# Making Inferences About the Location of Hidden Food: Social Dog, Causal Ape

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Domestic dogs (*Canis familiaris*) and great apes from the genus *Pan* were tested on a series of object choice tasks. In each task, the location of hidden food was indicated for subjects by some kind of communicative, behavioral, or physical cue. On the basis of differences in the ecologies of these 2 genera, as well as on previous research, the authors hypothesized that dogs should be especially skillful in using human communicative cues such as the pointing gesture, whereas apes should be especially skillful in using physical, causal cues such as food in a cup making noise when it is shaken. The overall pattern of performance by the 2 genera strongly supported this social-dog, causal-ape hypothesis. This result is discussed in terms of apes' adaptations for complex, extractive foraging and dogs' adaptations, during the domestication process, for cooperative communication with humans.

Much of cognition is concerned with going beyond the information given by making inferences. Different species are adapted for making inferences of different kinds, using different perceptually based cues, in different domains of activity. For example, recent research has demonstrated that great apes are skillful at making inferences about the location of hidden food on the basis of what may be called very generally *causality* (principles of how the physical world works). For example, Call (2004) presented apes with two opaque cups, only one of which contained food. Then, in one condition, he shook the cup that contained the food so that it produced an audible noise—a cue that all ape species used reliably to find the food. In another condition, he shook the empty cup so that no noise was produced, in which case apes chose the other cup reliably, apparently reasoning that because this cup is empty the other must have the food. Apes thus seem to understand something of the causal connection between objects, movements, and the noises that object movements can produce in different circumstances, and they use this understanding to locate hidden food (Call, 2004).

On the other hand, using this same basic experimental set-up—what has come to be called the *object choice task*—apes perform poorly when humans provide them with communicative cues such as pointing, gazing, touching, or placing a marker on the hidden food location (Call, Hare, & Tomasello, 1998; Call & Tomasello, 1998; Itakura, Agnetta, Hare, & Tomasello, 1999; Povinelli, Reaux, Bierschwale, Allain, & Simon, 1997; Tomasello, Call, & Gluckman, 1997). There are some task variations and some char-

acteristics of individual apes that improve their performance somewhat (Barth, Reaux, & Povinelli, 2005; Itakura & Tanaka, 1998), but overall the majority of great ape individuals in the majority of task variations perform at chance levels in the communication version of the object choice task (see Call & Tomasello, 2005, for a review). It is noteworthy for purposes of interpretation that apes reliably follow human gaze, including around barriers (Bräuer, Call, & Tomasello, 2005; Tomasello, Hare, & Agnetta, 1999), and so their difficulties in this task do not emanate from an inability to follow the directionality of the cue but rather from a seeming inability to make inferences about the communicative meaning of these directional cues—as indicating the location of hidden food—in this task setting.

Perhaps surprisingly, when this communicative task is changed slightly—so as to eliminate the specifically communicative component—apes do much better. Hare and Tomasello (2004) tested chimpanzees in an object choice task in which they simply reached effortfully (and unsuccessfully) toward the bucket containing the hidden food. Apes were much better at inferring the location of the hidden food from this straightforward behavioral cue than they were from a very comparable pointing cue (similar arm movement toward hidden food, but with pointing, no visible effort, and gaze alternation; Hare & Tomasello, 2004). One interpretation of this result is that reading behavioral cues depends on an understanding of the goal-directed actions of others, and chimpanzees are skillful at this (Call, Hare, Carpenter, & Tomasello, 2004; Call & Tomasello, 1998; Uller, 2004), but this is not the same thing as reading communicative cues in which one individual attempts to direct the others' attention to some third entity in order to provide them with needed information.

There is one species that is especially skillful at the communication version of the object choice task, and this is the domestic dog. Dogs are skillful at using a variety of cues, including pointing, looking, and bowing toward (Hare & Tomasello, 1999; Miklosi, Polgardi, Topal, & Csanyi, 1998; Soproni, Miklosi, Topal, & Csanyi, 2001). Their performance cannot be explained by the use of olfactory cues (various control conditions ruled these out), by learning during the experiment (they were skillful from the very

first trials), or by familiarity or past learning (they were skillful in many novel variations such as when the experimenter was standing closer to one cup and pointing to the other one, or when only a static cue was given; Hare, Call, & Tomasello, 1998). Notably, wolves (*Canis lupus*), as dogs' closest living relatives, are not skillful in this task. Moreover, very young puppies with almost no experience with humans are skillful (Hare, Brown, Williamson, & Tomasello, 2002; Miklosi, Kubinyi, Gacsi, Viranyi, & Csanyi, 2003). These facts suggest that dogs' ability to read human communicative cues is independent of their individual history, and it is very likely that this ability evolved in the context of the domestication process.

With regard to inferences based on causal cues, we have no reason to expect that dogs should be especially skillful relative to other mammals or primates. It is true that dogs can solve invisible displacement problems in an object permanence task. However, they have difficulties in encoding a complex sequence of events and representing a position change that is signaled but not directly perceived (Gagnon & Dore, 1993) and fail to show understanding of means–end connections (Osthaus, Lea, & Slater, 2005). Overall, very little is known about dogs' ability to make causal inferences, nor is much known about dogs' ability to understand behavioral cues, such as someone reaching or trying for something.

