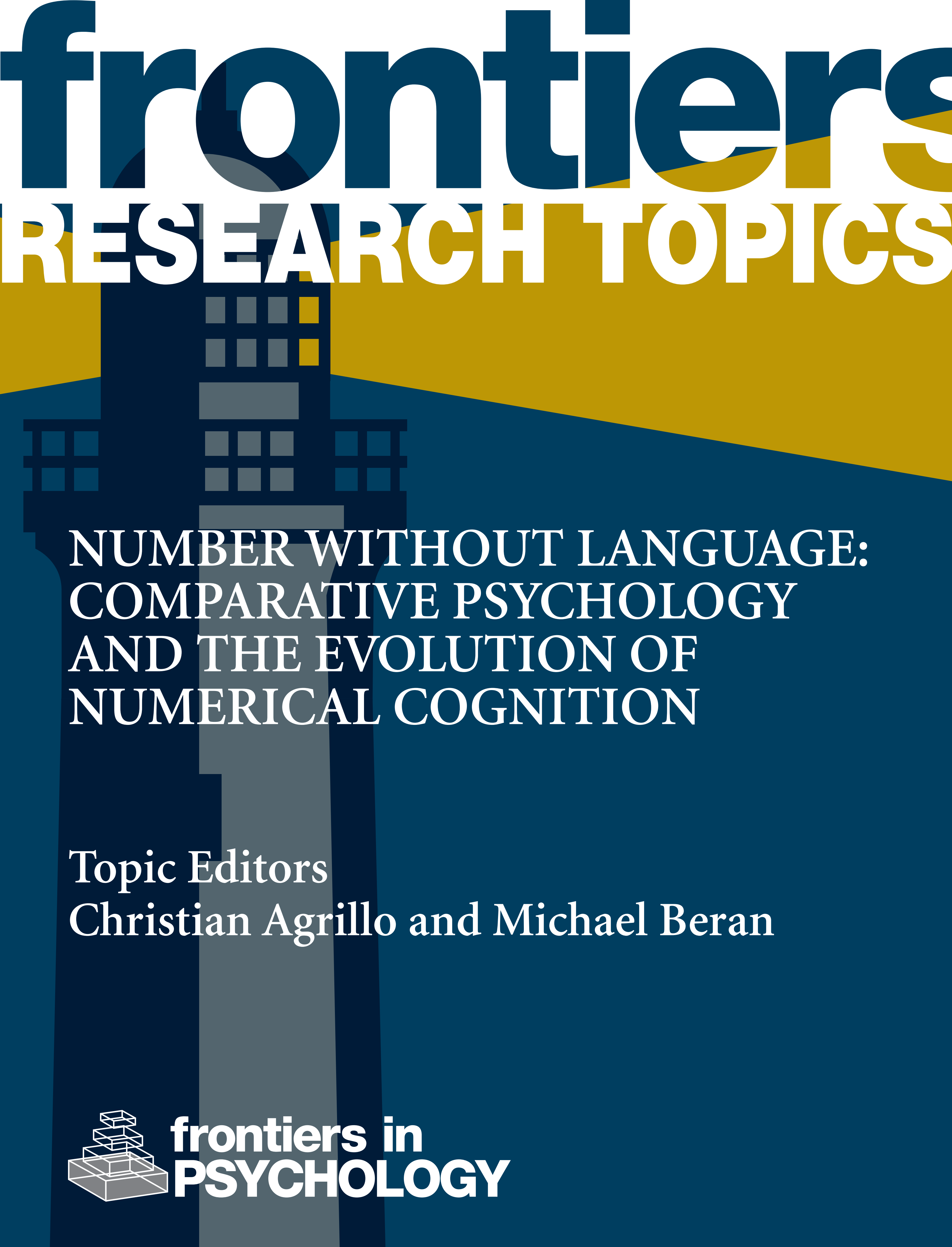

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NUMBER WITHOUT LANGUAGE: COMPARATIVE PSYCHOLOGY AND THE EVOLUTION OF NUMERICAL COGNITION

Topic Editors
Christian Agrillo and Michael Beran

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NUMBER WITHOUT LANGUAGE: COMPARATIVE PSYCHOLOGY AND THE EVOLUTION OF NUMERICAL COGNITION

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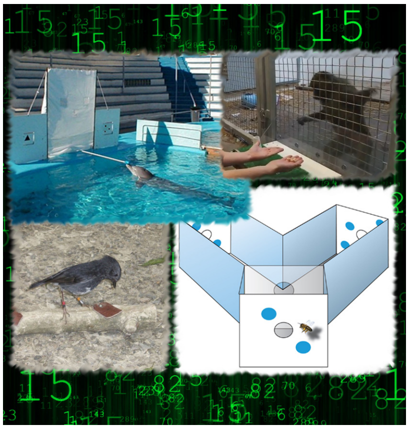

Figures taken from the following articles:

1. Yaman S, Kilian A, von Fersen L and Güntürkün O (2012) Evidence for a numerosity category that is based on abstract qualities of "few" vs. "many" in the bottlenose dolphin (*Tursiops truncatus*). *Front. Psychol.* 3:473. doi: 10.3389/fpsyg.2012.00473
2. Barnard AM, Hughes KD, Gerhardt RR, DiVincenti L Jr, Bovee JM and Cantlon JF (2013) Inherently analog quantity representations in olive baboons (*Papio anubis*). *Front. Psychol.* 4:253. doi: 10.3389/fpsyg.2013.00253
3. Armstrong N, Garland A and Burns KC (2012) Memory for multiple cache locations and prey quantities in a food-hoarding songbird. *Front. Psychol.* 3:584. doi: 10.3389/fpsyg.2012.00584
4. Pahl M, Si A and Zhang S (2013) Numerical cognition in bees and other insects. *Front. Psychol.* 4:162. doi: 10.3389/fpsyg.2013.00162

Despite once being reserved as perhaps a unique human ability, and one reliant on language, comparative and developmental research has shown that numerical abilities predate verbal language. Human infants and several non-human species have been shown to represent numerical information in varied contexts, and the capacity to discriminate both small and large numerosities has been reported in mammals, birds, amphibians, and fish. The similar performances often observed across such diverse species have led to the hypothesis that there may be shared core systems underlying number abilities of non-human species and human non-verbal numerical abilities. Thus, animal models could provide useful insight on our comprehension of numerical cognition, and in particular the evolution of non-verbal numerical abilities.

Several aspects need be clarified. For instance the ontogeny of numerical competence in animals has been rarely investigated. It is unclear whether all species can represent numerical information or, on the contrary, use non-numerical continuous quantities that co-vary with number (such as cumulative surface area, density and space). In addition, the existence of a specific mechanism to process small numbers (<4), traditionally called 'subitizing', is highly debated. Neuro-anatomical correlates of numerical competence need also to be clarified, as well as brain lateralization of non-verbal numerical abilities.

We solicit contributions in a variety of formats, from empirical research reports, to methodological, review and opinion papers that can advance our understanding on the topic. We particularly invite papers exploring the following issues:

1. Do non-human numerical abilities improve in precision across development as observed in human infants?
2. Can animals discriminate between quantities by using numerical information only? Is number a 'last resort' strategy adopted when no other continuous quantity is available?
3. To what extent do animals show similar numerical abilities? Do they show evidence of a subitizing-like process?
4. What kinds of things can be represented numerically by animals? What evidence is there for cross-modal numerical judgments, or judgments of sub-sets of stimuli, or perhaps even counting-like behavior in non-human species?
5. Do comparative studies help us to shed light on the neuro-anatomical correlates of number?

By bringing together different studies on these issues we aim to contribute to a more complete picture of numerical competence in the absence of language.

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EDITORIAL
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Number without language: comparative psychology and the evolution of numerical cognition

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Curiosity about the numerical abilities of non-human animals has been a topic in experimental psychology for about as long as such a science has existed. Some of the earliest comparative work looked at how well animals could use number as a cue in making different kinds of judgments. Early results were mixed, and in some cases were incredibly controversial (e.g., the case of the horse Clever Hans). After the "fall" of behaviorism and the "rise" of cognitive psychology, the question of numerical competence became one of the dominant research areas in the new field of comparative cognition. The present series of papers in this special topic represents the newest additions to that research area. This special topic also serves as an anniversary of sorts, as it comes 25 years after one of the most influential papers on the subject of numerical competence in animals (Davis and Perusse, 1988). Comparing the major themes of that paper to the topics in this special issue serves to highlight where we came from, and where we might be going with future research.

Davis and Perusse (1988) and the commentaries that were involved in that paper presented a number of critical issues in the area of numerical cognition research at that time. One of the largest was whether the use of the term "counting" was appropriate for much of what was being studied with non-human animals, and they cautioned against applying that term to methodologies that did not require the principles that underlie counting in humans (e.g., Gelman and Gallistel, 1978). This problem seems to be largely resolved, as most researchers in the area today recognize that animals are not counting, even in their most sophisticated demonstrations. Davis and Perusse (1988) attempted to standardize terminology. Some of the terms they offered have come to be re-defined (e.g., "sense of number") whereas others have come to be re-named (e.g., changing *relative numerousness judgments* to *relative quantity judgments* where it is clear that number is not the only stimulus dimension that an animal could use to perform a task). Subitizing remains an interesting phenomenon, sometimes evident in animal research but other times not evident (see Murofushi, 1997). Davis and Perusse (1988) also called for the use of transfer tests, and better controls in experimental work, and although those concerns still remain (e.g., Beran, 2012), in general the field has risen to that challenge. Perhaps the biggest change has been the shift from questioning whether number is used by animals only as a "last resort" (e.g., Davis and Memmott, 1982) to the now general consensus that number is a relevant stimulus cue to which animals are sensitive in a number of contexts (e.g., Cantlon and Brannon, 2007; Agrillo et al., 2011). As the papers in this special topic demonstrate, animals can and do use quantitative and numerical information in a variety of contexts, and in some cases may even be fairly described as numerate, although with certain caveats such as being far more "fuzzy" in how they represent numerosities than are humans above 5 or 6 years of age.

This special topic encompasses 16 novel studies, including mammals (e.g., Beran et al., 2012; Panteleeva et al., 2013), birds (Armstrong et al., 2012), fish (Gómez-Laplaza and Gerlai, 2012), and invertebrates (Pahl et al., 2013). We learned that numerical information is a potential relevant cue also in species that have been poorly investigated compared to primates (e.g., dolphins: Yaman et al., 2012, beetles: Carazo et al., 2012). Some non-numerical visual cues, however, may play a key role too: for instance, overall quantity of movement within the shoals is a necessary condition for large (but not for small) shoals discrimination in angelfish, with interesting implications for the theoretical debate about how non-human animals process small and large quantities (Gómez-Laplaza and Gerlai, 2012). Also the lack of a ratio effect reported in wolves in the range 1–4 is potentially in line with the idea of different ways to process small and large quantities (Utrata et al., 2012). In contrast, data against the existence of a subitizing-like process have been described in primates (Jones and Brannon, 2012; Barnard et al., 2013) and canids (Baker et al., 2012), highlighting that we are still far from solving the question raised by Davis and Perusse regarding whether animals subitize (see also Cutini and Bonato, 2012). Interspecific studies comparing different species (fish: Agrillo et al., 2012; canids: Baker et al., 2012) are also reported in the special topic: in both of these studies similarities among the species are greater than differences, suggesting the existence of similar numerical systems among vertebrates.

The special topic also includes theoretical and research studies on human infants. In particular, attention has been focused on number-space interaction (de Hevia et al., 2012), the relation between numerical and non-numerical cues (Uller et al., 2013) and the development of ordinal abilities (Anderson and Cordes, 2013). It has been suggested that human and non-human animals share the same non-symbolic numerical systems

(Feigenson et al., 2004). If so, we believe that an interdisciplinary approach including cognitive (non-verbal numerical judgments in adults), developmental (newborns and infants) and comparative psychology will represent the very frontier of numerical cognition studies, enabling us to understand both the evolutionary foundations of our numerical abilities and the exact mechanisms underlying quantity discrimination in the absence of language.

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Activity counts: the effect of swimming activity on quantity discrimination in fish

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Human infants and non-human animals can discriminate the larger of two sets of discrete items. This quantity discrimination may be based upon the number of items, or upon non-numerical variables of the sets that co-vary with number. We have demonstrated that angelfish select the larger of two shoals of conspecifics without using inter-fish distance or space occupied by the stimuli as cues. However, density appeared to influence the choice between large shoals. Here, we examine the role of another non-numerical cue, swimming activity of the stimulus fish, in quantity discrimination by angelfish. To control this variable, we varied the water temperature of the stimulus aquaria or restricted the space occupied by each fish in the stimulus shoals. We used the previously successfully discriminated contrasts consisting of large (10 vs. 5) and small (3 vs. 2) shoals. We also studied whether more active or less active shoals are preferred in case of equally sized shoals (10 vs. 10, 5 vs. 5, and 3 vs. 3). When differences in stimulus fish activity were minimized by temperature manipulation we found angelfish to prefer the larger shoal in the 3 vs. 2 comparison, but not in the 10 vs. 5 comparison. When activity was controlled by space restriction, angelfish preferred the larger shoal in both numerical contrasts. These results imply that the overall activity level of the contrasted shoals is not a necessary condition for small shoals discrimination in angelfish. On the other hand, the results obtained for the large shoals, together with results obtained in the control treatments (equal numerical contrasts and differing activity levels), suggest that activity is a sufficient condition for discrimination when large shoals are involved. Further experiments are needed to evaluate the influence of other continuous variables, and to assess whether the mechanisms underlying performance are comparable to those suggested for other animals.

