ORIGINAL ARTICLE

Quantity-based judgments in the domestic dog (*Canis lupus familiaris*)

Camille Ward · Barbara B. Smuts

Abstract We examined the ability of domestic dogs to choose the larger versus smaller quantity of food in two experiments. In experiment 1, we investigated the ability of 29 dogs (results from 18 dogs were used in the data analysis) to discriminate between two quantities of food presented in eight different combinations. Choices were simultaneously presented and visually available at the time of choice. Overall, subjects chose the larger quantity more often than the smaller quantity, but they found numerically close comparisons more difficult. In experiment 2, we tested two dogs from experiment 1 under three conditions. In condition 1, we used similar methods from experiment 1 and tested the dogs multiple times on the eight combinations from experiment 1 plus one additional combination. In conditions 2 and 3, the food was visually unavailable to the subjects at the time of choice, but in condition 2, food choices were viewed simultaneously before being made visually unavailable, and in condition 3, they were viewed successively. In these last two conditions, and especially in condition 3, the dogs had to keep track of quantities mentally in order to choose optimally. Subjects still chose the larger quantity more often than the smaller quantity when the food was not simultaneously visible at the time of choice. Olfactory cues and inadvertent cuing by the experimenter were excluded as mechanisms for choosing larger quantities. The results suggest that, like apes tested on similar tasks, some dogs can form internal representations and make mental comparisons of quantity.

C. Ward (✉) · B. B. Smuts
Department of Psychology, University of Michigan,
1012 East Hall, 530 Church Street, Ann Arbor,
MI 48109-1043, USA
e-mail: rameses@unich.edu
Tel.: + 1-734-761-6704
Fax: + 1-734-764-3520

Introduction

Animals that are able to judge quantities or amounts, even in a relative sense, should be at an advantage in determining which environments have the least number of predators or competitors, the most reproductive partners, and the largest amount of food resources (Dehaene 1997). Natural selection should favor optimal decision-making, but animals must first compare in order to optimize. Previous research has shown that children (Huntley-Fenner and Cannon 2000), infants (Feigenson et al. 2002), and variety of nonhuman animals such as dolphins (Kilian et al. 2003), monkeys (Hauser et al. 2000), apes (Rumbaugh et al. 1987; Boysen and Bernston 1995; Dooley and Gill 1997; Call 2000), rats (Meck and Church 1983), birds (Pepperberg 1987), and raccoons (Davis 1984) can discriminate between the quantities of various objects in their environments.

In some studies, researchers train or condition animals to make quantity comparisons. For example, rats learned to press one of two levers to distinguish two flashes of light from four flashes (Meck and Church 1983). Likewise, raccoons learned to select a transparent cube containing three grapes and ignore those cubes containing two or four grapes in order to receive a reward (Davis 1984). After years of training, an African grey parrot (*Psittacus erithacus*) could correctly identify the number of red keys present when researchers presented him with a group of objects containing red keys, green keys, red toys, and green toys (Pepperberg 1987).

Independent of training, selection should favor the natural development of such decision-making abilities in a number of ecological and social situations, including those involv-

ing parental investment, feeding competition, and intra- or intergroup aggression (Hauser 2003). For example, in the American coot (*Fulica americana*), an aquatic bird subject to conspecific brood parasitism, the number of eggs a female lays is directly related to the number or surface area of eggs already present in the nest. Females respond to their own eggs in a nest but ignore the number of parasitic eggs when regulating clutch size (Lyon 2003). Similarly, to maximize energetic rates of return, animals must make decisions between which patches of food to forage in (Stephens and Krebs 1986). Experiments using playbacks of conspecific calls in African lions (McComb et al. 1994), chimpanzees (Wilson et al. 2001), howler monkeys (Kitchen 2004), and wolves (Harrington and Mech 1979) showed that decisions about whether to respond aggressively to competitors reflected the size of the home group relative to the group size of competitors.

In this study, we examined how domestic dogs (*Canis lupus familiaris*) respond to differences in quantity naturally, without explicit training for a desired response. Previous research on chimpanzees (Dooley and Gill 1977; Rumbaugh et al. 1987; Beran 2001, 2004) and orangutans (Call 2000) addressed their ability to distinguish between two different quantities of food. Dooley and Gill (1977) reported that Lana, the chimpanzee, was able distinguish the larger quantity of cereal pieces from the smaller quantity in most trials. Lana was tested on all combinations between 1 and 10, and she performed better when the numerical distance (difference between quantities) was large (e.g., 1 vs. 4 was easier than 3 vs. 4), the ratio between quantities was small (e.g., 2 vs. 3 was easier than 5 vs. 6), and when the total number of pieces in both arrays combined was small.

Three orangutans performed similarly. When tested on all quantity combinations between 1 and 6, in most trials they chose the larger quantity of cereal over the smaller quantity (Call 2000), and their performance was positively correlated with the numerical distance between the two quantities and negatively correlated with ratio between quantities. For Lana, both quantities of cereal were always visually available at the time of choice. However, for the orangutans, in some trials the cereal was visually available, but in other trials, the experimenter covered the quantities with an opaque lid after the animal had an opportunity to visually compare them. Orangutans performed equally well whether the cereal was visually available or concealed at the time of choice. For all trials in both the chimpanzee and orangutan experiments, the subjects were positively rewarded whether they chose the larger or the smaller quantities, because they got to consume the quantity selected.