This pattern of findings points to a very interesting possible difference between the cognitive skills of great apes and those of domestic dogs based on differences in the ecological contexts in which these species evolved. That is, we might propose that great apes have evolved especially powerful inferential skills to solve problems in the physical world associated with finding food given that (a) they forage mostly for patchy food resources such as fruits and new leaves that mature in different times and places and that require complex spatial and memory skills (Milton, 1988) and (b) they often engage in so-called extractive foraging in which they must extract nonperceptible food items from hidden locations inside bark, husks/shells, underground nests, and so forth (Parker & Gibson, 1990). We might thus hypothesize that great apes have evolved cognitive skills for using a variety of visual and auditory cues to infer the location of food that is not currently perceptible. Apes may also have evolved inferential skills to solve problems in their social world, such as predicting what others will do next on the basis of their ability to determine the goals that others are pursuing in the context of a highly complex social field (Kummer, Dasser, & Hoyningen-Huene, 1990). However, they may not have evolved skills for understanding the special kinds of triadic cooperative communicative cues that humans use, for example, pointing or other gestures used to direct others to outside entities such as food in a cooperative manner. Some studies have shown that enculturated apes produced and understood pointing (e.g., Call & Tomasello, 1994; Hayes & Hayes, 1952), and it is also true that chimpanzees can lead others to food places under specific circumstances (Menzel, 1988). With specific reference to the object choice task, however, our knowledge of apes and other undomesticated species, however, suggests that they hardly ever experience a natural situation in which one individual cooperatively indicates for another individual the location of monopolizable food.

In contrast, domestic dogs very likely have evolved special cognitive skills for operating in human society. For example, it is very natural for them that humans inform them cooperatively about the location of food. Moreover, dogs work with humans in such activities as herding and hunting. In all of these social interactions, communicating effectively with humans should be highly adaptive, including communicating triadically and cooperatively by, for example, knowing that there is something relevant to be found in the direction of a human gesture such as pointing. On the other hand, there is no reason that dogs should have developed special cognitive skills for dealing with causal relations during domestication, and indeed it might even be that they have lost some of their skills for understanding causality as humans solve many causal problems for them (Frank, 1980).

All of this suggests the possibility of some specific differences between great apes and domestic dogs in the ability to make inferences from cues of different types. In the current study, we systematically compared which kinds of cues each genera was and was not able to use effectively to infer the location of hidden food in a series of object choice tasks. We presented three kinds of cues: communicative, behavioral, and causal. On the basis of previous research, we expected dogs to be especially skillful at using communicative cues such as human pointing and apes to be especially skillful at using causal cues (both visual and auditory) to infer the location of hidden food. These two predictions represent the core of the social-dog, causal-ape hypothesis (with the two genera's performance on behavioral cues not being strongly predicted). As causal conditions usually have a social dimension (i.e., the human touching the cup that she is shaking), we also included so-called ghost conditions in which subjects did not see the humans manipulating the cups. We expected that dogs would be more influenced by this social dimension than would apes. Nevertheless, it was unclear whether dogs would be more skillful than apes at using behavioral cues such as a human reaching toward a container.

Because the performance of different species in an object choice task partly depends on the experimental setup (Miklosi & Soproni, in press), we used exactly the same methods for the dogs and apes whenever possible. Note that the object choice task methodology has been used successfully with both dogs and apes in past research.

## Method

In this study, we systematically compared domestic dogs (*Canis familiaris*) and two species from the genus Pan (chimpanzees, *Pan troglodytes*, and bonobos, *Pan paniscus*) in their ability to use a variety of different types of cues—causal, behavioral, and communicative—to infer the location of hidden food in a series of object choice tasks. Because of the low number of available bonobos and given that they showed similar patterns to those of chimpanzees in object-choice tasks (Call, 2004), we analyzed the two species together. For practical reasons, the studies of the apes and the dogs were conducted separately, with three different experimenters and in different physical settings. However, we used exactly the same methods whenever possible, with deviations from this ideal indicated in the appropriate places below.

### Subjects

A total of 21 dogs (9 males and 12 females) of various breeds and ages (range = 1 to 11 years old) were tested (see Table 1). All subjects had been living as pets with their owners all of their lives and had received the normal obedience training typical for domestic dogs. The dog owners (except for one) were not present during the test and were not informed

Table 1
*Name, Breed, Gender, and Age of the Dog Subjects Included in the Study*

| Name | Breed | Gender | Age (years) |
|---|---|---|---|
| Alischa | Mongrel (Rottweiler × Doberman) | F | 5 |
| Andi | Dackel | M | 10 |
| Asaro | Mongrel | M | 6 |
| Aslan | Mongrel (Labrador × Münsterlander) | M[a] | 6 |
| Auguste | Mongrel (German Shepherd) | F | 2 |
| Ben | Mongrel (Briard) | M[a] | 5 |
| Ben2 | Labrador Retriever | M | 1 |
| Bora | Labrador Retriever | F | 1 |
| Floyd | Siberian Husky | M | 6 |
| Higgins | Mongrel (Border Collie × Boxer) | M | 3 |
| Jonas | Mongrel | M | 9 |
| Lea | Mongrel (German Shepherd × Rottweiler) | F | 2 |
| Linda | Mongrel | F | 11 |
| Lotte | Mongrel (Labrador Retriever) | F | 1 |
| Lowis | German Shepherd | F | 1 |
| Luna | White Shepherd | F | 4 |
| Mora | Mongrel (German shepherd × Mongrel Mix) | F | 5 |
| Pauline | Portuguese Waterdog | F | 2 |
| Rex | Mongrel (German Shepherd × Collie) | M[a] | 4 |
| Ronja | Mongrel (German Shepherd × Sheltie) | F | 6 |
| Sissi | German Shepherd | F[a] | 4 |

[a] Neutered.

about the design of the experiments before the test started. All dogs were tested individually by a female experimenter who did not change during the experiment.