Keywords: quantity discrimination, continuous variables, swimming activity, angelfish, shoal choice, numerical cognition

INTRODUCTION

In the past decades a wealth of studies have provided evidence suggesting that human infants and other animal species possess non-verbal numerical competence encompassing a diversity of categories (Gallistel and Gelman, 2000; Feigenson et al., 2004; Hauser and Spelke, 2004). The study of numerical competences is of importance in comparative research because of the potential implications for understanding the evolutionary origins and development of such capabilities. For example, a growing number of studies indicate that quantity discrimination, the ability to distinguish between sets of discrete elements of different numerical size is a robust phenomenon across a large number of animal species. This capability has been shown not just in human and non-human primates (e.g., Hauser et al., 2000; Xu, 2003; Cantlon and Brannon, 2006; Hanus and Call, 2007; Evans et al., 2009) where most work has been conducted, but also in other mammalian species such as elephants (Irie-Sugimoto et al., 2009), bears (Vonk and Beran, 2012), dolphins (e.g., Kilian et al., 2003), horses (Uller and Lewis, 2009), coyotes (Baker et al., 2011), voles (Ferkin et al., 2005), dogs (West and Young, 2002; Ward and Smuts, 2007), cats (Pisa and Agrillo, 2009), and rats (Capaldi and Miller, 1988), birds (e.g., Emmerton and Renner, 2006; Rugani et al., 2008; Al Aïn et al., 2009; Bogale et al., 2011; Fontanari et al., 2011), fish species (e.g., Buckingham et al., 2007; Bisazza et al., 2010; Agrillo et al., 2011; Piffer et al., 2012), amphibians (Uller et al., 2003; Krusche et al., 2010), and even in invertebrates (e.g., Gross et al., 2009; Reznikova and Ryabko, 2011). Findings in this large variety of organisms provide good evidence to support the idea that the ability to discriminate between differently sized quantities has ancient evolutionary roots. This may not be surprising considering that the ability to quantify may have an adaptive role with potential advantages in functionally different contexts. These include evaluation of food sources (e.g., Creswell and Quinn, 2004; Bar-Shai et al., 2011), parental investment (e.g., Lyon, 2003), threats, and social interactions (e.g., Benson-Amram et al., 2011; Bonanni et al., 2011), as well as protection from predators and from sexually pursuing males (e.g., Hager and Helfman, 1991; Agrillo et al., 2007).

In several studies, however, numerical information was confounded with a variety of other variables which co-vary with item number. Although in nature individuals may attend simultaneously to both number and continuous quantities (Davis and Perusse, 1988), the failure to control for continuous non-numerical properties of the stimuli such as perimeter, density, surface area, visual extent, or movement makes it difficult to evaluate whether numerical competence indeed exists in all species studied. Thus, whether individuals discriminate between discrete quantities of items relying solely on number or they respond to a variety of continuous variables is still a matter of debate (Mix et al., 2002).

This question has mostly been investigated in human infants and non-human primates, where experiments have specifically been designed to disentangle the influence of these confounds by using stringent controls for non-numerical continuous variables. Apparently contradictory results have been obtained. Some studies report that infants and non-human primates respond to continuous variables instead of number, mainly when discriminating between small numbers of elements (Clearfield and Mix, 1999; Feigenson et al., 2002; Stevens et al., 2007). Other studies, after controlling for continuous extent, have found that individuals base their discrimination on numerical differences (Feigenson and Carey, 2003; Xu, 2003; Xu et al., 2005; Beran, 2007; Cantlon and Brannon, 2007; Tomonaga, 2008). The picture emerging from these studies suggests that both infants and non-human primates can rely spontaneously on number even when continuous variables are available, indicating that the use of number for discrimination is not a last resort strategy for them (Cantlon and Brannon, 2007; Cordes and Brannon, 2009). Likewise, it appears that infants respond to number rather than continuous extent when presented with object sets of contrasting properties (color, pattern, texture) and rely on continuous extent over number when identical objects are presented (Feigenson, 2005). In line with this, Beran et al. (2008) conclude that chimpanzees preferentially attended to number over continuous variables or vice versa depending on the task and/or experimental conditions. Nevertheless, research has not provided a clear account of under what condition animals may rely on either number or continuous variables. Although in most studies controlling for numerous factors has been attempted, it is not possible to completely disregard the possibility that the discrepancies arose as a result of the effect of the subjects' experience or other ontogenetic factors (but see Feigenson et al., 2004).

In non-primate animals, research on whether individuals discriminate between two sets of stimuli on the basis of number or continuous dimensions is rather scarce. Nevertheless, empirical studies with birds, mainly pigeons (e.g., Xia et al., 2001; Machado and Keen, 2002; Emmerton and Renner, 2006; Scarf et al., 2011) and chicks (e.g., Rugani et al., 2008, 2009, 2010), resulted in findings comparable to those obtained with human infants and primates. Similarities have been found in newborn chicks even in the use of continuous extent or number: newborn chicks will also discriminate between set of objects based on continuous extent over number if objects are homogeneous rather than heterogeneous (Rugani et al., 2010). In other animals this issue has not generally been systematically investigated and findings indicate that whereas some species when confronted with quantity discrimination tasks use the type of information provided by continuous variables (e.g., Pisa and Agrillo, 2009; Krusche et al., 2010) other species have been shown to use number as the relevant cue (e.g., West and Young, 2002; Kilian et al., 2003; Gross et al., 2009; Bogale et al., 2011).

In fish, this issue has also received only little attention. Although fish can discriminate between groups (shoals) of conspecifics of different numerical size (Krause et al., 1998; Bradner and McRobert, 2001; Binoy and Thomas, 2004; Agrillo and Dadda, 2007; Agrillo et al., 2007, 2008a; Buckingham et al., 2007; Frommen et al., 2009; Piffer et al., 2012), generally no control for continuous variables has been attempted. To date the only comprehensive approach to unravel the cues that guide fish in selection of numerically different shoals has been carried out in mosquitofish, *Gambusia holbrooki*, (Agrillo et al., 2007, 2008b, 2009, 2010, 2011) and evidence indicates that this fish species is able to discriminate the larger of two shoals solely on the basis of number (Dadda et al., 2009), although perhaps not all factors were controlled. For example, in this study the requirement for the experimental fish to see only one stimulus fish at a time may not have been met due to the large visual field of the study species that likely allowed these fish to view more than a single stimulus fish at a time in the employed experimental set up. Studies in angelfish (*Pterophyllum scalare*) also indicate that this cichlid species can discriminate between shoals of conspecifics of different size both when large shoals (≥4 fish) and when small shoals (<4 fish) are contrasted (Gómez-Laplaza and Gerlai, 2011a,b). In these studies angelfish always showed preference for the larger shoal when placed in a potentially threatening novel environment, presumably because larger shoals provide greater safety. But the question whether this discrimination was based upon numerical abilities of the angelfish or perception of a co-varying quantitative variable remained unaddressed. In a subsequent study (Gómez-Laplaza and Gerlai, 2013 in press) we began a systematic analysis of the potential non-numerical factors affecting shoal choice decisions in angelfish. Our results show that density of the shoals did affect the selection when angelfish were comparing large shoals (10 vs. 5 fish), but not when they were choosing between small shoals (3 vs. 2 fish). Inter-fish distance and space occupied by the stimulus shoals were found to have no significant effect in test fish's preference when both large (10 vs. 5 fish) and small shoals (3 vs. 2 fish) were contrasted.

In the present study, to gain a better understanding of the potentially intervening variables that affect decision making we decided to assess the potential role played by another non-numerical cue. This allows further investigation of whether angelfish posses a strict form of numerical competence or use other quantitative cues to guide their responses. Specifically we analyze the influence of swimming activity of the stimulus shoals on the ability of angelfish to discriminate between two shoals of different numerical size simultaneously presented. The amount of movement in the larger shoal is likely to be greater than in the smaller shoal. More active shoals may provide a more salient stimulus for a solitary fish seeking a shoal with which to associate. Consequently, angelfish could respond to how much movement is present within each of the shoals. In fact, swimming activity has been shown to influence shoal association decisions in fish (e.g., Pritchard et al., 2001; Gómez-Laplaza, 2006; Agrillo et al., 2008b; Harcourt et al., 2009), and movement of the stimuli was shown to affect quantity discrimination in other animal species too (e.g., Krusche et al., 2010).

Here two numerical comparisons were used: 10 vs. 5 fish (large numbers in both shoals) and 3 vs. 2 fish (small numbers in both shoals). These contrasts have previously been found to be reliably discriminated by angelfish which chose the larger of the two contrasted shoals (Gómez-Laplaza and Gerlai, 2011b, 2013 in press). In the present study, we controlled for swimming activity by minimizing the potential difference in total level of activity of the shoals to be compared. This was achieved either by lowering the temperature of the water of the aquarium in which the shoals with the larger number of members was presented while increasing the temperature of the shoals with the smaller number of members (Experiment 1), or by keeping the stimulus fish in small individual compartments, thus allowing little swimming (Experiment 2). We also performed the opposite manipulation and kept the number of contrasted shoal members constant while making the equally sized contrasted shoals differ in their activity levels.

MATERIALS AND METHODS

SUBJECTS AND HOUSING CONDITIONS

Wild type juvenile angelfish (*Pterophyllum scalare*, 2.8–3.0 cm standard length) were obtained from local commercial suppliers. Since differences in color morph of the subjects can influence results (Gómez-Laplaza, 2009) only fish from the same color morph were used. Likewise, only juveniles of this sexually monomorphic species were studied so as to eliminate possible confounding effects arising from courtship or agonistic/territorial interactions. The fish were housed in glass holding aquaria (length × width × depth: 60 cm × 30 cm × 40 cm) in groups of 18–20 and were allowed a minimum of 2 week acclimation period before behavioral testing.

Test fish and stimulus fish (which were used to elicit test fish behavior) were randomly chosen and were housed separately, with no visual and olfactory communication being possible between fish in the separate aquaria. Aquaria were filled with dechlorinated tap water kept at 25°C using thermostat-controlled heaters. Each aquarium was illuminated by a 15 W white fluorescent tube on a 12:12 h light:dark cycle, with lights on at 08:30 h. External filters continuously cleaned the aquaria, which were provided with a 2 cm gravel substratum. The fish were fed commercial fish food (JBL GALA, JBL GmbH & Co. KG, Neuhofen, Germany) twice daily, at 10.00 h and at 18.00 h.

EXPERIMENTAL APPARATUS

The experimental apparatus to assess spontaneous shoaling preference in binary choice tests was similar to what we used in previous studies (Gómez-Laplaza and Gerlai, 2011a,b). It consisted of a test aquarium with one stimulus aquarium positioned at each end. The test aquarium was identical in all respects to the holding aquaria and was maintained under the same conditions, as also were the stimulus aquaria. The stimulus aquaria were of smaller dimensions (30 × 30 × 40 cm depth) but the side facing the test aquarium was of the same size as the short lateral sides of the latter (30 × 40 cm). The test aquarium and stimulus aquaria were illuminated with a 15 W white fluorescent light tube. A divider isolated a 10 cm compartment in the stimulus aquaria where the stimulus shoals were presented. In the other part of the stimulus aquaria, the stimulus shoals were placed before preference tests commenced. Except for the front, all exterior walls of the aquaria that were not adjacent to other aquarium walls were lined with white cardboard to prevent the fish from being influenced by external visual stimuli. Removable opaque white barriers placed outside the two end sides of the test aquarium were used to visually isolate the latter from the stimulus aquaria and these barriers were removed when preference tests commenced.

Five vertical lines drawn on the front and back walls of the test aquarium at a distance of 10 cm divided the test aquarium into six equal zones and facilitated measurements of the test fish's movements and position. The two 10 cm zones closest to the stimulus aquaria were considered as the preference zones. At least three-quarters of the body length of the fish had to be within the boundary for the fish to be included in a particular zone. Swimming activity of test fish was measured as the frequency (number of times) with which fish crossed the lines drawn on the walls of the aquarium during the tests.

GENERAL EXPERIMENTAL PROTOCOL: PREFERENCE TESTS

The experimental procedure was also similar to what has been described previously (Gómez-Laplaza and Gerlai, 2011a,b). In each trial a single test angelfish was given a choice between two numerically different shoals of conspecifics presented simultaneously and positioned in the stimulus aquaria on opposite sides of the test aquarium. The chosen number of fish that served as stimulus shoals were taken at random from the stimulus fish holding aquaria and were gently placed into the part of the stimulus aquaria not occupied by the stimulus compartment. To control for any potential side bias the allocation of the shoals to the stimulus aquaria was initially determined at random and then counterbalanced across trials. All fish were gently handled using dip netting and transferred between aquaria in small Perspex containers to minimize possible handling stress. In addition, all fish were allowed a 15 min acclimation period in the new aquaria (see below). Trials took place 15–30 min after feeding in the morning (i.e., they started around 10:15–10:30 h) when the stimulus shoals where gently transferred into the part of the stimulus aquaria not occupied by the stimulus compartment. Test fish were randomly selected from a test fish holding tank, and were introduced singly to the center of the test aquarium. Fish were allowed to swim freely with the barriers between aquaria removed, so they could see the 10 cm compartments where the stimulus shoals would be presented. This acclimation period in the absence of stimulus shoals lasted for 15 min and also allowed stimulus shoals to settle in the respective stimulus aquaria. At the end of this period, the barriers between aquaria were replaced and the stimulus shoals were gently placed into the 10 cm compartment. Test fish were placed in the center of the test aquarium via a transparent, open-ended, plastic cylindrical start box (7 cm diameter), where they remained for 2 min. During this time, the opaque white barriers between the aquaria were removed to reveal the stimulus shoals, thus allowing the confined test fish to view the stimulus shoals at both sides of the test aquarium. The start box was then gently raised and the test fish released. Shoaling behavior, recorded over a 15 min period, was defined as the time spent by the test fish in the 10 cm preference zones, i.e., within 10 cm from the wall adjacent to the stimulus shoal aquaria on either side. Behavioral responses of the test fish were recorded with a video camera (Sony video Hi8, model CCD-TR750E) concealed behind a blind. The recordings were later replayed for analysis.

At the conclusion of the recording session, the barriers between aquaria were replaced and the positions of the stimulus shoals were interchanged between stimulus aquaria to control for any potential directional bias (except for Experiment 1 in which replacing the water of the stimulus aquaria at different temperatures was not practical). After a second 15 min settling interval, another 15 min observation period was run with the same test fish following the same procedure as described above. After the second observation period, the aquaria were emptied and cleaned before being replenished with dechlorinated tap water. In the experiments individual fish were tested only once, and none of the fish in the stimulus shoals were used as test fish. Within each experiment, the order of testing was randomized according to different treatment conditions. Stimulus shoals were rearranged after each session, so that each test fish was exposed to a different stimulus fish set. The fish were returned to the suppliers at the end of the study. The experiments described here comply with the current laws of the country (Spain) in which they were performed (ref.: 13-INV-2010).