The performances of Lana and the orangutans suggest analog representations of quantity ("mental magnitudes") (Moyer and Landauer 1967; Gallistel and Gelman 2000) subject to scalar variability. Scalar variability describes a representation of quantity in which the "noisiness" of the estimate (measured by the degree of variation in response across trials) is directly proportional to the size of the quantity being estimated (Gallistel and Gelman 2000). Discrimination between mental magnitudes that are subject to scalar variability follows Weber's law, which states that two magnitudes are more easily distinguished as the ratio between the smaller divided by the larger magnitude decreases. Weber's law (Dehaene et al. 1998; Gallistel and Gelman 2000) reflects distance and size effects as described above for the chimpanzee and orangutan studies. Many other studies of quantity estimation report results consistent with Weber's law, implying that magnitude representations of quantity are widespread in both humans and nonhuman animals (Beran 2001, 2004; Cordes et al. 2001; Hauser 2003; Lewis et al. 2005; Jordan and Brannon 2006a).

In many natural situations, such magnitude representations may allow sufficiently accurate estimates of quantity. For example, for group-living, territorial species, the ability to assess and compare group sizes would allow for optimal decision-making during territorial disputes. In several studies, researchers used conspecific playbacks (playing calls from one to five individuals simultaneously) to simulate rival groups of conspecifics (chimpanzees: Wilson et al. 2001; lions: McComb et al. 1994; howler monkeys: Kitchen 2004, and wolves: Harrington and Mech 1979). In all of these species, animals were more likely to respond to perceived threats when numeric odds were in their favor, indicating an ability to accurately infer relative group size within this numerical range. Evidence from actual intergroup encounters supports the hypothesis that small groups avoid larger groups. For example, in 13 aggressive incidents between a pack of free-ranging, domestic dogs living in the mountainous region of central Italy and smaller packs or an individual dog, the smaller group always withdrew before aggression became physical (Macdonald and Carr 1995).

The importance of territoriality among wolves (Meier et al. 1995; Smith and Ferguson 2005) and their descendants, free-ranging domestic dogs, suggests at least one context in which the ability to judge relative quantities could prove important to survival and reproductive success. Since hunting in these species often involves discriminating the group size of potential prey, quantity comparisons could also be important during foraging. In this study, we took advantage of the availability and tractability of domestic dogs to investigate their discrimination abilities. Previous research that measured dogs' looking time at expected (e.g., $1 + 1 = 2$) versus unexpected outcomes (e.g., $1 + 1 = 1$ and $1 + 1 = 3$) showed that dogs looked longer at unexpected outcomes. Researchers suggested that dogs anticipated the outcome of the calculations and demonstrated a limited ability to count (West and Young 2002). In the current study, we tested a wider range of quantities than West and Young (2002) and employed meth-

ods similar to those used to investigate orangutans' abilities to distinguish between two quantities of food (Call 2000). We use the term "quantity" to signify amount without implying a reference to number or the ability to count (cf. Rumbaugh et al. 1987; Call 2000; Shumaker et al. 2001).

Our study had three main goals. First, we aimed to compare numerical performance in a quantity discrimination task by a carnivore to performances by nonhuman primates (previous studies on carnivores are lacking). Are dogs as skilled as nonhuman primates in discriminating small sets of quantities? Second, we wanted to determine whether the responses of dogs conformed to Weber's law, indicating a mental magnitude mechanism for quantity estimation. Based on studies of primates, we predicted that dogs would be more likely to choose the larger quantity when numerical distance between the two quantities was large, ratio was small, and total quantity being compared was small. Third, because the choices were visually available simultaneously in our original trials (e.g., experiment 1, conditions 1 and 2 of experiment 2, below), dogs could discriminate quantity based on perceptual cues alone. Therefore, to investigate the possibility that dogs can form and remember mental representations of quantity, we conducted preliminary tests requiring two subjects to choose between quantities that were visually available successively (condition 3 of experiment 2). We predicted that dogs, like orangutans tested under similar conditions (Call 2000), would choose the larger quantity regardless of whether or not the food was visually available at the time of choice.

Experiment 1

In experiment 1, we tested whether dogs overall (data combined for multiple subjects) could discriminate the larger from the smaller quantity of food when presented with the following eight combinations: 1 vs. 4, 1 vs. 3, 2 vs. 5, 1 vs. 2, 2 vs. 4, 3 vs. 5, 2 vs. 3, and 3 vs. 4. Results from a pilot study conducted prior to experiment 1 showed that all 12 adult dogs tested on the single quantity combination of 1 vs. 5 could discriminate the larger quantity over the smaller quantity.

Methods

Subjects

The 29 dogs used in the study were pets recruited from veterinarian offices, a local dog club, friends, neighbors, and people affiliated with the study. Of the 29 subjects, 18 were female and 11 male; 17 were purebred and 12 mixed breeds. Ages ranged from 1 to 12 years. Testing was conducted between June 2003 and August 2003.