A total of 16 apes from the genus *Pan* (4 bonobos and 12 chimpanzees) of various ages (range = 6 to 27 years old) were tested (see Table 2). All subjects lived in groups with conspecifics in the Wolfgang Köhler Primate Research Center in the Leipzig Zoo. They lived in stable groups consisting of 18 (for the chimpanzees) and 4 (for the bonobos) individuals and with access to an outdoor area (2,300–4,000 m²) and an indoor area (256–430 m²), both of which contained natural vegetation, climbing structures, trees, water streams, and various other natural features. In addition, various enrichment facilities were available in the indoor and outdoor habitats. At night the animals slept in a series of sleeping rooms (36–47 m²) with wood wool available for them to built nests. The subjects were fed various fruits, vegetables, and cereals several times per day. Subjects were tested individually in familiar testing rooms (16 m²) with a familiar experimenter. The subjects were never food deprived, and water was available at all times throughout the tests. Subjects could choose to stop participating at any time.

Table 2
*Name, Species, Gender, and Age of the Ape Subjects Included in the Study*

| Subject | Species | Gender | Age (years) |
|---|---|---|---|
| Corry | Chimpanzee | F | 26 |
| Dorien | Chimpanzee | F | 22 |
| Fifi | Chimpanzee | F | 9 |
| Fraukje | Chimpanzee | F | 26 |
| Frodo | Chimpanzee | M | 9 |
| Jahaga | Chimpanzee | F | 9 |
| Natascha | Chimpanzee | F | 22 |
| Riet | Chimpanzee | F | 25 |
| Robert | Chimpanzee | M | 27 |
| Sandra | Chimpanzee | F[a] | 9 |
| Gertruida | Chimpanzee | F | 9 |
| Ulla | Chimpanzee | F | 25 |
| Joey | Bonobo | M | 20 |
| Kuno | Bonobo | M | 6 |
| Limbuko | Bonobo | M | 7 |
| Ulindi | Bonobo | F | 9 |

[a] Neutered.

### Materials

We used two different pairs of "container" objects (opaque plastic cups: 8 cm × 12 cm with lids; wooden boards: 8 cm × 25 cm) to conceal the food from the subjects. During each trial, a human experimenter (E) placed a pair of these objects (either cups or boards) on each side of a platform that was located in front of her. A large opaque board (70 cm × 40 cm) served to occlude the baiting process from the subject. The sessions with the dogs took place in a small room with the dimensions 3.65 m × 2.80 m. E sat on the floor (Part 1) or on a small platform with wheels (part 2). The two objects stood on a wooden board (180 cm × 30 cm) on the floor separated by 1.3 m. When the trial started, the dog sat on a marked place 1.7 m away from E and was held on a leash by a second person. In the causal ghost conditions, the dog waited outside with the second person until the baiting was finished and entered the room when the trial started. Small pieces of dry dog food were used as rewards.

The sessions with the apes took place in a caged testing room (2.5 m × 2.2 m). The two objects were placed on a wooden platform (85 cm × 32 cm) located just outside the subjects' enclosure flushed against and perpendicular to a Plexiglas testing panel. At the bottom of the Plexiglas panel were two holes forming a straight line separated by 52 cm so that apes could indicate their choice of cup. At the time of choice, the objects were aligned with the outside holes, approximately 50 cm apart. When the trial started, the ape stood or sat in front of the experimenter behind the Plexiglas panel in its cage (except for the causal ghost condition where it was in another cage and entered the testing cage as soon as the trial started). Grapes and small pieces of banana were used as rewards.

## Design

We used a within-subjects design. The conditions (described below) were presented in the four different Sessions A, B, C and D.[1] Subjects received sessions in one of the following four orders: ABCD, ABDC, BACD, or BADC. The order of the conditions within a session was always the same (the order in which they are mentioned in the footnote), but subjects started with different conditions. That means that, for example, one subject started Session A with "point," and went on with "reach–first version," "shape," "noise–ghost," and so forth, whereas another subject started with "reach–first version," and went on with "shape," "noise–ghost," and so forth. Subjects received 6 trials per cue condition in each session. Moreover, there were 2 or 1 no-cue control trials in every session (2 trials in Sessions A and B, and 1 trial in Sessions C and D, for a total of 6 trials). Therefore, each session consisted of either 25 or 26 trials (4 cue conditions × 6 trials + 2 or 1 no-cue control trials).

The location of the food was counterbalanced left and right, with the stipulation that it was not hidden in the same location in more than two consecutive trials. After half of each session, there was a break of at least 30 min for the dogs. Dogs and apes usually received one session per day, but if an ape was not motivated, the session was continued the next day. One group of dogs (11 dogs) was tested by experimenter JK and the other group (10 dogs) was tested by experimenter JB, whereas the apes were all tested by experimenter JR. All trials were videotaped.

## Procedure

Each of the two test parts for both genera began with a short pretest (to help the subject become familiar with the testing situation) in which E placed food under one cup in full view of the subject, and the subject then chose one cup. The pretest ended after the subject chose the correct cup on four consecutive trials.

In test trials, E showed a piece of food to the subject, lowered it behind the occluder, which was placed between the subject and the objects (except for the condition "shape–block"), and concealed the food in one of the containers. E also sham baited the other container, removed the occluder, and displaced the containers simultaneously to their predetermined locations to the left and right of the subject. Depending on the experimental condition, E then gave a cue (duration = 4 s) to indicate the location of the food. After the 4 s had elapsed, E turned toward the subject and looked straight ahead (except for the "point–continuous" and "look–continuous" conditions, in which E continued giving the cue until the subject made a choice). In the case of the apes, E then moved the table so that the containers stood immediately in front of the left and right holes in the Plexiglas panel. For the dogs, the second experimenter released the subject. Subjects then made their choice. If the subject was correct, E turned over the container and gave the food to the subject. If incorrect, the subject was shown the empty container, and the food was taken from under the correct container and discarded. Subsequently, a new trial started.

There were 14 experimental conditions (each representing a different cue) and one control condition in which no cue was given. The experimental conditions were grouped into one of the following three types of cues: communicative, behavioral, and causal.