EXPERIMENT 1: CONTROL FOR SWIMMING ACTIVITY IN LARGE (10 VS. 5) AND SMALL (3 VS. 2) SHOALS BY MANIPULATING WATER TEMPERATURE

The aim of this experiment was to examine whether the preference previously shown by angelfish for the larger shoal, in both 10 vs. 5 and 3 vs. 2 contrasts, could have been influenced by the swimming activity of the stimulus fish within the shoals regardless of shoal numerical size. One common way of controlling for swimming activity is by varying water temperature. Because teleost fishes are ectothermic, swimming activity is generally linked to water temperature as body temperature influences metabolic efficiency for many physiological processes (e.g., Bennett, 1990). Therefore, it is possible to modify the swimming activity of angelfish by increasing or decreasing water temperature, a procedure that has been used in choice situations in a number of fish species (Pritchard et al., 2001; Agrillo et al., 2008b). Angelfish is a gregarious Amazonian cichlid species which is widely distributed over a vast area and is adapted to a highly variable natural environment (White, 1975). In the laboratory, angelfish has also been shown to be able to live in a broad range of temperatures (Pérez et al., 2003). Here, initially to test whether indeed swimming activity of angelfish can be manipulated through temperature, we used three thermostat-controlled water temperatures, 21, 25, and 29˚C, that are within the temperature tolerance limit for this species. First, three groups of 14 fish were placed each in one holding aquarium whose temperature was 25˚C. In one of the aquaria the temperature was gradually raised 1˚C per day, for 4 days, until a temperature of 29˚C was reached, whereas in other aquarium the temperature was gradually lowered 1˚C per day, also for 4 days, until a temperature of 21˚C was reached. Fish in the remaining aquarium were kept at 25˚C. Once the final temperatures were reached, groups were maintained at these temperatures for 10 days. Then, fish of each of the groups were individually transferred to a new aquarium (60 cm × 30 cm × 40 cm) where swimming activity was measured. The water temperature of the new aquarium was adjusted to the corresponding temperature of the previous holding aquarium of the fish to be tested (21, 25, or 29˚C). After a 15 min acclimation period, fish locomotor activity was recorded for 15 min with the video camera. We quantified swimming activity by counting the number of cells entered (5 × 6 cm high) of a grid drawn on the frontal wall of the new aquarium. Each fish was used only once.

Thereafter, to control for the potential effects of swimming activity on quantity discrimination, we gave test fish the choice between two shoals of different numerical size presented at two different water temperatures. These preference tests were carried out as indicated above. When testing preference between two large shoals (10 vs. 5), fish in the larger stimulus shoal were presented in the stimulus compartment with water at 21˚C (the same temperature as their corresponding holding aquarium), whereas fish in the smaller shoal were presented in water at 29˚C (the same temperature as their corresponding holding aquarium). Similarly when testing preference between shoals in the small number range (3 vs. 2): the larger shoal was presented in water at 21˚C, whereas the smaller shoal at 29˚C. The water temperature in the test aquarium, where the test fish were introduced, was at 25˚C (the same temperature as test fish holding aquarium). The position of the stimulus shoals was counterbalanced across subjects. Fourteen fish were observed for each of the two sets of choices (i.e., a total of 28 experimental fish). To ensure that swimming activity was equated between the stimulus shoals, while the focal fish were being tested we also recorded, with an additional concealed video camera (Sony Handycam HDR-XR160E), the activity of the stimulus fish in their respective compartments. Recordings were carried out with the camera angled to allow activity to be observed, and were alternated between the two stimulus compartments, thus obtaining seven recordings of each stimulus shoal in each contrast. For two randomly selected fish in each shoal, we measured the number of cells crossed (5 × 6 cm high) by these stimulus fish over the 15 min period. The number was averaged for the two fish to give a mean value for each stimulus shoal size. Given the difficulty of monitoring fish in the 10 fish shoals, the fish to be observed were identified by previously making small cuts on some of their fins. This process took less than 30 s with fish recovering immediately and no effect on their later behavior was observed.

A set of control experiments were also performed. These consisted of exposing test angelfish to pairs of shoals composed of the same number of fish: 10 vs. 10, 5 vs. 5, and 3 vs. 3 but presented in different water temperature (i.e., one of the shoals was placed in water at 21˚C, slow moving, whereas the other, of equal numerical size, was placed in water at 29˚C, fast moving). Fourteen fish were observed in each set of choices, giving a total of 42 fish tested.

EXPERIMENT 2: CONTROL FOR SWIMMING ACTIVITY IN LARGE (10 VS. 5) AND SMALL (3 VS. 2) SHOALS BY RESTRICTING SWIMMING OF THE FISH IN THE STIMULUS SHOALS

In this experiment we used another way of controlling for the potential effect of swimming activity on quantity discrimination in an attempt to further clarify the role of this variable on performance of angelfish. It consisted of equating activity in the shoals by ensuring that all stimulus fish had a similar level of activity.

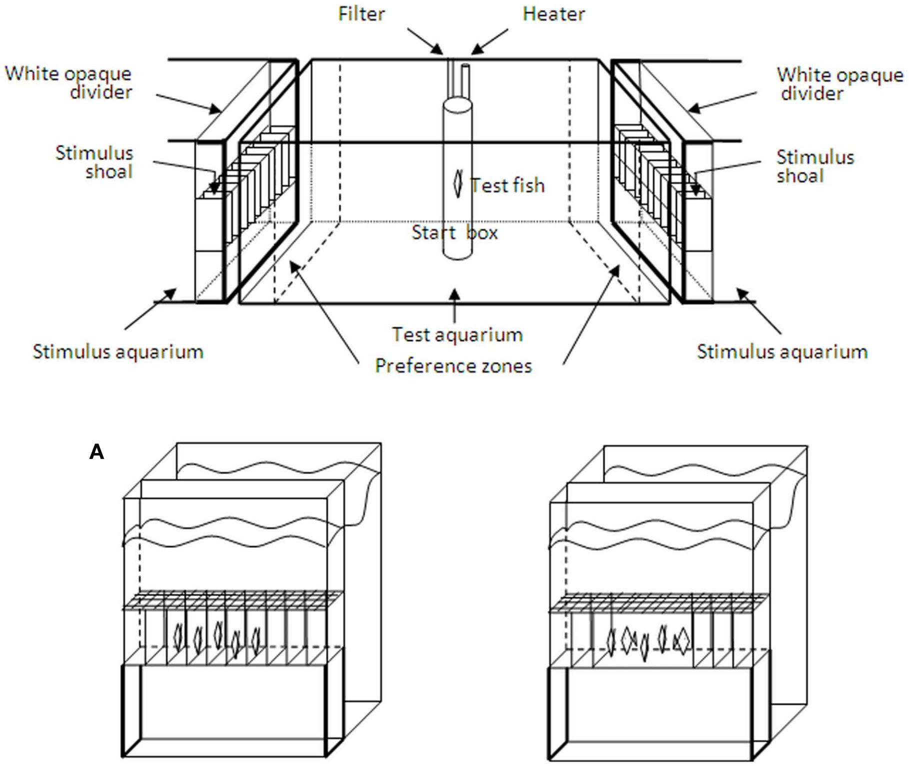

FIGURE 1 | The experimental apparatus with the central test aquarium and the two stimulus aquaria. In the latter, removable opaque dividers were used to delimit a 10 cm compartment where the stimulus shoals were placed. Opaque barriers were used to visually isolate the two stimulus aquaria from the test aquarium. These barriers were removed when the preference test commenced. The time spent by the test fish within 10 cm of the stimulus shoals (preference zones) was recorded. The frames delimiting 10 small identical sectors where fish of the stimulus shoals were placed in Experiment 2 are also shown. Figure is not to scale. **(A)** The stimulus aquaria with the stimulus compartments utilized in Experiment 2. To control for the overall swimming activity of the shoals, the stimulus compartments were divided into 10 sectors by transparent partitions and each fish of the stimulus shoals was individually placed into the adjacent sectors. In the control treatments (one shoal more stationary and the other moving), the central partitions were removed and fish in one of the shoals were allowed to swim freely in that space (illustrated in the case of 5 vs. 5 fish in the Figure). Presentation of the stimulus shoals in the stimulus compartments was balanced between the two stimulus aquaria.

Two removable transparent Plexiglas frames delimiting 10 small identical sectors (length × width × depth: 3 cm × 10 cm × 13 cm) were constructed and introduced into each stimulus compartment (**Figure 1**). Stimulus fish were confined in these small sectors that allowed little movement, thus providing control over movement and orientation. The stimulus shoals were presented in midline of the aquaria. When testing preference between large shoals, each single stimulus fish of the 10 fish shoals was confined into each of the 10 separate small sectors, whereas each of the fish of the five fish shoals was confined into each of the five central small sectors of the frames. Similar procedure was followed when the test fish were presented with a binary choice between three fish shoals and two fish shoals, stimulus shoals being now confined in the central small sectors. Note that by positioning the stimulus fish in this way, density and inter-fish distance was also equated; therefore these three non-numerical continuous variables were simultaneously controlled. Fourteen test fish were observed for each of these two sets of choices (i.e., a total of 28 experimental fish were tested).

In addition, to control for general effects of swimming activity we ran a further set of control experiments. The treatments consisted of presenting pairs of equally sized stimulus shoals in which fish in one of them were confined into each of the small sectors, thus remaining stationary, whereas fish of the other stimulus shoals were allowed to swim within the entire space occupied by the fish in the confined shoal. This was done by removing the corresponding partitions delimiting the sectors in the frame (see **Figure 1A**, as an example). Thus, the overall space occupied by the contrasting shoals was the same because the outermost walls were kept in position, but in one of the shoals the individuals could move around in the entire space instead of being confined into the small sectors. Three control conditions were employed: 10 vs. 10 fish, 5 vs. 5 fish, and 3 vs. 3 fish, each including 14 experimentally naive test fish (i.e., a total of 42 fish were observed).

STATISTICAL ANALYSIS

The time spent in the preference zones was recorded as a measure of each test fish's social preference for a particular stimulus. We calculated a preference index for each test fish as follows: time spent in the preference zone near the larger stimulus shoal was divided by the total time spent shoaling (i.e., the time spent within 10 cm from either stimulus shoals). A preference index equaling 1 would indicate complete preference for the larger shoal, whereas an index value of 0 would indicate complete preference for the smaller shoal. In the control treatments, with equal number of fish in the contrasting shoals, the preference index was calculated similarly but the numerator referred to the warm-water shoal (Experiment 1) or free-swimming shoal (Experiment 2). A one sample two-tailed t-test was used to compare the observed proportions against a chance value of 0.5 (null hypothesis). The proportions were normally distributed. Statistical probabilities reported are two-tailed. The null hypothesis was rejected when its probability (P) was less than 0.05.

The effect of water temperature on swimming activity was investigated with one-way ANOVA for independent samples. In case of a significant effect, Tukey Honestly Significant Difference (HSD) *post hoc* multiple comparison test was performed to determine where significant differences lay.

In Experiment 1, occasionally test fish did not enter both preference zones during the test. When this occurred the subjects were excluded and replaced by another fish. Five subjects (7%) were replaced: two subjects in 5 vs. 10, one in 10 vs. 10, and two in 5 vs. 5 contrasts.

RESULTS

EXPERIMENT 1: CONTROL FOR SWIMMING ACTIVITY BY MANIPULATING WATER TEMPERATURE

In the initial experiment, fish tested at different temperatures showed different overall levels of swimming activity, with the number of cells crossed decreasing with water temperature. Fish in the lower temperature group showed displacements at low speed, whereas at higher temperature fish moved faster (mean ± SEM, 21˚C: 88.86 ± 12.21; 25˚C: 145.79 ± 18.06; 29˚C: 169.36 ± 25.94). Temperature had a significant effect upon fish activity (ANOVA: $F_{2,39} = 4.475$, $P = 0.018$), and the Tukey HSD test confirmed a significantly reduced locomotor activity of fish in the lower temperature group (21˚C) relative to that of fish in the higher temperature group (29˚C; $P = 0.016$). Activity of fish tested at 25˚C was intermediate and not significantly different from that of fish in either of the other groups ($P > 0.05$).

When test fish were placed in a novel test aquarium in the absence of stimulus shoals they generally swam actively mainly along the rear wall of the aquarium. All fish were observed to enter both ends of the test aquarium and during this period they showed a significantly higher swimming activity (number of lines crossed) compared to that shown in the presence of the stimulus shoals (mean ± SEM: 53.07 ± 3.31 and 37.04 ± 2.23, respectively; paired t-test: $t_{69} = 4.528$, $P < 0.001$). The reduced shuttling activity during the presence of stimulus shoals is due to experimental fish staying longer in the preference zones close to the stimulus fish. This pattern was similar under the two experimental treatment conditions (10 vs. 5 and 3 vs. 2: overall mean ± SEM: 51.43 ± 4.97 before test and 38.71 ± 3.33 during test; $t_{27} = 2.216$, $P = 0.035$) as well as in the three control situations (10 vs. 10, 5 vs. 5, and 3 vs. 3: overall mean ± SEM: 54.17 ± 4.45 before test and 35.93 ± 3.00 during test; $t_{41} = 4.038$, $P < 0.001$).

When presented with the 10 vs. 5 fish contrast test fish failed to show preference for either shoal ($t_{13} = 0.297$, $P = 0.771$; **Figure 2**). In this test situation the larger shoal contained slow moving (21˚C temperature) and the smaller shoal contained fast moving (29˚C temperature) stimulus fish, which made the overall swimming activity of these two contrasted stimulus shoals statistically indistinguishable (mean ± SEM: large shoal 197.50 ± 23.57, small shoal 232.36 ± 22.40; unpaired t-test, $t_{12} = 1.072$, $P = 0.305$). Thus, it appears, that when overall swimming activity is similar despite the numerical difference between the contrasted shoals, angelfish were unable to distinguish the two shoals, a result that suggests that indeed angelfish perceives and responds to swimming activity when making a choice between shoals. Interestingly, however, when small shoals (3 vs. 2 fish) were contrasted, experimental angelfish reliably chose the larger shoal ($t_{13} = 3.420$, $P = 0.005$; **Figure 2**) despite that both shoals had statistically indistinguishable levels of overall activity (mean ± SEM: large shoal 139.71 ± 13.71, small shoal 151.86 ± 19.52; unpaired t-test, $t_{12} = 0.509$, $P = 0.620$). Thus, we conclude that activity of the contrasted shoals did not play a significant role when experimental angelfish fish had to discriminate between small quantities. This result was confirmed in the control condition in which small shoals of equal numerical size (3 vs. 3 fish) but with expected different overall levels of swimming activity were contrasted. In this test situation, experimental angelfish did not discriminate the shoals and performed at a level not significantly different from chance ($t_{13} = 0.497$, $P = 0.627$; **Figure 2**).

