that are readily perceived as goal-directed and those which can be learned through reinforced experience. To be clear, these conclusions are restricted to the particular details of our testing procedures, a point that links to our final comment concerning methods.

Experiments on canine cognition and behaviour often videotape each trial, with the camera focused on the subject; this is also the case for the majority of studies of captive primates and other animals. We are unaware of any canine study in which not only the subject, but the experimenter and handler, are also filmed, followed by blind coding of each of these three individuals. Based on our results, we believe this is a critical procedural detail, and one that we would urge others to take seriously. Though all experimenters went through a rigorous training session before running the experiments, and although all handlers were provided with clear instructions, our offline coding nonetheless detected errors in presentation and unintentional biases. For example, handlers often released their dogs too early or cued their dog by pushing it toward one container. Experimenters also made errors in performing the actions as described, including unintentional presentation of additional cues (e.g., eye gaze, head orientation), inaccurate gestures, and improper setup of the containers. It is certainly more time consuming to videotape and code the experimenter, handler, and dog. The payoff however, is a data set that is clean with respect to errors and unintentional cueing. We believe that this point applies with equal force to all studies of captive animals involving human experimenters, including those that the first author has carried out with nonhuman primates (e.g. Hauser et al., 2003, 1999).

In conclusion, our results suggest that a single-trial approach with a large sample of dogs generates interpretable data, and in particular, shows that dogs can use certain human cues to find hidden food following only a single experimental trial. Specifically, dogs readily located the baited food following a single presentation of the distal hand point, step, and foot point with hands occupied. Dogs did not, however, locate the hidden food following the foot point with hands free cue, suggesting that previous success with this action may have been driven by a reinforcement history over repeated presentations, perhaps within a few trials. The difference in performance between foot point hands free and hands occupied suggests that dogs are sensitive to environmental constraints, and use such information to distinguish rational from irrational action. In addition, when different cues were put into competition, we found no evidence that dogs perceived a communicative point as more important than step, a proximity cue. This suggests that distal hand point and step are equally communicative as goal-directed actions, at least within the context that we tested these actions. Lastly, we found that our warm-up criteria (i.e., lifting the lid to the container) allowed us to distinguish between slow and fast learners, with the latter out-performing the former on the critical test trials. Such variation is not surprising, but may be useful in future research aimed at understanding some of the causes of individual differences among dogs.

Acknowledgments

For help in running and coding these experiments, we thank Natalie Shelton, Alexandra Protopopova, Caroline Pires, Brittany Monteiro, Dana Bruck-Segal, Kelly Dunagan, Puja Singh, Marc Aidinoff, Kelley Humbert, Gracia Angulo, Lys Stevens, Erin Washington, and Alex Kell. Funding for this project was provided by an NSF-Human Social Decision grant to MDH. These

studies were approved by Harvard's Animal Care and Use Committee.