## Communicative

*Point.* E sat in front of the two cups and pointed to the correct cup with the extended index finger of the ipsilateral hand, alternating her gaze between the subject and the cup four times before the choice was presented. The arm was more stretched, and the distance between the finger and the cup was larger for dogs than for apes.

*Point–continuous.* The procedure in this condition was the same as in the "point" condition, but the cue was given continuously until the subject made a choice.

*Look.* E sat in front of the two cups/boards and alternated her gaze between the subject and the correct cup/board four times before the choice was presented.

*Look–continuous.* The procedure was the same as in the "look," condition but the cue was given continuously until the subject made a choice.

## Behavioral

*Try-to-open.* E grasped the correct cup with both hands and acted as if she wanted to open it by removing the lid while looking at it. Throughout the trial, the cup stayed in the same place.

*Reach.* E tried unsuccessfully to reach the correct cup, which was out of reach because the wheeled stool on which she sat "accidentally" rolled away from the cups so that they were out of reach. E extended the ipsilateral arm while looking only at the cup.

## Causal: Auditory Cues

*Noise.* E shook the baited cup four times so that the food (and a small stone that enhanced the sound) made a noise. E looked only at the cup and replaced it after shaking.

*Noise–empty.* This procedure was the same as in the noise condition except that E acted on the unbaited cup.

*Noise–ghost.* This procedure was the same as in the noise condition except that E left the cup untouched. Instead, the cup was shaken by a second experimenter by pulling on a fishing line connected to the cup. During baiting, the subject was outside the room to ensure that he or she did not see the experimenter touch the cups at any time.

*Noise–arbitrary control.* The baited cup contained (besides the food) a cellular phone that rang three times after the baiting had been completed. E gave no additional cues.

## Causal: Visual Cues

*Shape.* E hid the food under one of two small boards so that it became inclined. E manipulated the other board in a similar way (sham baiting it), but it remained flat on the platform.

*Shape–ghost.* The procedure in this condition was the same as in the shape condition, but in this case E did not touch the boards in sight of the subject because E placed the food under one of the small boards while the subject was outside of the testing room.

*Shape–smell control.* Both boards had the same inclination, but food was only under one of them. This condition assessed whether the subjects could perceive the location of the food under the inclined board using some other cue such as odor.

*Shape–block control.* E placed the food in plain view on her knee not under any of the boards and proceeded to place a wooden block under one of the two boards so that it became slanted. E manipulated the other board in a similar way but placed it flat on the platform. The subject was rewarded with the food for choosing the slanted board. This condition assessed whether the subjects were simply attracted to slanted boards. Note that although none of the boards concealed any food, the subjects were rewarded for choosing the slanted board.

## Control

*No-cue control.* E turned toward the subject and looked straight down or up for 4 s without giving any cue at all.

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[1] Session A = "point"/"reach–first version"*/"shape"/"noise–ghost"/"no-cue control"; Session B = "look"/"try-to-open"/"noise"/"shape–ghost"/"no-cue control"; Session C = "point–continuous"/"reach"/"shape–smell"/"noise–arbitrary control"/"no-cue control"; Session D = "look–continuous"/"try-to-open"/"noise–empty"/"shape–block"/"no-cue control."

## Scoring and Reliability

We scored which container the subject chose from the videotapes. Subjects of the two genera indicated their choice in different ways depending on their natural tendency. Dogs chose by touching the container with the muzzle (or moving the muzzle to within 10 cm of the cup/board), while apes indicated their choice by poking a finger through the Plexiglas hole in front of the chosen container. One person scored all trials of the apes (JR), and another person scored all trials of the dogs (JB). A third independent observer, who did not know the purpose of the studies, scored a randomly selected sample of 20% and 23% of trials for dogs and apes, respectively, to assess interobserver reliability. Reliability was excellent for both dogs (Cohen's $\kappa = .95$, $N = 430$) and apes (Cohen's $\kappa = .97$, $N = 421$).

## Data Analysis

Because the studies with the two genera were done separately and our initial overall analyses had shown important interaction effects between genus and condition, we analyzed the data for the two genera separately, but we present the analyses together to facilitate the comparison across groups. We used statistics appropriate for a priori hypotheses for comparisons testing the social-dog, causal-ape hypothesis. With respect to learning and order effects, we compared the first half of trials to the second half of trials for each condition for each genera separately and found no significant differences except a significant decrease of performance of the dogs in the "noise–empty" condition, $t(20) = 2.42$, $p = .025$. We therefore concluded that whatever was found, it was not due to learning during the experimental sessions but rather reflects skills the animals brought to the experiment. Because of the large number of conditions involved and their nested nature, we analyzed the data in a stepwise manner. We began with broad comparisons across cue types such as social versus causal cues by collapsing all cues of a given type. Later, we compared the various cues within each particular cue type and against the corresponding control conditions, which was deemed a more conservative analysis than comparing the cue conditions against chance (50%).

## Results

### Social Versus Causal

As the most general analysis, we grouped the various experimental (not control) cues into the two general categories social (communicative and behavioral cues: "point," "point–continuous," "look," "look–continuous," "try to open," "reach") and causal ("noise," "noise–ghost," "noise–empty," "shape," "shape–ghost") on the basis of whether or not the inference was about a human being's behavior or about the physical world. We also included the overall no-cue control condition. Figure 1 shows the mean percentage correct for dogs and apes on these three categories.

Results showed that dogs successfully used the social but not the causal cues. A repeated measures ANOVA with cue type (social vs. causal vs. control) showed a significant effect, $F(2, 40) = 10.34$, $\varepsilon^2 = 0.34$, $p = .002$. Planned pairwise comparisons revealed that compared with the control condition, dogs performed significantly better in the social condition ($p < .001$) but not in the causal condition ($p = .146$). Moreover, dogs performed significantly better in the social compared with the causal condition ($p < .001$).