In the other control treatments using large shoals, however, we obtained different results. We found experimental angelfish not to show a significant discrimination between shoals of differing activity levels in the 10 vs. 10 fish comparison ($t_{13} = 0.846$, $P = 0.403$; **Figure 2**) although they still appeared to prefer the faster swimming shoal. However, experimental angelfish did exhibit a significant preference in the 5 vs. 5 fish comparison, spending significantly more time close to the shoal that was kept at the high temperature (29˚C, and thus was expected to show increased activity) compared to the other shoal that was kept at the low temperature (21˚C, expected low activity; $t_{13} = 2.890$, $P = 0.013$; **Figure 2**).

EXPERIMENT 2: CONTROL FOR SWIMMING ACTIVITY BY RESTRICTING THE SPACE AVAILABLE TO FISH

As in the former experiment, during the acclimation period with no stimulus shoals, all test fish entered both ends of the tanks and exhibited a significantly higher swimming activity as compared to that shown in the presence of the stimulus shoals (mean ± SEM: 61.11 ± 4.13 and 42.34 ± 3.00, respectively; paired t-test: $t_{69} = 4.35$, $P < 0.001$). This pattern was also found in the two treatments in which the stimulus shoals were of different numerical size (mean ± SEM: 57.96 ± 4.61 and 29.32 ± 3.59, respectively; paired t-test: $t_{27} = 7.801$, $P < 0.001$), suggesting that during the test period experimental fish stayed close to the stimulus shoals, thus reducing shuttling activity. However, such overall reduction of activity during tests was not significant relative to the acclimation period when the shoals had equal numerical size (10 vs. 10, 5 vs. 5, and 3 vs. 3: overall mean ± SEM: 63.21 ± 6.19 before test and 51.01 ± 3.88 during test; paired t-test: $t_{41} = 1.844$, $P = 0.072$). This finding may possibly be due to greater difficulty in decision making by experimental angelfish during the control treatments, resulting in experimental fish moving more frequently from one stimulus shoal to the other.

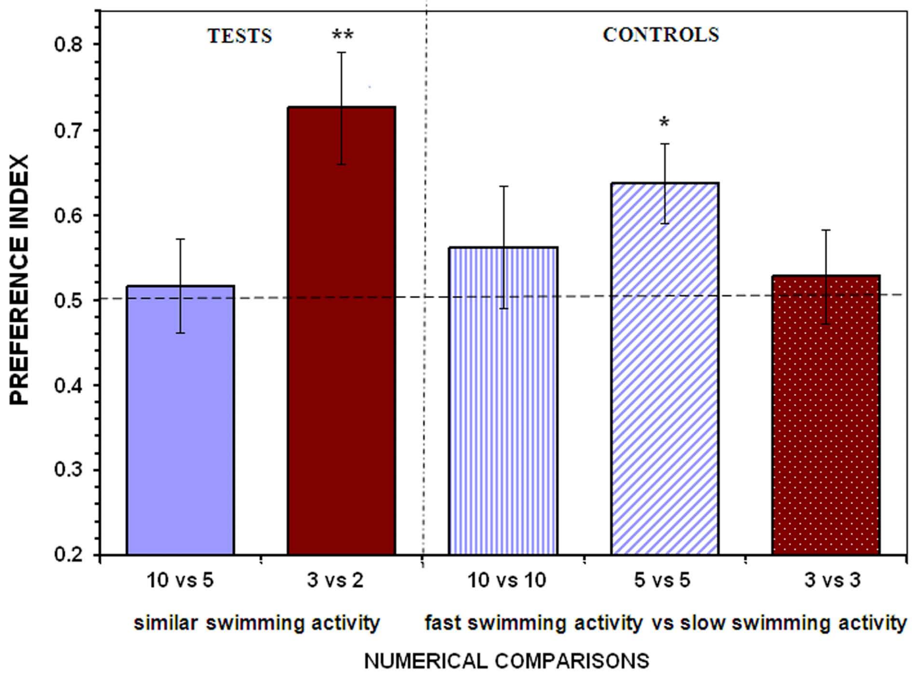

FIGURE 2 | Control for the overall activity of the contrasting stimulus shoals. To minimize differences in the overall levels of swimming activity between the shoals, the water temperature was varied. The large shoal was presented in water at 21˚C in the stimulus compartment, whereas the smaller shoal at 29˚C. The water temperature in the test aquarium, where the test fish were introduced, was at 25˚C. In the control treatments one of the equally sized shoals was presented at 29˚C and the other at 21˚C. Proportion of time (*preference index*) spent by test fish in the 10 cm preference zone close to stimulus fish (mean ± SEM) is shown. Values above 0.5 indicate a preference for the more numerous shoal of stimulus fish or a preference for the more active, faster moving shoal when the stimulus shoals are of the same numerical size. Significant departure from the null hypothesis of no preference is indicated by asterisks: $^{**}P < 0.01$, $^{*}P < 0.05$.

When given a choice between two large stimulus shoals (10 vs. 5 fish) in which the movement of the fish within each stimulus was restricted, a significant preference for shoaling with the larger shoal was found ($t_{13} = 2.892$, $P = 0.013$; **Figure 3**). Likewise, when the two contrasting shoals were numerically small (3 vs. 2 fish) a significant preference for the larger shoal was again detected ($t_{13} = 3.166$, $P = 0.007$; **Figure 3**). These results suggest that the swimming activity of the shoals is not a fundamental cue when angelfish make shoaling decisions, at least within the range of the numerical size of the shoals and under the experimental conditions employed in this study.

The control experiments, however, suggested that the activity of the shoals did affect shoal preferences in the large number range. When test angelfish were presented with two shoals of identical numerical size in which one of the shoals had quasi-stationary members whereas the other had fish swimming freely, a significant preference for the more active shoal was found in both the 10 vs. 10 fish, and the 5 vs. 5 fish comparisons ($t_{13} = 2.237$, $P = 0.043$; $t_{13} = 2.788$, $P = 0.015$, respectively; **Figure 3**). In contrast, when the choice was between two small shoals of identical numerical size (3 vs. 3 fish), angelfish performed at a level not significantly different from chance, showing no preference for any of the stimulus shoals ($t_{13} = 0.967$, $P = 0.351$; **Figure 3**). These control treatments demonstrate that angelfish is sensitive to the activity of the stimulus shoals and that this variable can be an important cue that guides the choice of angelfish when large numbers are involved.

DISCUSSION

At the origin of the present research is the broader issue of whether fish discriminate between shoals of conspecifics of different size on the basis solely of number or they respond to continuous variables that co-vary with number. In preceding studies we found that angelfish preferred the larger stimulus shoal to the smaller one both when large shoals (10 vs. 5 fish) and when small shoals (3 vs. 2) were contrasted (Gómez-Laplaza and Gerlai, 2011b, 2013 in press). But in these experiments we did not control for the potential influence of swimming activity of the stimulus shoals. The present experiments were designed to examine the potential role of swimming activity, a prominent non-numerical cue. Experiment 1 showed that when large shoals were contrasted (10 vs. 5) and the difference between overall activity level in the numerically different shoals was minimized, angelfish showed no preference for the larger shoal. In contrast, when comparisons involved small shoals (3 vs. 2) fish did prefer the larger shoal even when potential differences in activity levels were minimized between the contrasted stimulus shoals. This latter result was confirmed in Experiment 2 using a different method of controlling the influence of activity (by restricting the movement of fish in the stimulus shoals). Again fish exhibited a preference for the larger shoal (three fish)

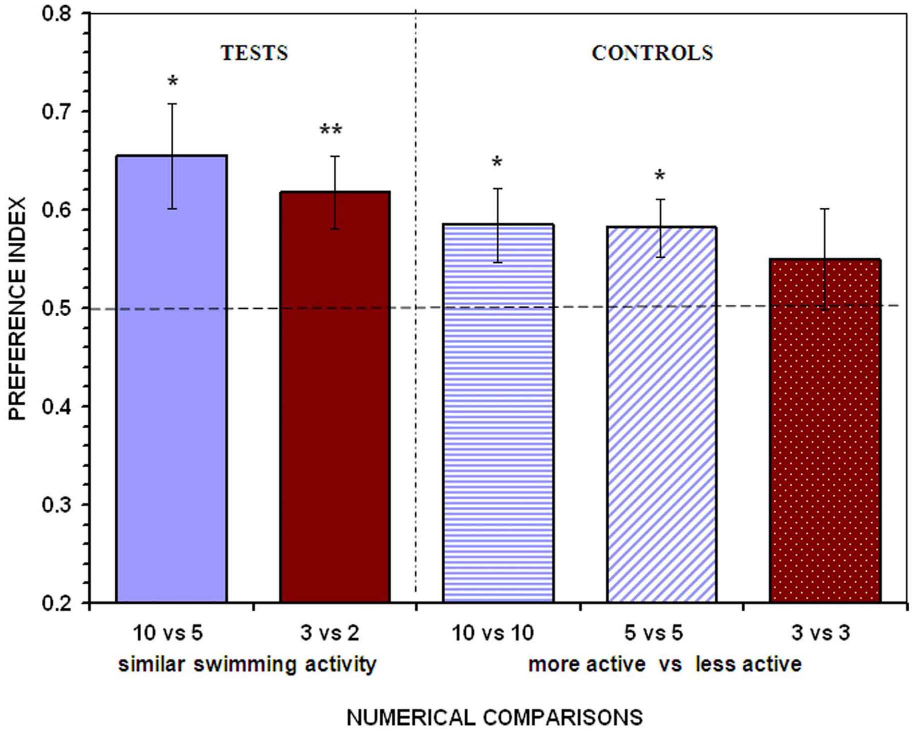

FIGURE 3 | Control for the overall activity of the contrasting stimulus shoals. To equate swimming activity between the members of the shoals, the stimulus compartments were divided into 10 small sectors using transparent partitions. Each fish of the shoals was individually confined into each of the adjacent sectors, where activity was restricted. In the case of shoals of five, three, and two fish, these were restrained into each of the central sectors. In the control treatments one of the shoals remained in the small sectors (i.e., stationary) while the other was allowed to swim (i.e., active). Proportion of time (*preference index*) spent by test fish in the 10 cm preference zone close to stimulus fish (mean ± SEM) is shown. Values above 0.5 indicate a preference for the more numerous shoal of stimulus fish or a preference for the active shoal when the stimulus shoals are of the same numerical size. Significant departure from the null hypothesis of no preference is indicated by asterisks: $^{**}P < 0.01$, $^{*}P < 0.05$.

over the smaller one (two fish). In summary, we found that overall activity of stimulus shoals had no significant influence on the decision making of angelfish when selecting between two shoals within a small number range. Further support for these results comes from the outcome of the control treatments. Neither in Experiment 1 nor in Experiment 2 did we find a significant preference for the stimulus shoal (3 vs. 3 fish) that was expected to be more active (because of warmer water, or more freedom to swim around). Thus, we conclude that when it comes to comparing shoals of small size, overall activity level of the contrasted shoals is not a necessary characteristic upon which angelfish base their discrimination. It is notable that although the preference did not reach significance (control treatments), it is possible that with a larger sample size, and a greater statistical power, the tendency would have been found significant, a question that needs further clarification in the future.

One could argue that even for small shoal comparisons angelfish might have used other continuous cues. However, our previous findings already ruled out the potential role of density, inter-fish distance, and space occupied by the stimulus shoals (Gómez-Laplaza and Gerlai, 2011b, 2013 in press). Others studying another fish species, the mosquitofish, have also showed that overall swimming activity does not affect discrimination between small shoals (Agrillo et al., 2008b). Furthermore, using the method of sequential presentation of the fish, Dadda et al. (2009) reported that density and the proportion of space occupied by the shoals did not affect preference, and using a training procedure with geometric figures Agrillo et al. (2009) found that density of the elements, total luminance, or the sum of perimeters of the stimuli did not affect performance in mosquitofish. Thus, it appears that when discriminating between small shoals fish do not use some prominent continuous variables. Nevertheless, other non-numerical variables such as overall space occupied and cumulative surface of the sets of geometric figures (Agrillo et al., 2009), as well as the surface area of the stimulus fish (Agrillo et al., 2008b) were found to influence discrimination of small quantities. In different animal species, surface area (or cumulative amount) has also been shown to provide a basis for discrimination (e.g., Stevens et al., 2007; Beran et al., 2008; Tomonaga, 2008; Pisa and Agrillo, 2009), and studies with human infants indicate that they may rely on surface area or contour length when discriminating between small quantities (Clearfield and Mix, 1999; Feigenson et al., 2002; Xu, 2003; Cordes and Brannon, 2008). Thus, surface area (and/or contour length) seems to be a salient stimulus property affecting discrimination in several species including fish. We have not tested the potential influence of the surface area of the stimulus shoals in angelfish preference, but at present, after controlling for a number of non-numerical variables, one at a time, (i.e., inter-fish distance, linear extent, density, and now swimming activity of the stimulus shoals) our results indicate that at least these variables have little effect on angelfish's discrimination of small shoals. Nevertheless, further research is needed to assess the importance of other stimulus properties, particularly surface area and boundary length of the stimuli. Furthermore, we may also need to control for all confounding variables simultaneously to conclusively ascertain the capacity of angelfish to utilize number representation when small shoals are encountered.