Procedure

We tested all dogs individually. Each dog's owner brought his or her dog into the testing room, and the dog had 5 min to explore the testing environment. Prior to trial 1, the experimenter fed the dog a piece of hotdog – the food used in the experiments. We wanted to be sure that the dog liked the food and was motivated to obtain it before proceeding. To increase motivation, we asked owners to refrain from feeding their dogs just prior to testing. All subjects were motivated by hotdogs.

In preparation for testing, the owner took the dog to a marked location. The owner positioned the dog into place, usually by gently holding the dog from behind. A few dogs maintained a sit and stay without aid, in which case the owner stood behind the dog. While the dog waited in place,

Fig. 1 Procedure followed in experiment 1 (open condition) and each of the three conditions in experiment 2 (modeled after Call 2000). Numbers next to plates refer to the steps of each procedure. See text for full description

a. Condition 1 (open)

b. Condition 2 (simultaneous closed)

c. Condition 3 (successive closed)
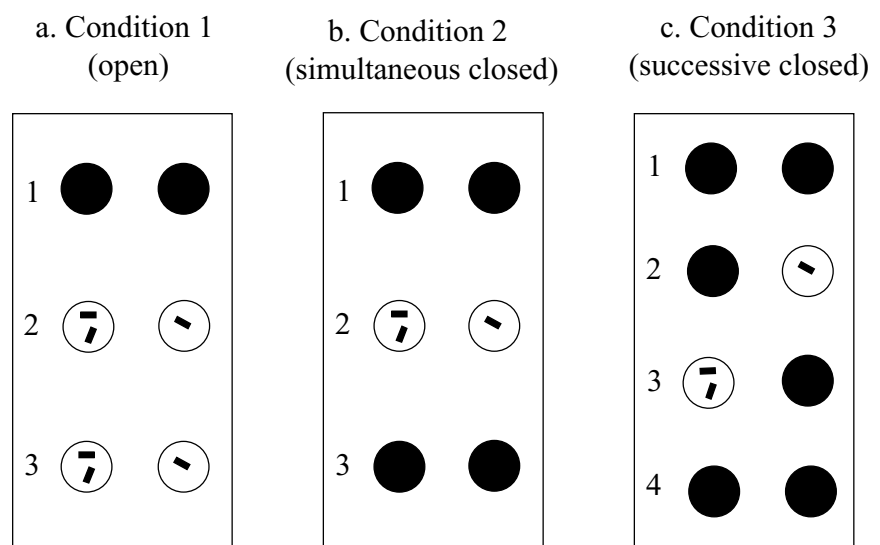
the experimenter baited two plates outside of the dog's view. The experimenter randomly dropped a set number of hotdog pieces onto each plate, depending on the quantity combination being tested, making no attempt to arrange the pieces into a consistent pattern. Plate construction was blue plastic with a 19 cm diameter, and each piece of food was 1/8th of a standard hotdog.

After baiting, the experimenter covered each plate with an opaque lid (Fig. 1a, step 1). Hare et al. (2002) reported that dogs could follow a human gaze to locate hidden food, so the experimenter wore dark sunglasses to avoid inadvertently cueing the dog with her eyes. Visual cueing by the owners was unlikely because they stood behind the dog. However, as an extra precaution, we asked owners to refrain from looking at the plates and instead focus their attention straight ahead at the wall in front of them. The experimenter approached the dog and put both plates down on the ground at the same time in front of the subject. The plates were set 1.2 m apart with the midpoint between them 1 m directly in front of the dog. The experimenter uncovered both plates at the same time (Fig 1a, step 2) and simultaneously tapped lightly on the edge of each plate in order to get the dog to look at both plates. Once the dog had visually examined both quantities, the experimenter waited 5 s and then said "okay", which meant that the owner could release the dog to choose (Fig 1a, step 3). The dog chose by going over to the plate and eating the hotdogs from that plate. As the dog was eating, the experimenter quickly removed the un-chosen plate from the dog's access. We provided no additional reinforcement.

We tested each of the 29 dogs once on each of the eight quantity combinations over four sessions, with two trials per session. Successive sessions for each subject were separated by a minimum of 2 days. We also wanted to test for a learning effect across sessions, so we randomly selected 14 of the dogs to begin testing with what we called the "small ratio group" and end their testing with the "large ratio group". The remaining dogs began with the "large ratio group" and ended with the "small ratio group". Ratio was simply the smaller quantity in the comparison divided by the larger quantity (e.g., 1 vs. 4 combination had a ratio of 0.25). We included combinations 1 vs. 4, 1 vs. 3, 2 vs. 5, and 1 vs. 2 in the small ratio group and combinations 2 vs. 4, 3 vs. 5, 2 vs. 3, and 3 vs. 4 in the large ratio group. Although the combinations 1 vs. 2 and 2 vs. 4 had the same ratio (i.e., 0.50), we assigned one combination to the small ratio group (1 vs. 2) and the other to the large ratio group (2 vs. 4) to equate sample sizes across groups. We assigned dogs to each ratio group in a counterbalanced manner. We counterbalanced the left–right presentation of quantities across trials for each combination and randomly assigned the order of presentation within each group.