Apes showed a very different pattern of results. Apes successfully used the causal but not the social cues compared with the control condition. A repeated measures ANOVA with cue type (social vs. causal vs. control) showed a significant effect, $F(2, 30) = 4.40$, $\varepsilon^2 = 0.23$, $p = .028$. Planned pairwise comparisons
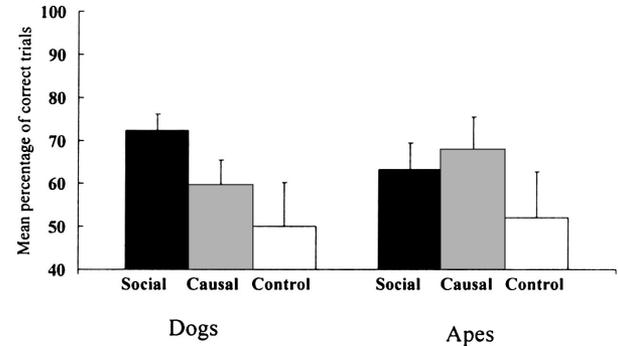


*Figure 1.* Mean percentage correct (plus confidence interval) for the two genera on the three categories social, causal and control.

revealed that compared with the no-cue condition, apes performed significantly better in the causal condition ($p = .018$) but not in the social condition ($p = .090$). Nevertheless, there were no significant differences between the causal and the social conditions ($p = .275$).

### Communicative Versus Behavioral

We next took a closer look at the social category by splitting it into communicative cues ("point," "point–continuous," "look," "look–continuous") and behavioral cues ("try-to-open," "reach") on the basis of whether the human was attempting to help the subject find the food communicatively or just behaving toward an object. We then compared these again with the general no-cue control condition. Figure 2 shows the mean percentage correct of the two genera on these three conditions.

Dogs found the food more often with communicative than with behavioral cues. A repeated measures ANOVA with cue type (communicative vs. behavioral vs. control) showed a significant effect of cue type, $F(2, 40) = 15.06$, $\varepsilon^2 = 0.43$, $p < .001$. Planned pairwise comparisons revealed that compared with the control condition, dogs performed significantly better both in the communicative condition ($p < .001$) and the behavioral condition ($p = .007$). Moreover, dogs performed significantly better in the communicative condition than in the behavioral condition ($p = .011$). In contrast, a repeated measures ANOVA showed no significant effect for type of cue on the successful searching of apes, $F(2, 30) = 3.02$, $\varepsilon^2 = 0.17$, $p = .08$.

### Communicative Cues

Within the communicative type of cues, there were two cues involving pointing ("point" and "point–continuous") and two involving looking ("look," "look–continuous"). One might say that pointing is more directly communicative given that it is a human convention, whereas looking might be considered more general (as many species follow the gaze direction of conspecifics spontaneously (Kaminski, Riedel, Call, & Tomasello, 2005; Tomasello, Call, & Hare, 1998). Figure 3 presents the mean percentage correct in these conditions for both genera.

Dogs found the food more often with pointing than with looking as communicative cues. A repeated measures ANOVA showed an effect of cue, $F(2, 40) = 33.08$, $\varepsilon^2 = 0.62$, $p < .0001$. Planned
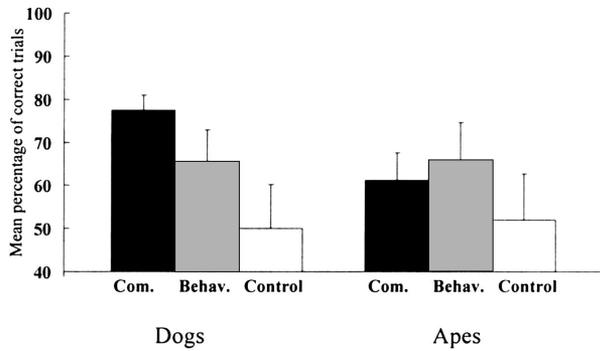
*Figure 2.* Mean percentage correct (plus confidence interval) for the two genera on communicative (com.), behavioral (behav.), and control type of cues.

pairwise comparisons revealed that compared with the control condition, dogs performed significantly better in both the point condition ($p < .001$) and the look condition ($p = .02$). In contrast, a repeated measures ANOVA showed no significant effect for type of cue on the successful searching of apes, $F(2, 30) = 1.48, \varepsilon^2 = 0.09, p = .246$.

Notably, for both point and look, dogs performed better when the cue was given continuously than when it was given and then withdrawn at the moment of choice. Dogs used the "point–continuous" cue more effectively than the "point" cue, $t(20) = 3.76, p = .001$, and the "look–continuous" cue more effectively than the "look" cue, $t(20) = 4.37, p < .001$. Three of these four cues were also used more effectively than the no-cue control condition: for point, $t(20) = 5.05, p < .001$; for point continuous, $t(20) = 8.77, p < .001$; for look–continuous, $t(20) = 3.60, p = .002$; and for look, $t(20) = 0.72, p = .479$.