Although we found angelfish not necessarily to show discrimination between small shoals on the basis of overall activity levels of the shoals, when large shoals were contrasted the results yielded a different picture. As noted earlier, in Experiment 1 with the potential differences in level of activity minimized between the shoals, subjects were not able to distinguish between shoals of 10 vs. 5 conspecifics. Preference for the more active shoal apparently increased but did not reach significance when the number of fish in the shoals was equated (10 vs. 10). Swimming activity of the stimulus shoals was also found to influence discrimination in the other control treatment (5 vs. 5). Here experimental angelfish did exhibit a significant preference for the more active of the two equally sized shoals. We can conclude from these results that the overall activity difference can be a sufficient condition for discrimination in angelfish, and it seems to be a necessary condition as indicated by the results when the overall difference in swimming activity between the numerically different shoals was minimized (10 vs. 5). These results are fairly consistent with the discrimination of large shoals found in mosquitofish. In this latter species, subjects responded at chance level when presented with shoals of four vs. eight individuals as long as swimming activity was equated between shoals through manipulation of water temperature (Agrillo et al., 2008b). Salamanders, another simple vertebrate, have also been reported to discriminate between large quantities on the basis of movement (Krusche et al., 2010). Furthermore, other continuous variables such as density (Frommen et al., 2009) and surface area (Agrillo et al., 2008b) have also been shown to play a role in discrimination of large shoals in fish. Cumulative surface area also affected discrimination of large quantities of geometric figures in mosquitofish (Agrillo et al., 2010). Although in a previous study neither overall space occupied by the shoals nor inter-fish distance were found to be necessary conditions for the angelfish's choice between large shoals (10 vs. 5), density was shown to play a role in the choice (Gómez-Laplaza and Gerlai, 2013 in press). It is possible that the denser 10 fish shoal relative to the 5 fish shoal had a potentially greater overlap among individuals, reducing the visibility of the shoal, and the test fish thus could not have perceived it as large enough to be selected. This seems unlikely since fish in the 10 fish shoal were moving slowly and the formation of denser shoals tends to be greater at higher temperatures (see below). Therefore, the role played by density and swimming activity (current experiment) indicates that angelfish are not necessarily able to discriminate large quantities on purely numerical basis. Interestingly, in some fish species it has been reported that, after controlling for non-numerical variables, individuals are able to discriminate between large quantities, apparently with number controlling the selection (Agrillo et al., 2010; Bisazza et al., 2010), but the use of some non-numerical variables could not completely be excluded. Results with human infants and non-human primates suggest that these subjects rely mainly on number when discriminating large sets (Lipton and Spelke, 2003; Brannon et al., 2004; Xu et al., 2005), even though the sets were composed of moving items (Beran, 2008; Beran et al., 2011).

We have not controlled for all continuous variables simultaneously, and also have not systematically examined the potential effect of surface area and contour length. Also notably, in one of our control conditions, the one in which we presented two 10-member fish shoals kept at low vs. high water temperatures (inactive vs. active), preference for the more active shoal was apparent but did not reach significance. It is not clear why angelfish were unable to make a significant choice under this condition and why they could show a preference for the more active shoal in the 5 vs. 5 condition. As mentioned above, it is possible that larger sample sizes would have allowed us to find this apparent effect significant. Another possible explanation for lack of significance is that at the higher temperature, with fish moving faster within the shoal, individuals can temporarily overlap with each other and may not be always simultaneously visible. The effect of overlap is likely to be greater in larger shoals than in smaller ones thus resulting in different outcomes for the 10 vs. 10 and 5 vs. 5 contrasts. In other words, due to the greater overlap, choice could be affected by the total surface area of the fish which could have been reduced in the more active shoal. A smaller overlap of individuals in the low temperature shoal allowing for all fish to be distinguished from each other appears to be a prerequisite for optimal discrimination, even if discrimination is not based on density perception (see Kramer et al., 2011). The existence of conflicting preferences (e.g., more active shoal with reduced overall surface area at 29˚C vs. greater surface area shoal with low swimming activity at 21˚C) has been demonstrated to lead to individual variation in discrimination and lack of clear choice (e.g., Wong and Rosenthal, 2005). Until the effect of the surface area with two fully visible shoals is evaluated in angelfish the above arguments remain speculative. Alternatively, it is also possible that fish in the shoals adopted different spatial configuration which could affect discrimination. It has been shown that some fish species increase shoal cohesion and form more compact shoals at higher water temperature (Weetman et al., 1998). Although such shoals may be preferred because they are expected to provide better protection from potential danger, aggregating closely may also indicate greater potential predation risk (i.e., it is an antipredator behavior, Gotceitas et al., 1995; Speedie and Gerlai, 2008) and these conflicting cues could restrain test fish from clearly selecting the more active shoal. Thus, the potential benefit of an active shoal may be outweighed by the potential cost of increased risk exposure and this could affect selection of shoal. Position in the water column, postural changes, or other more subtle behavioral differences between shoals could likewise affect the spatial configuration of the shoals and provide cues that influence the decision making of fish, as it has also been suggested for other animal species (e.g., Kilian et al., 2003; Beran, 2006; Krusche et al., 2010). Specific experimental studies are needed before a precise explanation of the behavior exhibited by test fish in this condition can be offered.

In contrast to the results of Experiment 1, Experiment 2 suggests that a clear choice between numerically different shoals is exhibited even when differences in activity of these shoals is minimized. Angelfish were capable of assessing differences in shoal size, preferring the larger shoal (10 fish) over the smaller one (5 fish) even though the activity level of both shoals was similar. Although linear extent of the contrasted shoals was different, this continuous variable has previously been shown not to have much influence on shoal choice (Gómez-Laplaza and Gerlai, 2013 in press). Notably, however, surface area also differed between the above shoals and effect of this variable has not yet been tested. It is also notable that when confronted with shoals of equal size (10 vs. 10, and 5 vs. 5), with one of the two confined to a small space (leading to reduced activity) and the other not (high level of activity), angelfish did spend significantly more time near the active shoal, revealing that angelfish are able to use activity level as a cue in their choice. These results suggest that the activity level, as controlled in this experiment, may contribute to discrimination and that it can be a sufficient cue with large shoal size (see discrimination between more and less active shoals in case of 10 vs. 10 and 5 vs. 5 contrasts). However, the possibility exists that restraining the stimulus fish provides some yet uninvestigated cue that experimental subjects may perceive. For example, fish in the restrained condition could be more stressed than freely swimming fish and this could favor the approach to the more active shoal. Although we did not observe any particular postural or body coloration change or other signs of stress in the restrained fish, some subtle changes could have been perceived by the subjects and could potentially affect the choice made by the experimental subjects. In several animal species, it has been shown that restrained conspecifics may elicit withdrawal rather than approach. Although approach of restrained conspecifics, in order to explore their state, is also observed, this is often a short-term behavior as compared to the longer lasting approach to and preference for free moving conspecifics (e.g., see Watanabe, 2012). These complex effects will be evaluated in the future and may better illuminate our results obtained in the control treatments with large shoal sizes in Experiment 2. Notably, however, one may expect such features of the restrained shoals to also occur in the 3 vs. 3 contrasts, but in this case no significant preference was exhibited by angelfish. Clearly, further research is needed to disentangle these possible explanations.

It is also possible that fish used swimming activity in combination with inter-fish distance, since shoals could also differ in this latter variable. More active shoals may be particularly important in natural situations. Shoals containing fast swimming fish may be preferred because activity levels can indicate increased chances of finding food or anticipation of food (Reebs and Gallant, 1997), and therefore may convey fitness benefits. The ability to quantify moving stimuli as opposed to stationary stimuli has also been shown in primates (e.g., Beran, 2008).

Considering findings published in the literature as well as these above results, it is likely that angelfish as well as other species can base their discrimination upon several attributes of the contrasted stimulus sets. These can include actual number, continuous variables and/or combination of certain continuous features, and numerical attributes. It is also likely that individuals may preferentially rely on one or another such factor depending upon task and context. In summary, further investigation of the relations among these variables is needed. Additionally, our results also underscore what Agrillo and Miletto Petrazzini (2012) stated. These authors argued that it is important to assess different methods and to obtain replication of results. Application of these different approaches will help us better understand the perceptual and cognitive mechanisms that underlie context-dependent differences observed in quantity discrimination and numerical competence across a variety of species.

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Quantity estimation based on numerical cues in the mealworm beetle (*Tenebrio molitor*)

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In this study, we used a biologically relevant experimental procedure to ask whether mealworm beetles (*Tenebrio molitor*) are spontaneously capable of assessing quantities based on numerical cues. Like other insect species, mealworm beetles adjust their reproductive behavior (i.e., investment in mate guarding) according to the perceived risk of sperm competition (i.e., probability that a female will mate with another male). To test whether males have the ability to estimate numerosity based on numerical cues, we staged matings between virgin females and virgin males in which we varied the number of rival males the experimental male had access to immediately preceding mating as a cue to sperm competition risk (from 1 to 4). Rival males were presented sequentially, and we controlled for continuous cues by ensuring that males in all treatments were exposed to the same amount of male–male contact. Males exhibited a marked increase in the time they devoted to mate guarding in response to an increase in the number of different rival males they were exposed to. Since males could not rely on continuous cues we conclude that they kept a running tally of the number of individuals they encountered serially, which meets the requirements of the basic ordinality and cardinality principles of proto-counting. Our results thus offer good evidence of "true" numerosity estimation or quantity estimation and, along with recent studies in honey-bees, suggest that vertebrates and invertebrates share similar core systems of non-verbal numerical representation.

Keywords: numerical cognition, quantity estimation, sperm competition, numerosity discrimination, sperm competition risk, mate guarding

INTRODUCTION

Understanding the evolution of numerical abilities is a mayor challenge in the study of cognition (Shettleworth, 2010). Reports accumulated during the last few years suggest that human and non-human animals share the ability for quantity estimation, which is believed to be the cognitive foundation of higher numerical skills (Dehaene et al., 1998; Hauser, 2000; Feigenson et al., 2004; Hauser and Spelke, 2004; Beran, 2008; Shettleworth, 2010). Quantity estimation has been reported in every mayor group of vertebrates excepting reptiles (mammals, Beran et al., 2008; birds, Rugani et al., 2009; amphibians, Uller et al., 2003; Krusche et al., 2010; fish, Agrillo et al., 2009); and in a few invertebrates (ants, Reznikova and Ryabko, 2011; bees, Dacke and Srinivasan, 2008; beetles, Carazo et al., 2009).

Despite these advances, it is yet unclear whether quantity estimation in non-human animals is based on the same cognitive system as in humans and, if so, how evolutionary ancient this system might be. Part of the problem lies in the difficulty of establishing whether quantity estimation in non-human animals is based on a computation of numerosity itself (i.e., quantity estimation *sensu stricto*), or on non-numerical continuous cues that co-vary with numerosity (i.e., amount estimation; Agrillo et al., 2011; Shifferman, 2012). Quantity estimation is often investigated by exploring the capacity of animals to discriminate between two sets of objects differing in numerosity (e.g., Carazo et al., 2009). However, several continuous features will co-vary with numerosity as more objects are added to a given group of items, such as temporal duration, area, volume, luminance, shape, or perimeter (Agrillo et al., 2009), which may allow for discrimination of numerosity based on non-numerical cues. Therefore, one of the current challenges of research on numerical cognition is hence to understand the relative importance of amount versus quantity-based numerosity mechanisms, particularly in invertebrates, which have so far received considerably less attention than vertebrates in this respect (Menzel et al., 2007; Reznikova and Ryabko, 2011).

A fruitful approach to study cognitive abilities is to stage tasks with ethological validity, where a clear link between cognition and individual fitness can be established (Dukas, 1998; Shettleworth, 2010). As a matter of fact, the field of numerical cognition has experienced a gradual shift from extensive training in captivity or in artificial settings to considering spontaneous expression of numerical competence, and toward understanding how numerical competence functions for particular animals in their natural environments (e.g., Hager and Helfman, 1991; McComb et al., 1994; Uller et al., 2003; Flombaum et al., 2005; Hanus and Call, 2007). Sperm competition provides an ideal context in which to study numerical cognition in many invertebrates (Shifferman, 2012). Sperm competition makes reference to the evolutionary battle of males for the fertilization of a given set of ova (Parker, 1970). A main prediction of sperm competition models is that male allocation of sperm and/or mate guarding should vary according to the probability that a female will re-mate with a different male before laying her eggs (i.e., sperm competition risk; hereafter SCR), and according to the number of males she is expected to mate with (i.e., sperm competition intensity; hereafter SCI). This prediction rests on the assumption that males are somehow able to assess sperm competition levels, which may be accomplished in two ways. First, males may directly determine the risks from past matings by detecting whether a female has recently mated with other males; for example, by assessing the presence of semen in her reproductive tract (e.g., Cook and Gage, 1995; Siva-Jothy and Stutt, 2003). Second, males may assess the future probability that a female will engage in further matings. Several studies with insects have shown that males assess either male density or the operational sex ratio at the time of mating (e.g., Gage, 1991; Simmons, 2001). Both SCR and SCI will co-vary with the number of males present around the time of mating, and males of many species have been show to respond to increasing numbers of rival males by increasing their allocation to sperm competition strategies (e.g., sperm investment and/or mate guarding; Simmons, 2001). Unfortunately, amount and quantity estimation are confounded in most available sperm competition studies, so we know very little about whether quantity estimation in this context relies on numerical or non-numerical cues (reviewed in Shifferman, 2012).

The mealworm beetle (*Tenebrio molitor*) is a highly polygynandrous beetle that has evolved several strategies reflecting an evolutionary history of intense sperm competition (e.g., Happ, 1969; Siva-Jothy et al., 1996; Drnevich et al., 2000; Griffith, 2001; Drnevich, 2003; Carazo et al., 2004). Sperm transfer in this species begins when males fill a pre-formed spermatophore with sperm and transfer it to the female's bursa during the first 30–60 s of copulation (Gadzama and Happ, 1974). Once inside the female, the spermatophore undergoes a series of eversions before eventually bursting and releasing sperm, about 7–10 min after the end of copulation (Gadzama and Happ, 1974). When a female re-mates with a second male before the sperm from the first male's spermatophore has been released into the bursa, the second male is capable of preventing sperm release from the first male's spermatophore (i.e., spermatophore inhibition) and achieves near complete sperm precedence (Drnevich et al., 2000). In response to spermatophore inhibition, males have evolved a short-term anti-aphrodisiac that they transfer to females during mating, and that increases female re-mating intervals by decreasing long-range female attractiveness (Happ, 1969; Griffith, 2001; Seybold and Vanderwel, 2003). However, this anti-aphrodisiac does not prevent re-mating once a female encounters another male, and is probably only effective in avoiding rapid re-mating (<7 min) when male densities are low (Griffith, 2001; Drnevich, 2003). The probability of suffering from spermatophore inhibition is thus likely to be quite low when male densities are low, and males of this species normally devote very little time to mate guarding under such circumstances (Carazo et al., 2004, 2007). However, local populations of *T. molitor* often reach high densities when they colonize pockets of stored grain (Thompson, 1995, 1998), so the risk of spermatophore inhibition is bound to vary considerably depending on varying levels of relative male density at the time of mating. In accordance, males have been shown to respond to high male densities by increasing the amount of time they allocate to guarding their spermatophore (i.e., spermatophore guarding; Carazo et al., 2007). During spermatophore guarding, a male remains in contact with a female, and will actively fight against a rival male attempting to copulate with the guarded female. Despite considerable size differences, spermatophore guarding normally allows males to delay female re-mating sufficiently to enable sperm release into the bursa (Carazo et al., 2007). Hence, short-term mate guarding appears to be an effective mechanisms to prevent spermatophore inhibition, and the fact that its duration depends on existing levels of SCI suggest that males may be capable of assessing the number of rival males present during or immediately preceding mating.