Data analysis

For statistical analyses in all experiments, alpha was set at 0.05 for rejection of the null hypothesis. Statistical tests were conducted using SPSS® version 11.5 and SAS® version 8.1. Tests are one-tailed for all directional predictions: (1) dogs would choose the larger quantity more often than the smaller quantity and (2) their performance (the percentage of times, out of eight trials, that the dog chose the larger over the smaller quantity) would improve as the numerical distance between quantities (the larger minus the smaller quantity) being compared increased and as the ratio between quantities (defined previously) and the total quantity (the larger plus the smaller quantity) decreased. Results from our pilot study and research on human children and nonhuman animals support these directional predictions (Dooley and Gill 1977; Boysen and Bernston 1995; Call 2000; Huntley-Fenner and Cannon 2000; Feigenson et al. 2002). For all parametric statistics, the assumptions of homogeneity and normality were met.

We used a GEE (generalized estimating equation) model to test whether the dogs' ability to choose the larger quantity varied with (1) ratio between quantities, (2) numerical distance between quantities, and (3) total quantity of hotdogs available at the time of choice. The GEE model is appropriate for use here because it extends the GLM (general linear model) algorithm to accommodate correlated observations within subjects, and it allows for comparison across subjects (Diggle et al. 1994; Hardin and Hilbe 2002).

To test whether dogs chose the larger quantity significantly more often than the smaller quantity in each of the eight individual combinations (see above), we conducted binomial tests and compared the numbers of dogs choosing the larger and smaller quantities within each combination.

Results and discussion

Of the 29 dogs tested, three never finished with the testing, and we excluded them from the analyses. Eight dogs exhibited a laterality bias, going to the same side on every single trial regardless of the quantity presentation. We excluded them as well, which left 18 dogs for data analysis. Of the 18 subjects, 12 were female and 6 male; 10 were purebred and 8 mixed breeds. Fifteen out of the 18 remaining dogs (83%) chose the larger quantity more often than the smaller quantity across the eight trials (sign test, $p < 0.0001$); two chose the larger and smaller quantities equally often, and one chose the smaller quantity more often. There was no effect of age (Pearson correlation, $r = -0.163$, $p = 0.518$, $n = 18$) or sex (independent sample t-test, $t(16) = 0.230$, $p = 0.821$, $n_{female} = 12$, $n_{male} = 6$) on performance. Males chose the larger plate 73% of the time, and females 71% of the time.

We found no learning effect across trials. Dogs that started or ended with the smaller ratios got an equal percentage
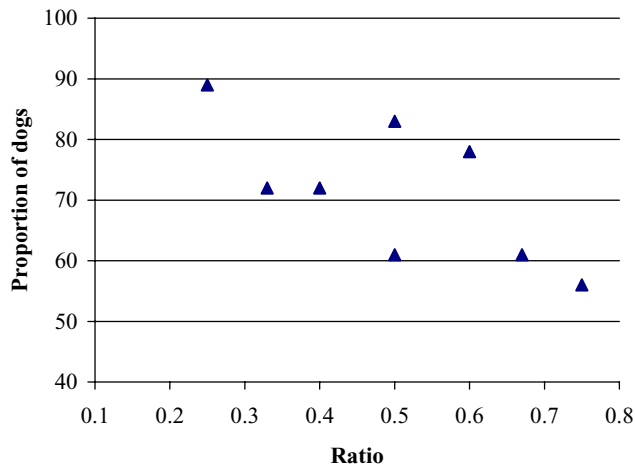
Fig. 2 Proportion of dogs selecting the larger quantity in experiment 1 as a function of ratio between quantities on two plates. Generalized estimating equation (GEE), $Z = -2.69$, $p = 0.007$, $n = 18$

Fig. 3 Proportion of dogs selecting the larger quantity in experiment 1 as a function of the numerical distance between quantities on two plates. Generalized estimating equation (GEE), $Z = 2.86$, $p = 0.004$, $n = 18$

(75%) of the small ratio trials correct (independent sample t-test, $t(16) = 0.00$, $p = 1.000$, $n_{female} = 12$, $n_{male} = 6$). Likewise, there was no significant difference in the percentage correct between the dogs that started with (73% correct) or ended with (59% correct) the large ratio trials (independent sample t-test, $t(16) = 0.971$, $p = 0.346$, $n_{started} = 8$, $n_{ended} = 10$).

Dogs as a group followed Weber's law: they were more likely to choose the larger quantity when the ratio between quantity combinations was small (GEE, $Z = -2.69$, $p = 0.007$, $n = 18$) (Fig. 2) and when the numerical distance between quantity combinations was large (GEE, $Z = 2.86$, $p = 0.004$, $n = 18$) (Fig. 3). Previous research obtained similar results for orangutans (Call 2000) and chimpanzees (Dooley and Gill 1977) when tested under similar conditions. There was no significant relationship between total quantity and the dogs' overall performance (GEE, $Z = 0.29$, $p = 0.769$, $n = 18$). Again, similar results were obtained for orangutans (Call 2000) but not for Lana, the chimpanzee, who was more likely to choose the larger quantity when total quantity available at the time of choice was small (Dooley and Gill 1977). However, the chimpanzee data contained a wider range of total quantity values compared to this study and the orangutan study. This difference may account, at least in part, for the discrepancy in total quantity results among the studies.