For the apes, "point–continuous" led to better performance than "point," $t(15) = 2.77, p = .014$, but "look" and "look–continuous" did not differ, $t(15) = 1.65, p = .12$. Only the "point–continuous" cue differed from the no-cue control condition for the apes, $t(15) = 3.05, p = .008$. None of the three other conditions was significant: "point" vs. no-cue control, $t(15) = 0.13, p = .90$; "look" vs. no-cue control, $t(15) = 0.57, p = .58$; "look–continuous" vs. no-cue control, $t(15) = 1.77, p = .10$.
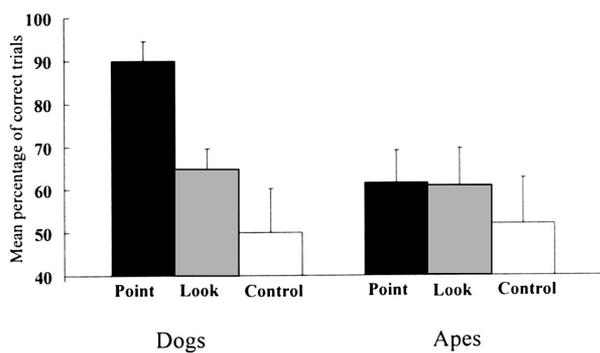
### Behavioral Cues

Figure 4 presents the mean percentage correct with the behavioral cues for both genera. Dogs found the food more often with reaching compared with trying cues. A repeated measures ANOVA with cue type (reaching vs. trying vs. control) showed a significant effect of cue type, $F(2, 40) = 7.06, \varepsilon^2 = 0.26, p < .003$. Post hoc comparisons (Bonferonni corrected as we had no a priori hypotheses) revealed that compared with the control condition, dogs performed significantly better in the reaching condition ($p < .012$) but not in the trying-to-open condition ($p = .093$). Nevertheless, there were no significant differences between the reaching and trying-to-open conditions ($p = .268$). As they were so similar, we also compared the pointing condition with the reaching condition for the dogs, and interestingly, dogs performed significantly better in the pointing compared with the reaching condition, $t(20) = 3.30, p = .004$. In contrast, a repeated measures ANOVA showed no significant effect for type of cue on the successful searching of apes, $F(2, 30) = 2.43, \varepsilon^2 = 0.14, p = .105$.

### Causal Cues

We examined causal cues in detail by analyzing visual and auditory cues separately. Additionally, we investigated the effect of presenting these cues in a social situation compared with a nonsocial one (i.e., ghost conditions).

### Auditory

Figure 5 presents the mean percentage correct of trials in each condition. A repeated measures ANOVA showed a significant effect of condition, $F(3, 60) = 9.89, \varepsilon^2 = 0.33, p < .0001$. Planned pairwise comparisons revealed that dogs performed significantly better in all three conditions with auditory cues compared with the condition without an auditory cue (noise–empty; $p = .001$ in all three cases). Moreover, there were no significant differences between those conditions with auditory cues ($p > .05$ in all cases). This means that dogs treated causal and noncausal auditory cues equally and, additionally, that they were not capable of inferring the absence of the food on the basis of a silent shaken cup.

In the "noise–empty" condition, dogs were attracted to the container shaken by the experimenter, which suggests that dogs in this condition chose on the basis of the contact between the
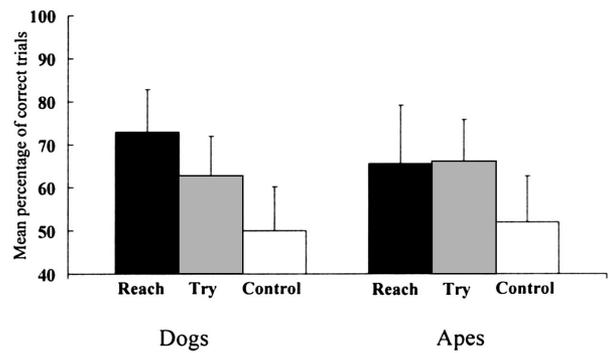


*Figure 3.* Mean percentage correct (plus confidence interval) for the two genera on pointing, looking, and control cues.



*Figure 4.* Mean percentage correct (plus confidence interval) for the two genera on reaching, trying, and control cues.
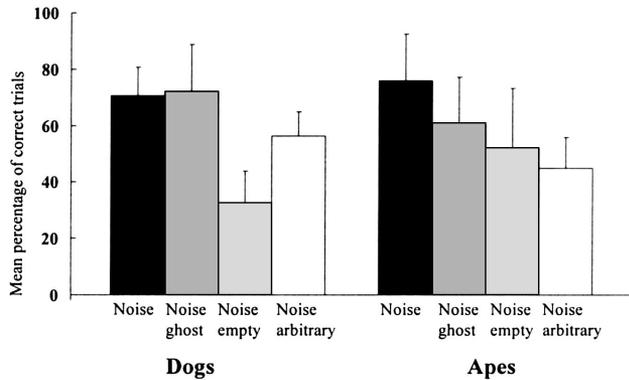
*Figure 5.* Mean percentage correct (plus confidence interval) for the two genera on auditory cues.

experimenter and the cup, independently of the auditory cue. We therefore decided to investigate the joint effect of the presence of the auditory cue and contact with the cup on the percentage of correct responses. Note that four of the conditions ("noise," "noise–arbitrary," "noise–empty," no-cue control) represent the perfect crossing between presence of auditory cue and contact with the cup. A 2 × 2 repeated measures ANOVA with auditory cue and contact as within-subjects variables revealed no significant main effects but did show an Auditory Cue × Motion interaction effect, $F(1, 20) = 8.48$, $\varepsilon^2 = 0.29$, $p = .009$. Inspection of the mean values in each cell indicated that the auditory cue had a higher effect on performance when the human touched the cup (noise condition). Moreover in the "noise–empty" condition, in which the wrong cup was touched, the dogs were correct only in 32.5% of the cases, which is significantly below chance, $t(20) = 3.20$, $p = .004$. Thus, these results suggest that dogs mostly prefer the cup touched by the experimenter, again indicating the crucial importance of human actions on dogs' behavior.