In support of this idea, *T. molitor* males have been shown to be capable of numerosity discrimination, albeit in a different context. Recently, we investigated the existence of quantity discrimination in this species by using a spontaneous two-choice procedure in which males were simultaneously exposed to substrates bearing odors from different numbers of females (≤ 4). Our results show that *T. molitor* males discriminate between odor sources reflecting different numbers of donor females when given the choice between odors from 1 versus 4 or 1 versus 3 female donors. In particular, and as predicted, males spent more time inspecting sources with odors from more donor females (Carazo et al., 2009). These results suggest that males can discriminate sources of odors reflecting different numerosities with a signature ratio of 1:2, although we were not able to rule out the possibility that males could have been using continuous cues (Carazo et al., 2009).

Our aim here was to test whether *T. molitor* males are capable of estimating numerosity in a different but biologically relevant context in which only numerical cues are available. We designed an experimental setup in which we simulated the situation faced by a male that has to assess the risk of suffering spermatophore inhibition by assessing relative male density (i.e., male-female encounter rate) immediately prior to mating. We staged matings between virgin females and virgin males in which we varied the number of rival males the experimental male had access to immediately preceding matings (i.e., the risk of suffering spermatophore inhibition). We controlled for the temporal duration of male–male contact across treatments, and rival males (1–4) were presented sequentially (and were not present during mating). In these circumstances, experimental males would need to keep a running tally of the number of different rivals encountered before mating in order to gage the risk of spermatophore inhibition (Shifferman, 2012).

MATERIALS AND METHODS

All the beetles used in this study originated from stock cultures maintained in our laboratory. These cultures have been running for more than 10 years with regular contributions from other cultures. All growth stages are kept together in plastic trays with a rearing medium consisting of white flour and wheat bran to which chunks of fruit, bread, and various vegetables are added periodically. The culture is covered with filter paper that is sprayed with water for moisture on a daily basis. All containers are kept in well-ventilated, dark storage cabinets, at ambient humidity, and under temperature-controlled conditions.

Subjects used in our experiments were collected from the stock cultures and sexed as pupae by inspection of developing genitalia on the ventral side of the eighth abdominal segment (Bhattacharya et al., 1970). Individuals were examined under a dissecting microscope both as pupae and after eclosion and those with obvious malformations were discarded. Sexed adults of the same age were kept separately in plastic containers measuring approximately 15 cm(height) × 13 cm × 20 cm until used in the experiments. Plastic containers were maintained in the same way as stock cultures. Males and females participating in mating interactions were virgin, sexually mature (i.e., at least 10 days post-eclosion), and never older than 30 days. After staged matings, experimental males were transferred to a plastic container (same conditions as above) and participated in successive trials as introduced rival males (i.e., males introduced to experimental males in the 20 min prior to mating). Trials were conducted at a temperature of 22–25°C, at ambient humidity, and under dim light.

To test whether males are capable of estimating numerosity based exclusively on numerical cues, we staged matings between virgin females and virgin males in which we varied the number of rival males the experimental male had access to immediately preceding matings (**Figure 1**). Twenty minutes before having access to a virgin female, males were subject to the following protocol. Each male was introduced into a small arena (i.e., a 5 cm diameter inverted Petri dish) with another male for 3 min and then isolated in an empty arena for 2 min. We repeated this protocol four times in a row (i.e., overall duration 20 min) before introducing the experimental male into a mating arena with a virgin female. Males were assigned to one of our four treatments: (a) in the "one male" treatment, the male introduced during the four 3 min periods was always the same, (b) in the "two males" treatment, we alternated between two different males (i.e., the same male was never introduced twice in a row), (c) in the "three males" treatment, we introduced three different males in a random order and, in the last 3 min period, we haphazardly selected and introduced one of the first two males again, and (d) in the "four male" treatment, each introduced male was different. We randomized rival male size by randomly selecting males from the sexed cultures. Each of these treatments simulated different average encounter rates with a novel male (i.e., a novel male is encountered once every 20 min in the "one male" treatment, once every 10 min in the "two male" treatment, once every 6.7 min in the "three males" treatment, and once every 5 min in the "four males" treatment). All arenas were clean and free of odors prior to the introduction of "rival" and/or the experimental males. Mating trials begun immediately after the 20 min period in which males were exposed to rival males; i.e., at the end of this period, males were immediately transferred to a mating arena where they had access to a virgin female. If the

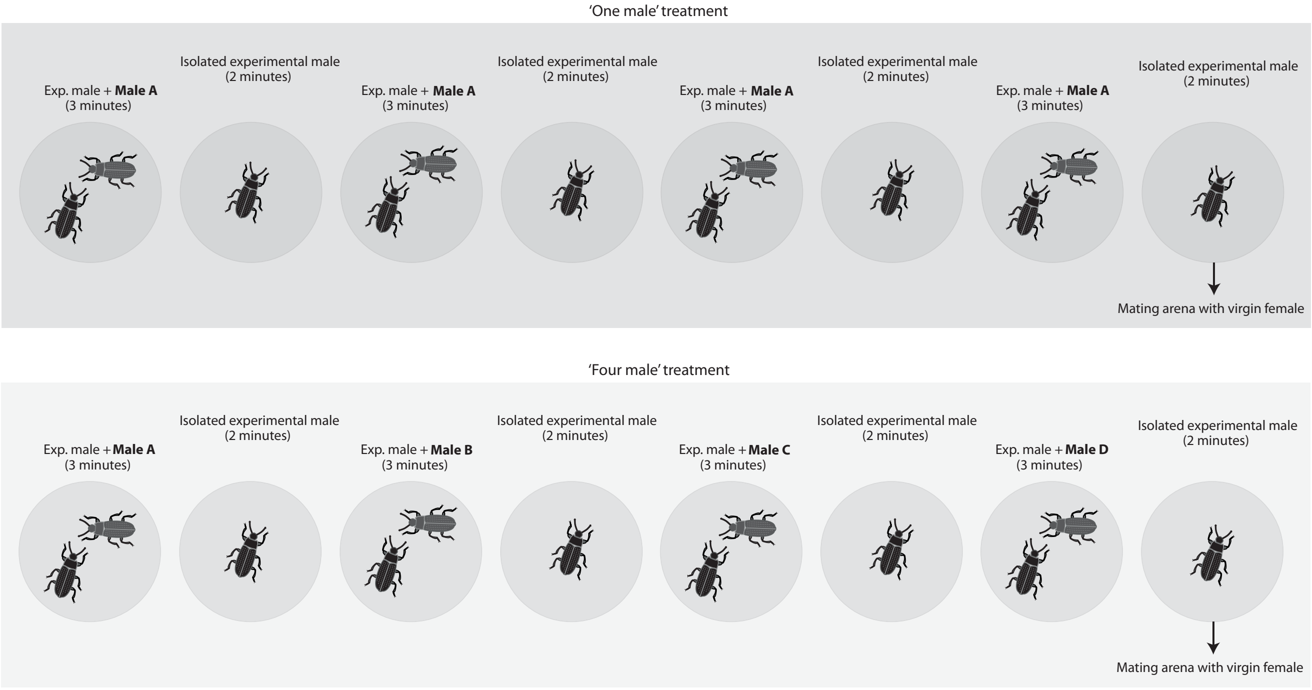

FIGURE 1 | Two of the four treatments employed (i.e., the "one male" and the "four males" treatments) as an example to illustrate the experimental designed used. We staged matings between virgin females and virgin males in which we varied the number of rival males the experimental male had access to immediately preceding matings. Each male was introduced in a small 5 cm diameter arena with another male for 3 min and then isolated in a new blank arena for 2 min. We repeated this protocol four times in a row (i.e., overall 20 min) before introducing the experimental male in a mating arena with a virgin female. Each male was subject to one of four different treatments. In the "one male" treatment, the male introduced during the four 3 min periods was always the same. In the "two males" treatment, we used two different males that were alternated. In the "three males" treatment, we introduced three different males and repeated one of the first two males in the last presentation. Finally, in the "four male" treatment each introduced male was different.

experimental male failed to initiate courtship within 10 min, the trial was terminated. We used a laptop computer equipped with event-recording software (JWatcher 0.9, Blumstein et al., 2000) to record the duration of the following behaviors:

i) Courtship: begins with the male rapidly tapping the female with its antennae in a rhythmic way. The male then climbs on top of the female making rapid scraping movements with its prothoracic legs against the female's sides and then proceeds to move its copulatory organ across the female's rear end until achieving intromission (end of courtship). Tapping with the antennae typically continues through courtship and ends with the onset of copulation.
ii) Copulation: the female lowers her last abdominal sternite and the male introduces the copulatory organ. The pair remains attached by the genitalia for a variable length of time.
iii) Mate guarding: after withdrawing his copulatory organ, the male remains on top of the female and/or dismounts the female and stays immediately adjacent to (i.e., less than 1 cm apart) and usually in direct physical contact with her. Mate guarding typically occurs in bouts that are interrupted by periods in which the members of the pair briefly lose contact with each other. Consequently, the duration of total mate guarding duration is difficult to measure. Our operational measure was restricted to the first bout of mate guarding, which ended when the male and the female were apart from each other (i.e., ca. 1 cm or one body length away from each other) for more than 5 s. Even though this measure is bound to underestimate actual mate guarding, it is an objective conservative measure that correlates strongly with overall mate guarding (Carazo et al., 2007).

Final sample sizes were: "one male" treatment ($n = 27$), "two males" treatment ($n = 29$), "three males" treatment ($n = 29$), and "four males" treatment ($n = 28$). Behavioral data were rank-transformed due to the presence of a few extreme outliers. To look for differences in the time males allocated to courtship, copulation and mate guarding across treatments we performed a robust one-way ANOVA for each of these variables. Significant treatment effects were followed by *post hoc* multiple comparisons using Tukey's HSD (Quinn and Keough, 2002). As a complementary robust analysis, we winsorized raw data at $\alpha = 0.05$ to minimize the influence of outliers (i.e., outliers were replaced by the next highest or lowest value, depending on the tail of the distribution), and re-run the one-way ANOVA analyses for all variables. All tests were performed in R v 2.14.0 (R Development Core Team, 2011). All research was conducted in accordance with the animal care and experimentation guidelines provided by the Association for the Study of Animal Behaviour.

RESULTS

Our ANOVA analyses on ranked data did not detect significant treatment effects for courtship duration ($F_{3,\ 109} = 1.428$, $p = 0.239$) or copulation duration ($F_{3,\ 109} = 0.510$, $p = 0.677$; **Figure 2**). ANOVA analyses on winsorized data yielded similar results (i.e., "courtship duration," $F_{3,\ 109} = 2.011$, $p = 0.117$; "copula duration," $F_{3,\ 109} = 0.328$, $p = 0.805$). We did detect a highly significant treatment effect in the time devoted to mate guarding using both rank-transformed ($F_{3,\ 109} = 11.46$, $p < 0.001$) and winsorized data ($F_{3,\ 109} = 10.48$, $p < 0.001$). In both analyses (for brevity, we report only the ranked data), there was a highly significant difference in mate guarding duration between the "four males" treatment and the "one male" treatment (estimate ± standard error; 29.746 ± 7.810, t-value $= 3.809$, $p < 0.001$), but not between the "two males" (-11.904 ± 7.744, t-value $= -1.537$, $p = 0.127$) or "three males" (-5.559 ± 7.744, t-value $= -0.718$, $p = 0.474$) treatment and the "one male" treatment. Tukey's HSD test confirmed that the significant treatment effect detected in the ANOVA model was due to the existence of significant differences between the "four males" treatment and the "one male" (difference $= 29.746 \pm 20.378$, $p = 0.001$), "two males" (difference $= 41.650 \pm 20.017$, $p < 0.001$), and "three males" (difference $= 35.305 \pm 20.016$, $p < 0.001$) treatments (again, we found no difference when using winsorized data).

DISCUSSION

We did not find any evidence that male treatment affected courtship or copula duration (**Figure 2**). The absence of a treatment effect on courtship duration was expected because it is not involved in spermatophore guarding, and a previous study in this same species reported that courtship duration does not increase with increasing male density (i.e., Carazo et al., 2007). In contrast, in the same study copulation duration was reported to increase in response to increasing male density (as a putative mechanism to extend spermatophore guarding). However, this was in response to higher male densities than those simulated in our experiment (i.e., 10 males; Carazo et al., 2007), which may explain why we did not find an effect on this variable. Finally, we found a highly significant treatment effect on the duration of mate guarding, which is the variable we predicted should be directly affected by increasing male density (i.e., risk of spermatophore inhibition). Our results thus show a marked increase in mate guarding in the "four males" treatment, but we did not detect any significant differences in male behavior when exposed to two or three rival males.