Finally, we examined the ability of dogs to discriminate the larger from the smaller quantity within each of the eight individual quantity combinations. Dogs as a group chose the larger quantity significantly more often than the smaller quantity for all combinations except those that differed by one piece (binomial test, 1 vs. 4: $p = 0.001$; 1 vs. 3: $p = 0.048$; 2 vs. 5: $p = 0.048$; 1 vs. 2: $p = 0.240$; 2 vs. 4: $p = 0.004$; 3 vs. 5: $p = 0.015$; 2 vs. 3: $p = 0.240$; 3 vs. 4: $p = 0.407$; $n = 18$ for
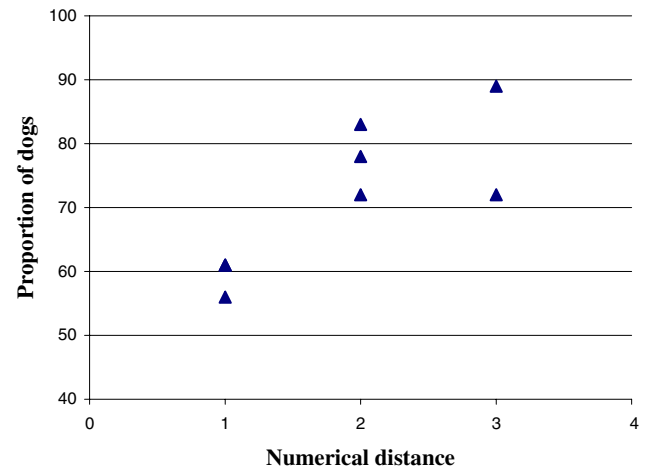
each combination). Our findings parallel the data obtained for orangutans when tested under very similar experimental conditions. Although Call (2000) did not statistically examine the performance of orangutans within each quantity combination, the data he presented (Table 2, p. 139) enabled us to do so. He tested each subject 12 times in each quantity combination, and using his data, we calculated that two of the three orangutans did not discriminate above chance between 1 vs. 2 and 2 vs. 3, and one orangutan did not discriminate between 3 vs. 4 (binomial test, $p > 0.05$), similar to the dogs in the current study.

Experiment 2

In experiment 2, we examined, in greater depth, the abilities of two dogs from experiment 1. Experiment 2 consisted of three conditions that were presented successively. Progression from one condition to the next was dependent upon successful performance in the previous condition.

In condition 1, we verified the generality of the results from experiment 1, and in conditions 2 and 3 we tested to see if dogs could still choose the larger quantity when the food was visually unavailable at the time of choice. In conditions 1 and 2, the dogs could rely strictly on perceptual cues to choose the larger quantity, but success in condition 3 required some mental representation of quantity in order to choose optimally. For all three conditions, we tested the dogs multiple times on the eight combinations from experiment 1, and we also tested them on two additional combinations, 1 vs. 1 and 1 vs. 5. We included the 1 vs. 1 condition to see if a side preference might develop in a setup where the dogs would do equally well by choosing either plate. Condition 2 and 3 tests presented a potentially more difficult

challenge for the dogs, so we added a combination (1 vs. 5) that, according to Weber's law and the results from our pilot study (see experiment 1), should be relatively easy for them to discriminate. We also included the 1 vs. 5 combination in condition 1 to make it directly comparable to conditions 2 and 3.

Methods

Subjects

One of the dogs, Marty, an 8-year-old Labrador retriever, chose the larger quantity in seven out of eight trials in experiment 1; he missed only the 3 vs. 4 combination. The second dog, Acorn, a 5-year-old Doberman pincher, chose the larger quantity in all eight trials. Testing was conducted between August 2003 and January 2004.

Procedure

Condition 1: open The setup was nearly identical to that of experiment 1 (Fig. 1a), with some exceptions. First, we gave each dog four warm-up trials using 1 vs. 0 just prior to a session. If the dog chose the quantity of 1 in all four trials, we preceded to testing. If not, we gave two additional warm-up trials. We used warm-up trials as a pretest to screen for laterality preferences. We did not anticipate laterality preferences in experiment 1 and, therefore, did not screen for them. Second, we presented all 10 combinations in a single session. We randomized the order of presentation within sessions, and counterbalanced trials for side within sessions. Third, we tested Marty and Acorn 11 times in each quantity combination over the course of the experiment. Lastly, because we tested the two dogs numerous times within a session, we used smaller pieces of hotdogs to prevent them from becoming satiated early on, and we positioned the dogs slightly closer to the plates, so that they could more easily view the smaller individual pieces. Each piece of food was 1/16th a standard hotdog; the plates were 1 m apart with the midpoint between the plates being 0.8 m directly in front of the subject.