The performance of apes also varied across conditions (see Figure 5). A repeated measures ANOVA revealed a significant effect of condition, $F(3, 45) = 3.02$, $\varepsilon^2 = 0.17$, $p = .04$. Planned pairwise comparisons revealed that apes did differentiate between causally relevant auditory information and an arbitrary auditory cue if it appeared in a social setup (noise vs. noise arbitrary, $p = .001$) but not when it appeared in a nonsocial setup (noise ghost vs. noise arbitrary, $p = .114$). Moreover, in the "noise–ghost" condition, 9 of the 16 apes reacted with caution and sometimes even with withdrawal. Unlike dogs, they showed no significant differences between conditions with an auditory cue and the empty–noise condition ($p > .08$ in all three cases). This means that apes, unlike dogs, did not treat causal and noncausal noises equally: They understood the causality and were not attracted to the human actions, as were dogs. Second, they were capable of inferring to some extent the absence of the food on the basis of a silent shaken cup.

### Visual

Figure 6 presents the mean percentage correct of trials in each condition. A repeated measures ANOVA revealed a significant effect of condition, $F(3, 60) = 4.74$, $\varepsilon^2 = 0.19$, $p = .005$. Planned

pairwise comparisons revealed that dogs only used the causally relevant visual information when they had seen the human touching the boards ("shape" vs. "shape–smell," $p = .001$; "shape" vs. "shape-block," $p = .014$). However, if they had not seen the human touching the boards, they were incapable of using the visual information provided ("shape–ghost" vs. "shape–smell," $p = .367$; "shape–ghost" vs. "shape–block," $p = 1.00$). A direct comparison of the social compared with the ghost version of the cue also revealed a significant difference ($p = .030$). Thus, again the dogs were attracted to human actions.

The apes showed a different pattern of results. A repeated measures ANOVA indicated a significant effect of condition, $F(3, 45) = 8.48$, $\varepsilon^2 = 0.36$, $p < .0001$. Planned pairwise comparisons revealed that apes used the causally relevant visual information when they had seen the human touching the boards ("shape" vs. "shape–smell," $p = .0001$) and also when they had not seen the human touching the board ("shape–ghost" vs. "shape–smell," $p = .005$). Therefore, the social factor had no influence on the behavior of the apes in this situation, though a direct comparison of the social with the ghost condition approached significance ($p = .052$). However, the apes' capability of using the causally relevant visual information must be considered with some caution because apes did not show a significant difference between the conditions in which the visual information had a causal relation compared with the condition in which it did not ("shape" vs. "shape–block," $p = .718$; "shape–ghost" vs. "shape–block," $p = .30$). Moreover, a comparison of the "shape–block" condition with the control condition having no visual information ("shape–smell") showed a significant difference ($p = .001$). Recall, however, that even in this control condition, being attracted to the slanted board is not totally "wrong," as the slanted board is the only place food could possibly be (we return to this point in the Discussion).

### Discussion

Overall, the results of this study provide support for the social-dog, causal-ape hypothesis. Dogs were especially skillful at finding hidden food when the human experimenter gave a communicative cue, and they were slightly more skilled as well at finding the hidden food when the cue was human action with the goal of reaching or opening the container that had food in it. In contrast,
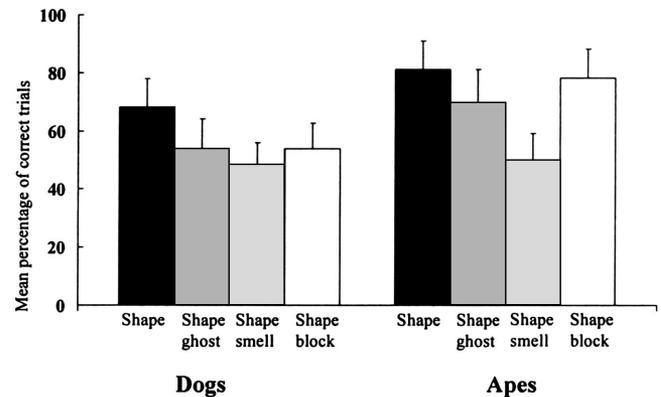


*Figure 6.* Mean percentage correct (plus confidence interval) for the two genera on visual cues.

apes were especially skillful at finding the hidden food when the food itself caused some perceptible change of state in the physical world (e.g., by making a noise or displacing another object). Notably, they did not choose the correct alternative when the cup shook in a ghostly manner ("noise–ghost"), a situation to which some apes reacted with caution and withdrawal.

The results with the communicative cues provided a very good fit to the hypothesis. As in many previous studies (see Call & Tomasello, 2005, for a review), the apes performed basically at chance with the pointing and looking cues, with better than control performance in only one of the four cues, namely, "point–continuous" in which the finger stayed in some proximity with the correct bucket throughout the subjects' choice. Other researchers have also found that apes only perform above chance when the pointing finger is close to the target bucket (Povinelli et al., 1997; see Miklosi & Soproni, in press, for a review), suggesting the possibility that some kind of local enhancement process is at work (see Barth et al., in press, for some other variables affecting apes' performance). The dogs, in contrast, performed skillfully with all four communicative cues, their rate of success with the pointing cues being almost 50% higher than the apes' (even though the pointing finger was farther from the cup than for the apes). Notably, dogs' performance was reliably better with the pointing cues than with the looking cues (there was no such difference for the apes). This is interesting because pointing is a conventional human gesture underlain by communicative intentions, whereas looking sometimes is and sometimes is not used by humans as an intentional communicative cue for others. Pointing is thus more communicative than looking, and it is dogs' best cue.

Apes performed well with causal cues, which was expected given previous research in this domain (e.g., Call, 2004). They used the shape of a slanted board to find the hidden food independent of whether the human had touched it before. It is true that in the control condition "shape–block," in which the food was in plain sight and the board's angle was being influenced by a wooden block under it, apes still showed a reliable preference for the slanted board. However, choosing the slanted board in this condition cannot be considered a mistake because food could be hidden under it, whereas this was not possible for the board lying flat on the platform. Apes also selected the cup that produced an auditory cue when the experimenter shook it but not when the cup shook on its own ("noise–ghost" condition). However, it is very likely that this result was a consequence of the unexpected sight of a cup moving independently, to which many subjects reacted with withdrawal and mild fear. Thus, these results can be interpreted as evidence that apes have some understanding of the causal relations between the food, the cup, and the effects that one can produce on the other.