It is important to note that this cannot be taken as evidence that males are not able to discriminate between the "two males" and "three males" treatments and the "one male" treatment. Theory predicts that, in this species, males should increase spermatophore guarding when they perceive a significant increase in the risk of suffering spermatophore inhibition (i.e., the risk that the female they have just mated with will re-mate with another male within the next 7 min, at which time sperm release begins). Female re-mating after sperm release from the first male results in a reduction of approximately 60% in the first male's paternity share due to sperm dilution by the second male (Drnevich et al., 2000; Drnevich, 2003). However, this outcome is clearly more beneficial than losing all paternity, which may happen if the female re-mates before sperm from the first male is released from the spermatophore. Also, the costs of mate guarding are very high given the mating system of this species, so males cannot prevent females from re-mating with other males before they lay their eggs (i.e., they cannot avoid sperm dilution by other males). In contrast, short-term mate guarding (i.e., spermatophore guarding) is much cheaper and provides males with a tool to avoid spermatophore inhibition

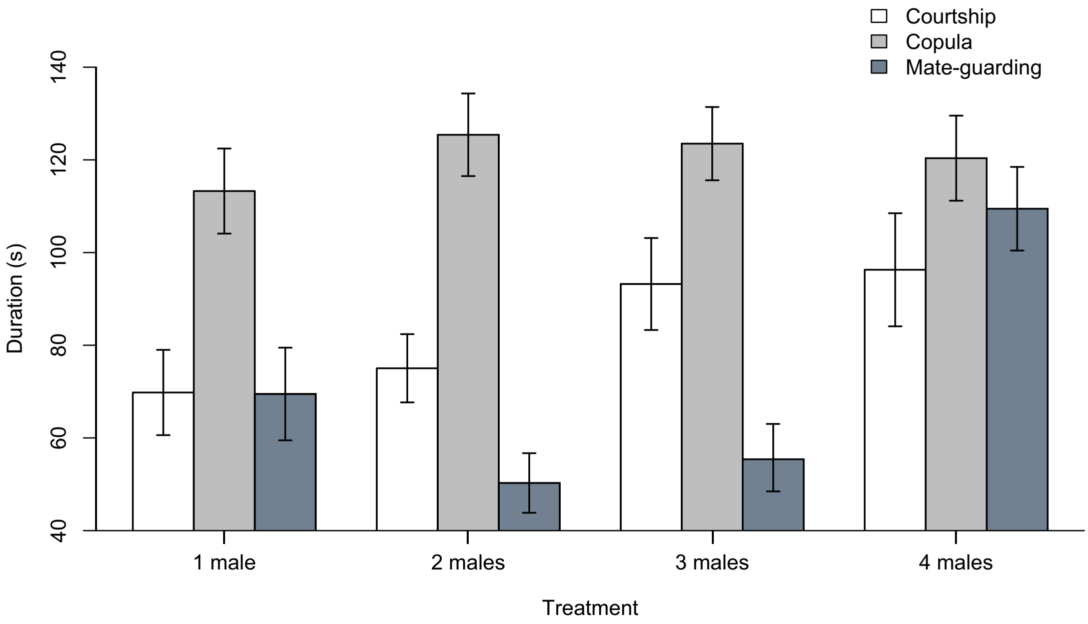

FIGURE 2 | Duration (in seconds) of courtship, copulation, and mate guarding behaviors in males subject to the "one male," "two males," "three males," and "four males" treatments. Bar plots show mean ± SEM constructed using data that were previously winsorized at $\alpha = 0.05$ to minimize the influence of outliers (i.e., outliers were replaced by the next highest or lowest value, depending on the tail of the distribution).

(Carazo et al., 2007). For a *T. molitor* male, the crucial question is not whether a female is going to re-mate or not, but whether it is going to do so fast enough so that spermatophore inhibition may take place.

It is hence perfectly possible that males in our experiment were able to assess the differences in the number of males in all the treatments, but only responded to the last treatment because it marks the point at which there is a significant increase in the risk of suffering spermatophore inhibition. As a matter of fact, this is exactly what seems to be happening. For sperm inhibition to take place, females have to re-mate with a new male within the first 7 min after the end of their previous mating, at which time sperm release from the first male begins. Given the average encounter rates simulated in our different treatments and the average courtship and mate guarding duration in this species, males should only increase their allocation to mate guarding in response to the last treatment as this is the only treatment in which they face (on average) a risk of loosing their paternity due to sperm inhibition by a second male (**Figure 3**). Our finding that males only responded to the "four males" treatment hence fits nicely with theoretical expectations.

For the reasons stated above, our results cannot be used to infer information about the operational limit of the cognitive mechanism males are using to assess numerosity (but see Carazo et al., 2009). They do, however, suggest that males of this species possess a sophisticated mechanism that allows them to assess male density, and with it the average risk of spermatophore inhibition that they face after mating with a female. Furthermore, our results suggest that such a mechanisms is probably based on a sequential accumulator model. Given that rival males were presented sequentially to experimental males, the only way for them to assess numerosity is by keeping a running tally of the number of males they encountered during trials. Furthermore, our experimental setup ensured they could only do this by assessing the number of *different* males they encountered because males in all treatments were exposed to the same overall amount of contact with other males. It is also worth noting that the competitive potential of the last male encountered and the average competitive potential of all the males encountered are both expected to be equal across treatments, so this could not explain observed differences in male mate guarding. All in all, these facts make it very unlikely that males could have been using any sort of continuous cue to estimate numerosity.

To conclude, we believe our results offer good evidence of "true" numerosity estimation (i.e., based exclusively on numerical cues) in an insect. Assessment of numerosity in our experimental setup entails a more sophisticated quantity estimation aptitude than mere amount estimation because males need to perform a continuous real-time monitoring of the number of individuals they encounter serially, which meets the requirements of the basic ordinality and cardinality principles of proto-counting (Shifferman, 2012). To our knowledge, in insects such proto-counting ability has only been previously reported conclusively in bees (Dacke and Srinivasan, 2008), although there is some indirect evidence that suggests it may be present in other species (Reinhardt, 2001). In conjunction, these studies suggest that vertebrates and invertebrates share similar non-verbal representational systems allowing quantity estimation based on numerical cues alone. As a corollary, our results also suggest that *T. molitor* males may be capable of individual recognition, a possibility that should be addressed by future studies.

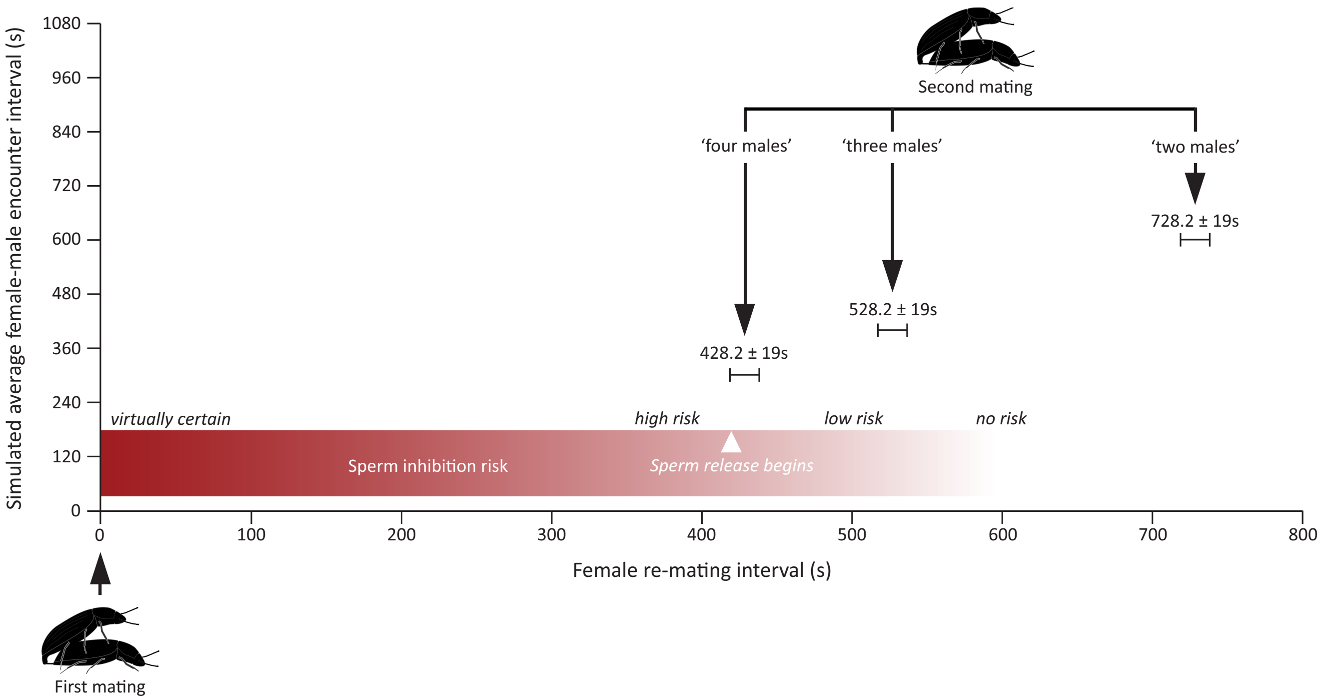

FIGURE 3 | Figure showing the expected risk of suffering from spermatophore inhibition under three of the four treatments assayed in this study. Expected female re-mating interval was calculated by summing up the average encounter rate with a new male simulated in each treatment (i.e., a novel male is encountered once every 1200 s in the "one male" treatment, once every 600 s in the "two male" treatment, once every 400 s in the "three males" treatment, and once every 300 s in the "four males" treatment) with the mean duration (mean ± SEM) of mate guarding and courtship taken from the "one male" treatment (i.e., 128.2 ± 19 s). Average courtship and mate guarding duration were calculated from winsorized ($\alpha = 0.05$) data to prevent overestimation of both parameters due to the presence of outliers (see Materials and Methods). The risk of suffering from spermatophore inhibition is virtually one for re-mating intervals <5 min, high for re-mating intervals around 7 min, and is then bound to drop fast for longer re-mating intervals as sperm release begins (Gadzama and Happ, 1974; Drnevich et al., 2000). This being so, the "four males" treatment is the only one simulating a situation in which males would face a significant increase in the risk of suffering spermatophore inhibition.

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Inter-specific differences in numerical abilities among teleost fish

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Adults, infants and non-human primates are thought to possess similar non-verbal numerical systems, but there is considerable debate regarding whether all vertebrates share the same numerical abilities. Despite an abundance of studies, cross-species comparison remains difficult because the methodology employed and the context of species examination vary considerably across studies. To fill this gap, we used the same procedure, stimuli, and numerical contrasts to compare quantity abilities of five teleost fish: redtail splitfin, guppies, zebrafish, Siamese fighting fish, and angelfish. Subjects were trained to discriminate between two sets of geometrical figures using a food reward. Fish initially were trained on an easy numerical ratio (5 vs. 10 and 6 vs. 12). Once they reached the learning criterion, they were subjected to non-reinforced probe trials in which the set size was constant but numerical ratios varied (8 vs. 12 and 9 vs. 12). They also were subjected to probe trials in which the ratio was constant, but the total set size was increased (25 vs. 50) or decreased (2 vs. 4). Overall, fish generalized to numerosities with a 0.67 ratio, but failed with a 0.75 ratio; they generalized to a smaller set size, but not to a larger one. Only minor differences were observed among the five species. However, in one species, zebrafish, the proportion of individuals reaching the learning criterion was much smaller than in the others. In a control experiment, zebrafish showed a similar lower performance in shape discrimination, suggesting that the observed difference resulted from the zebrafish's difficulty in learning this procedure rather than from a cross-species variation in the numerical domain.

Keywords: ***Xenotoca eiseni, Poecilia reticulata, Danio rerio, Betta splendens, Pterophyllum scalare,*** **Fish cognition**

INTRODUCTION

Though numerical abilities were once considered a unique human ability, numerous studies have now shown that other primates display the capacity to add, subtract, and order numerical information (Brannon and Terrace, 1998; Beran, 2004; Matsuzawa, 2009). The evidence collected in cognitive, developmental, and comparative research has led several authors to propose that adults prevented from verbal counting, infants and non-human primates possess similar numerical systems that are independent from language and culture (Feigenson et al., 2004; Hauser and Spelke, 2004; Beran, 2008). For instance, the performance of rhesus monkeys adheres to that of adult humans in two comparative studies where both species were presented identical stimuli (Cantlon and Brannon, 2006, 2007a). In chimpanzees, error rates and reaction times are constant in the subitizing range (1–4) while they increase monotonically for larger numbers, suggesting the existence of a subitizing-like mechanism in apes (Tomonaga and Matsuzawa, 2002).

Following the discovery of the remarkable numerical skills of primates, researchers initially believed in the existence of a sharp discontinuity in cognitive abilities between primates and other animal species. However, during the last decade, the presence of basic quantity abilities has been reported in other mammals (bears: Vonk and Beran, 2012; elephants: Perdue et al., 2012; dogs: West and Young, 2002; dolphins: Kilian et al., 2003), in birds (parrots: Pepperberg, 2006; Al Aïn et al., 2009; pigeons: Roberts, 2010), in fish (mosquitofish: Agrillo et al., 2009; angelfish: Gómez-Laplaza and Gerlai, 2011a,b; swordtails: Buckingham et al., 2007), and even in invertebrates (ants: Reznikova and Ryabko, 2011; bees: Gross et al., 2009; beetles: Carazo et al., 2009).

Such new evidence has prompted a debate as to whether or not all species share the same quantity systems. Some studies have reported interesting similarities between primates and non-primate species. For instance, different mammals (Ward and Smuts, 2007; Perdue et al., 2012), birds (Al Aïn et al., 2009), amphibians (Krusche et al., 2010), and fish (Gómez-Laplaza and Gerlai, 2011a) are affected by the numerical ratio when required to compare numerosities, as commonly reported in primates (Beran, 2004; Cantlon and Brannon, 2007a). Rhesus monkeys can discriminate 1 vs. 2, 2 vs. 3, and 3 vs. 4, but not 4 vs. 5 (Hauser et al., 2000), the same limit exhibited by distantly related species, such as Eastern mosquitofish (Agrillo et al., 2008), guppies (Agrillo et al., 2012a), and robins (Hunt et al., 2008). Domestic chicks and robins can make spontaneous use of numerical information instead of using non-numerical perceptual cues that co-vary with number, such as cumulative surface area or density (Hunt et al., 2008; Rugani et al., 2009), which aligns with what has been reported in human (Cordes and Brannon, 2008; Nys and Content, 2012) and non-human primates (Cantlon and Brannon, 2007b). Similar performance in the discrimination of small and large numbers recently has been reported in a study comparing humans and guppies (Agrillo et al., 2012a).