Condition 2: simultaneous closed The procedure and quantity combinations were the same as in condition 1 except the hotdogs were not visually accessible to the dogs at the time of choice. After the experimenter presented both plates (Fig. 1b, step 1), she uncovered them simultaneously and allowed the dog to examine the two quantities (Fig. 1b, step 2). She waited 5 s, re-covered the plates, and then waited an additional 3 s before releasing the dog to choose (Fig. 1b, step 3).

Condition 3: successive closed The setup and quantity combinations were the same as in conditions 1 and 2 with one

exception. After baiting both plates and placing them on the ground in front of the dog (Fig. 1c, step 1), the experimenter first uncovered the plate on her right and waited until the dog examined the quantity for 5 s before placing the cover back on the plate (Fig. 1c, step 2). Next, she uncovered the plate to her left and waited until the dog examined that quantity for 5 s before covering the plate (Fig. 1c, step 3). After both plates were covered, she waited an additional 3 s before releasing the dog to choose (Fig.1c, step 4).

Results and discussion

For all conditions, both dogs chose the larger quantity significantly above chance for all trials combined (binomial test, Marty: condition 1, 92% of trials, condition 2, 88%, condition 3, 84%, $p < 0.001$ for all, $n = 99$ for each condition; Acorn: condition 1, 93% of trials, $p < 0.0001$, condition 2, 65%, $p = 0.002$, condition 3, 64%, $p = 0.005$, $n = 99$ for conditions 1 and 3 and $n = 98$ for condition 2 [Acorn refused to choose in one trial]).

In conditions 1 and 2, Marty was more likely to select the larger quantity when the numerical distance between quantities was large and the ratio between quantities was small. Ratio and numerical distance were not significantly correlated with the percentage of correct trials in condition 3, and total quantity was not significant in any of the conditions (Table 1).

In condition 1, Acorn performed better when the ratio between quantities was small and the total quantity large. Ratio, numerical distance, and total quantity were not significantly related to performance in conditions 2 and 3, and numerical distance was not significant in condition 1 (Table 1).

Table 1 Spearman rho correlation coefficients[a] and associated *p* values from testing the relationship between the percentage of correct trials for each dog in three conditions of experiment 2 as a function of ratio between quantities, numerical distance, and total quantity ($n = 99$ for each dog in each condition with one exception[b])

Conditions	Ratio		Numerical distance		Total quantity	
	rho	*p*	rho	*p*	rho	*p*
Marty						
1	− **0.875**	0.001	**0.633**	0.03	− 0.397	0.15
2	− **0.699**	0.02	**0.612**	0.04	− 0.209	0.30
3	− 0.492	0.09	0.324	0.20	− 0.426	0.13
Acorn						
1	− **0.755**	0.01	0.377	0.16	**0.715**	0.02
2	− 0.368	0.17	0.332	0.19	− 0.151	0.35
3	− 0.069	0.43	0.332	0.19	0.532	0.07

Condition 1: open, condition 2: simultaneous closed, condition 3: successive closed.

[a]One-tailed tests; significant rho ($p < 0.05$) in bold.

[b]$n = 98$ for Acorn in condition 2; she refused to choose in one trial.

Table 2 Summary of results for individual quantity combinations for each dog in three conditions of experiment 2 ($n = 99$ for each dog and condition with one exception[a])

Conditions	Individual quantity combinations								
	1 vs. 5	1 vs. 4	1 vs. 3	2 vs. 5	1 vs. 2	2 vs. 4	3 vs. 5	2 vs. 3	3 vs. 4
Marty									
1	**<0.0005**	**<0.0005**	**<0.0005**	**<0.0005**	**<0.0005**	**0.01**	**0.01**	0.11	0.11
2	**<0.0005**	**0.01**	**<0.0005**	**<0.0005**	**0.03**	0.11	**0.03**	**0.01**	0.11
3	**<0.0005**	**0.01**	**<0.0005**	**0.03**	0.11	**0.03**	0.50	**<0.0005**	0.11
Acorn									
1	**<0.0005**	**<0.0005**	**<0.0005**	**0.01**	**<0.0005**	**<0.0005**	**0.03**	**0.01**	0.11
2	**0.01**	0.27	0.11	0.50	0.50	0.11	0.50	0.11	0.38
3	0.11	0.11	0.50	0.50	0.50	0.27	0.11	0.50	0.11

Condition 1: open, condition 2: simultaneous closed, condition 3: successive closed. Numbers in table are significant values ($p < 0.05$) in bold associated with one-tailed binomial tests.

[a] $n = 98$ for Acorn in condition 2; she refused to choose in one trial of 3 vs. 4.

Neither Marty nor Acorn showed a side preference in the 1 vs. 1 combination (binomial test, $p > 0.05$ for both dogs in each condition, $n = 11$ for each dog and condition), and with one exception (i.e., Marty in condition 2, $\chi^2 = 4.18$, $df = 1$, $p = 0.041$), the dogs' success choosing the larger quantity did not differ significantly between the first four and last four testing sessions (condition 1, Fisher's exact test; conditions 2 and 3, Pearson chi-square test; $p > 0.05$ for both dogs in each condition with the one exception [see above]).