In contrast, it seems that the dogs' performance with the causal cues was not based on causal understanding. They selected the noisy cup even if it did not move at all (i.e., arbitrary noise condition), indicating that no causal mechanisms were involved. Moreover, dogs selected the correct cup below chance in the "noise–empty" condition in which the experimenter shook the empty cup. A further analysis showed that dogs just preferred the cup that the experimenter manipulated, showing a strong attraction not to the causally correct answer but simply to the human's actions. In the shape condition, dogs found the food reliably when it was under the board, displacing it, but only when the dogs witnessed the human touching the boards before the trial. Of course, it is possible that the human experimenter gave an unintended cue while moving the slanted board. However, this seems unlikely because dogs could not find the food in the control conditions (when both boards were slanted or when a block was used instead of the slanted board). Instead, it is more likely that the dogs did not understand the situation when they just saw the boards without human intervention. In this sense, the social aspect of the problem appeared quite critical for dogs. Thus, overall, dogs' successful performance did not emanate from causal understanding whereas apes' arguably did.

With the behavioral cues, such as a human reaching or trying to open the baited container (during which E did not look at the subject at all), dogs performed a bit more skillfully than apes. Dogs were better than in the control with the reaching cue but not with the trying cue, which suggests the possibility that they might have interpreted this intentional action (wrongly) as a pointing gesture, or at least as some kind of purposeful communicative gesture. However, dogs performed significantly better with the pointing compared with the reaching cue, suggesting that the communicative aspect of the pointing gesture had an influence to some degree. Apes did not use either the reaching or the trying cue, which is a bit surprising given the results of Hare and Tomasello (2004), who found positive results for the reaching cue (see also Call et al., 2004; Call & Tomasello, 1998; Uller, 2004). In that study, however, the human first established a competitive relationship with the subject, so the reaching was seen in this context, and this may have affected the apes' motivation and performance. On the basis of the trying-to-open results, it might be argued that subjects could also choose the second cup because the experimenter was unsuccessful in opening the first one. There was always only one piece of food, however, and neither the dogs nor the apes used this strategy. In general, it is not clear that either of the genera has a clear advantage in reading human behavioral cues.

The good performance of the apes with causal cues makes sense because apes live in an environment in which they must make many causal inferences when they search for food, as they seek to extract nonperceptible foods from hidden locations inside underground nests and so forth, sometimes using tools in a way that requires some causal understanding. Previous experimental studies have shown that apes are very skillful in solving a variety of causal problems requiring inferential reasoning (Antinucci, 1989; Cacchione & Krist, 2004; Premack & Premack, 1994; Suda & Call, 2004). On the other hand, apes have no special connection to humans and their unique forms of cooperative triadic communication in which one individual informs another about the location of various things, including monopolizable food resources. Moreover, there is major intragroup food competition among chimpanzees (Wittig & Boesch, 2003) and also among bonobos (Van Elsacker, Beuleman, & Savini, 2001). It is thus to be expected that ape individuals should refrain from informing others cooperatively about the location of valuable food. Given these considerations, apes' struggles with the human communicative cues in this and other studies are not so surprising.

For dogs, on the other hand, understanding the communicative cues of humans was presumably an important aspect (either direct or indirect) of the domestication process, and many previous studies have found that they can use gaze and pointing gestures to locate hidden food (e.g., Hare et al., 2002; Miklosi et al., 2003).

Notably, across many studies the individuals or species that are best at using human communicative cues in the object choice task are invariably those that are either domesticated by humans or have been raised during ontogeny by humans. Thus, some individual apes raised by humans are skillful (Itakura & Tanaka, 1998; Call, Agnetta, & Tomasello, 2000), dolphins and seals raised and trained by humans are skillful (Pack & Herman, 2004; Scheumann & Call, 2004; Tschudin, Call, Dunbar, Harris, & van der Elst, 2001), and domestic goats also show some skills (Kaminski et al., 2005). On the other hand, monkeys must be trained for dozens or even hundreds of trials to learn to use human cues (Anderson, Sallaberry, & Barbier, 1995), and wolves are also not skillful (Frank & Frank, 1983; Hare et al., 2002). Thus, dogs' excellent performance with the communicative cues may plausibly be attributed to aspects of the domestication process. Dogs' struggles in the current experiment with the causal cues may or may not reflect general mammalian skills of causal inference; only future comparative research can determine this. One interesting possibility is that dogs have actually lost some skills in understanding causality during domestication, as humans solved many of their problems for them. It would be important to test dogs' closest living relatives, such as foxes and wolves, for the ability to make causal inferences. The prediction is that they would outperform dogs, and indeed there is some indication that wolves are better problem solvers than dogs (Miklosi et al., 2003), although the cognitive processes underlying this performance remain poorly understood.

The current results thus support the hypothesis that great apes are especially skilled at making inferences about the workings of the physical world. They have many skills in making inferences about the social world as well, of course, but perhaps not those required by the human form of cooperative, triadic communication in which one individual informs another about something in the outside world. In contrast, domestic dogs very likely have the same inferencing skills as other mammals for dealing with the physical world but, in addition, have an adaptive specialization for reading human behavior, especially cooperative communicative signs. The skills were very likely created, in one way or another, through many thousands of years of domestication in the context of human culture. If cognitive skills are adaptations to particular ecological contexts and problems, there is much to be done in discovering how this works in particular cases.

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