References

- Behne, T., Carpenter, M., Tomasello, M., 2005. One-year-olds comprehend the communicative intentions behind gestures in a hiding game. Developmental science 8. 492.
- Bradbury, J.W., Vehrencamp, S.L., 1998. Principles of Animal Communication. Blackwell, Oxford.
- Call, J., Agnetta, B., Tomasello, M., 2000. Cues that chimpanzees do and do not use to find hidden objects. Animal Cognition 3, 23–34.
- Call, J., Tomasello, M., 1994. Production and comprehension of referential pointing by orangutans. Journal of Comparative Psychology 108, 307–317.
- Csibra, G., 2008. Action mirroring and action understanding: an alternative account. In: Haggard, P., Rosetti, Y., Kawato, M. (Eds.), Sensorimotor Foundations of Higher Cognition: Attention and Performance, XXII. Oxford University Press, Oxford.
- Csibra, G., Gergely, G., Biro, S., Koos, D., Brockbank, M., 1999. Goal attribution witouth agency cues: the perception of "pure reason" in infancy. Cognition 72, 237–267.
- Gácsi, M., Gyoöri, B., Virányi, Z., Kubinyi, E., Range, F., Belényi, B., Miklósi, Á., 2009a. Explaining dog-wolf differences in utilizing human pointing gestures: selection for synergistic shifts in the development of some social skills. PLoS ONE 4, e6584.
- Gácsi, M., Kara, E., Belényi, B., Topál, J., Miklósi, Á., 2009b. The effect of development and individual differences in pointing comprehension of dogs. Animal Cognition 12, 471–479.
- Gergely, G., Csibra, G., 2003. Teleological reasoning in infancy: the naive theory of rational action. Trends in Cognitive Science 7, 287–292.
- Hare, B., Brown, M., Williamson, C., Tomasello, M., 2002. The domestication of social cognition in dogs. Science 298, 1636.
- Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R.W., Trut, L., 2005. Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. Current Biology 16, 226–230.
- Hare, B., Rosati, A., Kaminski, J., Brauer, J., Call, J., Tomasello, M., 2010. The domestication hypothesis for dogs' skills with human communication: a response to Udell et al. (2008) and Wynne et al. (2008). Animal Behaviour 79, e1–e6.
- Hauser, M.D., 1996. The Evolution of Communication. MIT Press, Cambridge.
- Hauser, M.D., Chen, K., Chen, F., Chuang, E., 2003. Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who give food back. Proceedings of the Royal Society 270, 2363–2370.
- Hauser, M.D., Glynn, D.D., Wood, J.N., 2007. Rhesus monkeys correctly read the goal-relevant gestures of a human agent. Proceedings of the Royal Society 274, 1913–1918.
- Hauser, M.D., Kralik, J., Botto-Mahan, C., 1999. Problem solving and functional design features: experiments with cotton-top tamarins (Saguinus oedipus). Animal Behaviour 57, 565–582.
- Helton, W.S., Helton, N.D., 2010. Physical size matters in the domestic dog's (Canis lupus familiaris) ability to use human pointing cues. Behavioural Processes 85, 77–79
- Krebs, J.R., Dawkins, R., 1984. Animal signals: mind-reading and manipulation. In: Krebs, J.R., Davies, N.B. (Eds.), Behavioural Ecology. Sinauer Associates Inc., Sunderland. MA.
- Lakatos, G., Soproni, K., Dóka, A., Miklósi, Á., 2009. A comparative approach to dogs' (Canis familiaris) and human infants' comprehension of various forms of pointing gestures. Animal Cognition 12, 621–631.
- Leavens, D.A., Hopkins, W.D., Bard, K.A., 1998. Indexical and referential pointing in chimpanzees. Journal of Comparative Psychology 110, 346–353.
- Liebal, K., Behne, T., Carpenter, M., Tomasello, M., 2009. Infants use shared experience to interpret pointing gestures. Developmental science 12, 264–271.
- Miklosi, A., 2008. Dog Behavior, Evolution & Cognition. Oxford University Press, New York.
- Miklosi, A., Soproni, K., 2006. A comparative analysis of animals' understanding of the human pointing gesture. Animal Cognition 9, 81–93.
- Owings, D.H., Morton, E.S., 1998. Animal Vocal Communication: A New Approach.
 Cambridge University Press, Cambridge.
- Pongracz, P., Miklosi, A., Doka, A., Csanyi, V. 2003. Successful Application of Video-Projected Human Images for Signalling to Dogs. Ethology.
- Range, F., Heucke, S., Gruber, C., Konz, A., 2009. The effect of ostensive cues on dogs' performance in a manipulative social learning task. Applied Animal Behaviour Science 120, 170–178.
- Range, F., Viranyi, Z., Huber, L., 2007. Selective imitation in domestic dogs. Current Biology 17, 868–872.
- Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. Nature Review Neuroscience 2, 661–670.
- Smith, B.P., Litchfield, C.A., 2010. Dingoes (Canis dingo) can use human social cues to locate hidden food. Animal Cognition 13 (2), 367–376.
- Soproni, K., Miklosi, A., Topal, J., Csanyi, V., 2001. Comprehension of human communicative signs in pet dogs (*Canis familiaris*). Journal of Comparative Psychology 115, 122–126.
- Soproni, K., Miklosi, A., Topal, J., Csanyi, V., 2002. Dogs' (Canis familiaris) responsiveness to human pointing gestures. Journal of Comparative Psychology 116, 27–34.
- Szetei, V., Miklósi, Á., Topal, J., Csanyi, V., 2003. When dogs seem to lose their nose: an investigation on the use of visual and olfactory cues in communica-

- tive context between dog and owner. Applied Animal Behaviour Science 83, 141–152
- Tomasello, M., Carpenter, M., Call, J., Behne, T., Moll, H., 2005. Understanding and sharing intentions: the origins of cultural cognition. Behavioral and Brain Research 28, 675–691.
- Udell, M.A.R., Dorey, N.R., Wynne, C.D.L., 2008a. Wolves outperform dogs in following human social cues. Animal Behaviour 76, 1767–1773.
- Udell, M.A.R., Giglio, R., Wynne, C.D.L., 2008b. Domestic dogs (Canis familiaris) use human gestures but not nonhuman tokens to find hidden food. Journal of Comparative Psychology 122, 84–93.
- Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D., Miklósi, Á., 2008. Comprehension of human pointing gestures in young humanreared wolves (Canis lupus) and dogs (Canis familiaris). Animal Cognition 11, 373–387.
- Wood, J.N., Glynn, D.D., Hauser, M.D., 2007. The uniquely human capacity to throw evolved from a non-throwing primate: an evolutionary dissociation between action and perception. Biology Letters 3, 360–364.