In condition 1, which is most comparable to experiment 1, the effects of ratio on performance for Marty and Acorn and the effect of numerical distance on performance for Marty are similar to what we found for the dogs as a whole in experiment 1. The finding that Acorn's performance was not related to numerical distance in condition 1 may have resulted from a ceiling effect that masked the distance effect for her. Such distance effects might become apparent if a larger range of quantity combinations are used. The results for individual quantity combinations varied with condition (Table 2), but neither dog chose the larger quantity in the 3 vs. 4 combination under any condition in experiment 2 (and dogs were unsuccessful at it in experiment 1), further suggesting a ratio effect.

Control tests

In experiments 1 and 2, we showed that dogs could discriminate based on quantity, but we do not know whether dogs were basing their decisions on number or some other parameter that varies with number such as surface area or volume. However, we can eliminate two other potentially confounding cues that could have affected the dogs' decision-making: (1) olfaction and (2) experimenter effects.

A dog's sense of smell is extremely sensitive (McCartney 1968; Passe and Walker 1985), serving to enhance social recognition (Fox 1971; Hepper 1986) and aiding in the iden-

tification and receptivity of potential mates (Beach et al. 1983). To address the possibility that choices were based on olfaction, we tested Marty and Acorn 10 times on the quantity combination of 1 vs. 5. The experimental setup was nearly identical to that of experiment 1 except instead of plates, we placed hotdog pieces in opaque bowls that were open at the top and tall enough so that the dogs could not see inside of the bowls. We hypothesized that if dogs were basing their choice on smell, they should go to the bowl containing five pieces in most of the trials. However, Marty chose the bowl containing five pieces in 50% of trials and Acorn chose the bowl containing five pieces in 60% of trials (binomial test, $p = 1.000$ for both dogs, $n = 10$ for each dog).

A second alternative explanation for the dog's performance is that the experimenter, despite wearing sunglasses, somehow inadvertently provided cues that aided subjects in selecting the larger quantity (i.e., the Clever Hans effect). In both experiments 1 and 2, a single researcher was responsible for both baiting the plates and presenting them to the dogs. To test for the possibility that the experimenter knowing which plates contained the larger and smaller quantities may have affected the dogs' performance, we conducted additional trials with Marty and Acorn. For all trials, an assistant baited both plates and handed them to the experimenter already covered. For half the trials (randomly chosen), the assistant informed the experimenter which plate contained the greater number of pieces ("informed" trials), and for the remaining six trials, the experimenter was not informed which plate contained more ("blind trials"). When the experimenter was informed, she presented the plates as described in the setup for experiment 2, condition 1, and in the other half, the experimenter presented the plates from behind an opaque screen that prevented her from seeing the two quantities until after the dog chose, precluding inadvertent cueing (the assistant, in all trials, was not visible to the dog).

We tested Marty and Acorn on the quantity combinations 1 vs. 4, 1 vs. 3, and 3 vs. 5. We presented each combination eight times over two sessions, with 12 trials per

session. Quantity combinations and screen/no-screen trials were counterbalanced within each testing session. If the experimenter inadvertently influenced the subjects' ability to choose the larger quantity, then the dogs should have performed better on no-screen trials. They did not. Marty chose the larger quantity in 92% of trials and Acorn in 83% of trials (binomial test, Marty: $p < 0.001$; Acorn: $p = 0.001$; $n = 24$ for each dog), and their ability to choose the larger quantity was independent of trial type (binomial test, Marty: $p = 0.832$; Acorn: $p = 0.503$; $n = 24$ for each dog).

General discussion

Our study had three primary goals. First, we examined the ability of dogs to discriminate between two quantities that differed in number and compared their performances to non-human primates. Pooling across all quantity conditions, dogs chose the larger quantity of food over the smaller quantity in all experiments. For all dogs in experiment 1 and Marty in conditions 1 and 2 (experiment 2), dogs chose the larger quantity most often when the numerical distance between quantities was large and ratio between quantities was small. These results parallel those obtained for orangutans (Call 2000) under testing conditions similar to those in experiments 1 and 2. In condition 1 (experiment 2), Acorn chose optimally when ratio between quantities and total quantity compared were small. Lana, the chimpanzee, was more likely to choose the larger quantity of food under these same two conditions (Dooley and Gill 1977). Overall, our results indicate that some dogs can perform on par with nonhuman primates in these particular tasks.

Second, we examined aspects of the mechanism responsible for quantity discrimination. Does the pattern of discrimination conform to an analog (magnitude) model of quantity representation, or do the results suggest an alternative explanation? The detrimental effect on performance of smaller numerical distances between quantities, larger ratios between quantities, and larger total quantities (i.e., for Acorn in condition 1) suggests that dogs rely on an approximate mechanism of quantity representation that conforms to Weber's law and fits an analog model (Gallistel and Gelman 2000). However, correlations between the subject's performance and numerical distance between quantities, ratio, and total quantity broke down for Acorn in condition 2 and for Marty in condition 3. Therefore, these latter results do not conform to an analog model of representation. Nor do they resemble the results for orangutans (Call 2000), whose performance conformed to the predictions of Weber's law under all testing conditions, including those comparable to our conditions 2 and 3. Beran (2004) found a similar breakdown effect with chimpanzees. Chimpanzees chose the larger quantity when presented with two and three sets of non-visible food items. Their decreased performance when sets were close in number and large in magnitude suggested an analog model of magnitude representation. However, when chimpanzees were given the more challenging task of choosing the larger of two sets after the experimenter removed two or three of the initially presented food items, ratio was no longer associated with performance, even though one of the two subjects still chose the larger quantity at levels above chance. Future work should explore the mechanisms responsible for outcomes in condition 2 and especially condition 3 (also see the discussion on mental representation below).

One commonly cited alternative to the analog model of quantity representation is the object file model (although there are other models, e.g., Siegler and Opfer 2003). In this model, performance is not subject to Weber's Law, but instead is limited by set size. Mental files are opened, one for each object in the set. This mechanism is precise, rather than approximate, representing quantity exactly up to a set size limit of approximately three or four (Hauser et al. 2000, Hauser 2003; Feigenson et al. 2002). If dogs were using an object file model of quantity representation, we would have expected success at 1 vs. 2 and 2 vs. 3, but this was not typically the case (see experiment 1 and Table 2).

Our third goal for the study was to examine whether dogs could form mental representations of quantity, rather than rely strictly on perceptual cues to choose the larger quantity. In experiment 1 and experiment 2 (condition 1), dogs were most likely using some perceptual mechanism (Rumbaugh et al. 1987) to approximate differences in quantities when both plates of food were visually available at the time of choice (Fig. 1a). In conditions 2 and 3 (Fig. 1b and c), the tasks were potentially more difficult because the food was visually unavailable at the time of choice. As the tasks became more difficult, individual performances decreased somewhat; however, both subjects performed above chance at selecting the larger quantity across all trials in both conditions. In condition 2 (Fig. 1b), Marty visually compared both quantities and then sometimes focused and held his attention on the plate containing more, so that even after the experimenter covered both plates, his gaze was fixed on his final choice. With this strategy, Marty could still choose the larger quantity using strictly perceptual cues. However, the successive presentation in condition 3 (Fig. 1c) made visual fixation impossible because subjects had to examine each plate in turn and form some mental representation of quantity, rather than rely solely on perceptual mechanisms (Call 2000) to choose optimally.

A number of studies have examined the ability of dogs to encode and maintain the spatial location of objects in working memory using a series of retention intervals. In one such study, dogs' working memory for locating hidden objects was very good up to 30 s and then gradually deteriorated up

to 240 s, but even at 240 s, the subjects still performed above chance (Fiset et al. 2003). Other studies show that dogs can remember the spatial location of auditory information for up to 120 s (Kowalska 1995, 2000). Although these experiments examine how memory relates to spatial location rather than to quantity discrimination, the current study does contain a spatial component. The dogs in condition 3 (experiment 2) showed evidence of an ability to encode in memory which of the two locations contained the plate with more food. Future studies could examine the effects of increasing delays on the dog's performance in two-choice tasks like the ones used in conditions 2 and 3 (experiment 2).

The current study addressed the potential for dogs to judge differences in food quantity. The question remains whether quantification ability in dogs is context-specific or a more general mechanism – i.e., does the ability to quantify in a foraging context transfer to quantities in a social or territorial context? Research in this area is sparse. However, some experimental work suggests the existence of cross-modal transfer in quantification. For example, both human infants and rhesus monkeys (*Macaca mulatta*) were able to match the number of vocalizations they heard (i.e., auditory task) with the corresponding number of adult humans or monkeys (i.e., visual task) in 2 vs. 3 comparisons (Jordon et al. 2005; Jordan and Brannon 2006b). Likewise, adult humans approximated the difference between large sets of elements presented successively when one array consisted of dots on a screen and a second array consisted of auditory sequences, and their ability to discriminate decreased as the ratio between the two comparisons increased (Barth et al. 2006).

We demonstrated that domestic dogs can perform similarly to apes when required to judge relative quantities of food. Our study focused on what domestic dogs can do in general (experiment 1) and what two "high performing" dogs can do given increasingly demanding tasks (experiment 2), rather than on the potential for differences in quantification abilities among breeds. Dogs have descended from group-living wolves (Vilà et al. 1999), but we have since modified form and function to meet our requirements. The American Kennel Club classifies purebred dogs into seven breed groups based on intended function (AKC 1992). The 10 purebred dogs in this study represented only three out of the seven breed groups (one working group dog, three herding dogs, and six sporting group dogs). Systematic investigation of breed differences in quantity judgment tasks could reveal relationships between specific cognitive abilities and "ecological niche" (i.e., the jobs the dogs were bred for) *within* species, as previously demonstrated in comparisons across species (Gould-Beierle 2000; Brodin 2005). For example, some herding dogs bred to keep track of livestock might naturally be more attentive to quantity differences than breeds bred primarily for chasing game or human companionship.

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