However, many other studies have evidenced that performance varies across species in many respects. For example – unlike primates, chicks and robins – cats and dolphins seem to use numerical information only as a "last-resort" strategy, when no other continuous information is available (Kilian et al., 2003; Pisa and Agrillo, 2009). Horses, chicks, salamanders, and angelfish seem to be able to discriminate between groups differing by one unit up to 2 vs. 3 items (Uller et al., 2003; Rugani et al., 2007; Uller and Lewis, 2009; Gómez-Laplaza and Gerlai, 2011b), while mosquitofish, guppies, and robins discriminate up to 3 vs. 4 items (Agrillo et al., 2008, 2012a; Hunt et al., 2008). Trained pigeons can discriminate up to 6 vs. 7 items (Emmerton and Delius, 1993), well above the limit of number discrimination of 2 vs. 3 items observed in trained chicks (Rugani et al., 2007). Differences have been reported even between closely related species. For example, the ability to discriminate between large quantities appears to be affected by numerical ratio in African elephants (Perdue et al., 2012), but not in Asian elephants (Irie-Sugimoto et al., 2009).

Despite the wealth of comparative data, cross-species comparison has been difficult because the tasks investigated, the methodology employed, the sensory modality involved, and the context of species investigation vary considerably from one study to another. In some cases, the inconsistency is clearly to be ascribed to the different methods adopted. For example, when required to discriminate 1 vs. 2 and 2 vs. 3, the numerical ratio plays a key role in infants' performance using auditory stimuli (vanMarle and Wynn, 2009), but not visual stimuli (Feigenson et al., 2002). Similarly, in goldbelly topminnows, the performance in a quantity discrimination task was affected by the type of procedure, with fish able to discriminate 2 vs. 3 only in one of two different procedures (Agrillo and Dadda, 2007).

To date, cross-species comparison using the same methodology rarely has been attempted; such studies have related exclusively to primates (Cantlon and Brannon, 2006, 2007a; Hanus and Call, 2007). To fill this gap, the present study compares the numerical abilities of five teleost fish (redtail splitfin, guppies, zebrafish, Siamese fighting fish, and angelfish) using the same procedure, stimuli, and numerical contrasts. Subjects were trained with a food reward to discriminate between two sets of geometrical figures differing in numerosity. Fish initially were trained on an easy numerical ratio (0.50). Once they reached the learning criterion, they were tested in non-reinforced probe trials for their ability to generalize to more difficult ratios (0.67 and 0.75), or to a larger or a smaller total set size. In addition, because the proportion of individuals reaching the initial learning criterion was very low in one species, we conducted a control experiment on shape discrimination to assess if this difference was specific to the numerical domain or was due to a more general cross-species difference in learning with this procedure.

EXPERIMENT 1

SUBJECTS

The initial subjects of this experiment were 16 *Xenotoca eiseni* (redtail splitfin, total length: mean ± SD: 3.02 ± 0.25 cm), 16 *Poecilia reticulata* (guppies, 2.01 ± 0.30), 16 *Betta splendens* (Siamese fighting fish, 3.36 ± 0.32), 16 *Pterophyllum scalare* (angelfish, 4.09 ± 0.38), and 16 *Danio rerio* (zebrafish, 2.84 ± 0.27). All subjects were adult females with the exception of the group of angelfish composed by unsexed juvenile individuals. Redtail splitfin came from the stocks maintained in our lab; guppies were also maintained in our lab and were fifth generation descendants of wild-caught fish from the Tacarigua River in Trinidad. Siamese fighting fish, angelfish, and zebrafish were obtained from local commercial suppliers. As few zebrafish reached the criterion, we increased the sample size for this species by adding 10 more specimens of the same strain (hereafter called "commercial stock") and by testing 22 more specimens from another strain coming from the outbreed stock maintained at the Biology Department of University of Padua (hereafter called "lab stock").

Subjects were stocked at the Laboratory of Comparative Psychology (University of Padua) for at least 15 days before the beginning of the experiments and maintained in 150 l stock aquaria; each species was housed separately. Aquaria were provided with natural gravel, air filters, and live plants. Both stock aquaria and experimental tanks were maintained at a constant temperature of 25 ± 1˚C and a 14:10 h light:dark (L:D) photoperiod; stock aquaria were lit by an 18-W fluorescent light, experimental tanks were lit by two 36 W fluorescent lamps. Before the experiment, fish were fed twice daily to satiation with commercial food flakes and live brine shrimp (*Artemia salina*).

APPARATUS AND STIMULI

We followed the apparatus and procedure described in a recent study (Agrillo et al., 2012b). The experimental apparatus was composed of a 50 cm × 19 cm × 32 cm tank (**Figure 1**) filled with gravel and 24 cm of water. The long walls were covered with green plastic material, while the short ones were covered with white plastic material. Two mirrors (29 cm × 5 cm) were placed in the middle of the tank, 3 cm away from the long walls, in order to reduce the potential effects of social isolation (Miletto Petrazzini et al., 2012). In addition, an artificial leaf (9 cm × 8 cm) was placed in the middle to provide some shelter for the subjects. In correspondence with the sides in which stimuli were presented, two "choice areas" were defined by white rectangles (14 cm × 12 cm) covered by a green net.

Stimuli were inserted in a 6 cm × 6 cm square and were presented at the bottom of a 6 × 32 transparent plexiglass panel. There were groups of black geometric figures differing in size on a white background. We presented different numerical contrasts: 5 vs. 10 and 6 vs. 12 (0.50 ratio) in the training phase; 8 vs. 12 and 9 vs. 12 (0.67 and 0.75 ratios) in phase 1; 2 vs. 4 and 25 vs. 50 in phase 2. Stimuli selected for the experiment were extracted from a pool of 24 different pairs for each numerical contrast. Both the size and position of the figures were changed across sets to avoid the fish having to discriminate the overall configuration of the stimuli instead of using numerical information. In addition, it is known that numerosity co-varies with other physical attributes, such as cumulative surface area, overall space occupied by sets, or density of the elements; human and non-human animals can use these non-numerical cues to estimate which group is larger/smaller (Pisa and Agrillo, 2009; Gebuis and Reynvoet, 2012). Cumulative surface area was controlled to reduce the possibility of

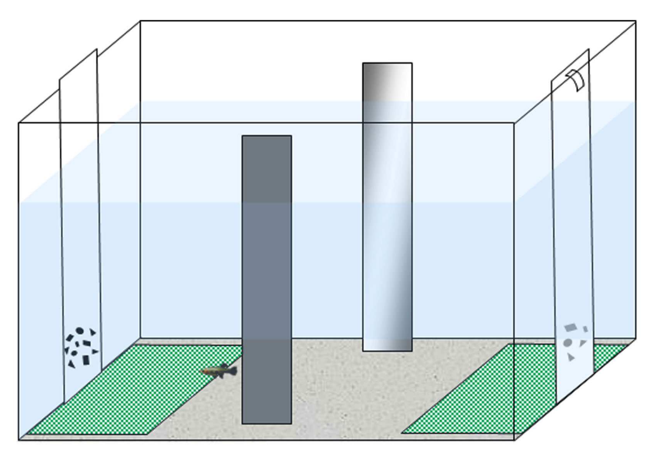

FIGURE 1 | Experimental apparatus. Subjects were housed in the experimental tank for the entire experiment. Stimuli (two groups of geometric figures differing in numerosity) were presented at the bottoms of the tank.

fish using non-numerical cues. In particular, for one-third of the stimuli, the two numerosities were equated for cumulative surface area (100%). However, as a by-product of equaling cumulative surface area, smaller than average figures were more frequent in the larger groups, and fish could have used this cue instead of numerical information. To reduce this possibility, in another third of the stimuli, cumulative surface area was controlled to 85%, and, in a final third of the stimuli, it was controlled to 70% (**Figure 2**). In addition, since density and overall space encompassed by the stimuli are negatively correlated, half of the sets was controlled for density, whereas the second half was controlled for overall space. Cumulative surface area, density and overall space represent the most non-numerical continuous variables controlled in numerical cognition studies (Vos et al., 1988; Durgin, 1995; Kilian et al., 2003; Pisa and Agrillo, 2009). They also represent the only cues that proved to be sometimes used by fish with static stimuli (Agrillo et al., 2008, 2009, 2010; Gómez-Laplaza and Gerlai, 2011b).

Sixteen identical experimental tanks were used. They were placed close to each other on the same table. A video camera was suspended about 1 m above the experimental tanks and used to record the position of the subjects during the tests.

PROCEDURE

The experiment was divided into three different steps: (a) pre-training, (b) training, and (c) test.

Pre-training (a) was set up to permit fish to familiarize themselves with the experimental apparatus. Subsequently (b), all fish were singly trained to discriminate an easy numerical ratio (0.50) with the purpose of selecting those fish that successfully accomplished the numerical task.

Fish who reached the criterion were subsequently tested with novel numerical contrasts (c). This was divided in two phases: in phase 1, we observed the ability to discriminate between large numbers with two different numerical ratios: 8 vs. 12 (0.67) and 9 vs. 12 (0.75); in phase 2, we assessed whether fish showed the ability to generalize the numerical rule to novel numerosities having the same ratio (0.50), but very different total set size (2 vs. 4 and 25 vs. 50).

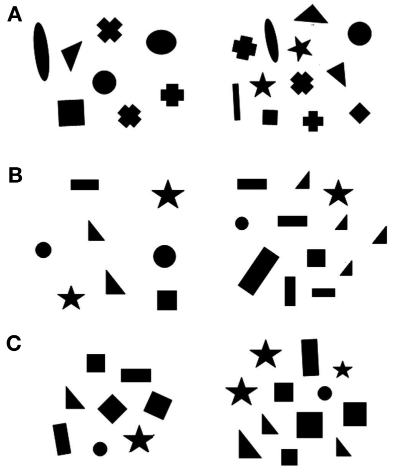

FIGURE 2 | Schematic representation of the stimuli used. Each panel contained black geometric figures differing in numerosity inserted in a white background. In the figure we depicted a 8 vs. 12 contrast with cumulative surface area controlled to 100% **(A)**, to 85% **(B)** and to 70% **(C)**. In **(A)** and **(B)** stimuli are controlled for overall space, whereas in **(C)** they are controlled for density.

Pre-training

During the 6 days preceding the beginning of training, fish gradually were familiarized with the apparatus. On days 1–2, groups of 4 subjects of the same species were inserted in the experimental apparatus for a total of 4 h; on days 3–4, two subjects of each species were inserted in the apparatus for 4 h, while on days 5–6, fish stayed singly in the apparatus for the whole day. During this latter period, fish were fed twice a day. *Artemia* nauplii (*A. salina*) were inserted in the morning and in the afternoon near the two short walls.

Siamese fighting fish are known to be poorly social, as a consequence they were the only exception to this procedure. For this species, pre-training was identical but subjects were individually inserted in the apparatus starting from day 1.

Training

On days 7–9, fish received four trials per day (three consecutive days, for a total of 12 trials). Each trial consisted of inserting the two stimuli panels on the short walls. Two numerical contrasts were presented in a pseudo-random sequence: 5 vs. 10 and 6 vs. 12. Half of the fish were reinforced to the larger numerosities, while the second half was reinforced to the smaller numerosities. Soon after the stimuli were inserted into the tank, a Pasteur pipette was inserted to release the food reward (nauplii of *A. salina*) in correspondence with the reinforced numerosity; an identical syringe was simultaneously used to insert pure water close to the non-reinforced numerosity. Subjects were left free to feed for 7 min. After this time, stimuli were removed from the tank. The inter-trial interval lasted 3 h. We counterbalanced the position of the stimuli (left-right) over trials.

On days 10 and 11, two probe trials were alternated with two reinforced trials each day (four probe trials). In probe trials (two trials with 5 vs. 10 and two trials with 6 vs. 12, presented in a pseudo-random sequence), stimuli were inserted for 4 min in the tank without any reinforcement (extinction procedure). Pipettes were not inserted. The proportion of time spent in the "choice areas" was recorded as a measure of their capacity to discriminate the two numerosities. In particular subjects were considered as selecting a stimulus when their heads were inside the choice area associated to that stimulus. Reinforced trials were identical to those described for days 7–9. Only fish that met the criterion (defined as 60% of the time spent near the reinforced numerosity in probe trials) were selected for the test. A previous study (Agrillo et al., 2012b) has shown that, in easy tasks, such a criterion permits to distinguish fish that learn discriminations from those fish that continue to choose randomly. In a recent experiment we observed that fish that do not meet this criterion after the first 12 trials do not improve their performance even after extensive training (unpublished data).

Subjects were moved from one tank to another one at the end of each day in order to avoid the possibility of using the local/spatial cues of the tank. The latter was previously occupied by conspecific subjects.

Test

After a short interval (days 12–13) in which subjects received two reinforced trials each day with the same numerical contrasts presented during training, fish started the test. The test was composed of two different phases. In phase 1, three probe trials were presented each day for four consecutive days (days 14–17). Fish were presented with two different numerical ratios, 0.67 (8 vs. 12) and 0.75 (9 vs. 12), six presentations for each ratio in a pseudo-random sequence. The inter-trial interval lasted 3 h. Two reinforced trials presenting the numerical contrasts of the training (5 vs. 10 and 6 vs. 12) were alternated in the probe trials.

In phase 2, four probe trials were presented each day for two consecutive days (days 18–19). Fish were observed for their ability to generalize to small (2 vs. 4) and large (25 vs. 50) numbers; there were four presentations for each ratio in a pseudo-random sequence. The numerical ratio was equal to 0.50.

In both phase 1 and 2, we considered the proportion of time spent in the "choice areas" (accuracy) during probe trials as the dependent variable. Proportions were arcsine (square root)-transformed (Sokal and Rohlf, 1995). Mean ± SD are provided. Statistical tests were carried out using SPSS 18.0.

RESULTS

Training

In zebrafish, 5 out of 26 fish in the commercial stock and one out of 22 of the lab stock reached the criterion. The two strains of zebrafish did not differ in performance [independent t-test, $t(46) = 1.48$, $p = 0.148$] and were pooled together in subsequent analyses. A total of 42 fish reached the criterion and were admitted to the following phases (10 out of 16 redtail splitfin, 8/16 guppies, 10/16 Siamese fighting fish, 8/16 angelfish, and 6 out of 48 zebrafish). We found a significant difference among the species in the number of subjects reaching the criterion [chi square test, $\chi(4) = 23.48$, $p < 0.001$]. This finding results from the fact that the number of individuals reaching the criterion in zebrafish was significantly lower compared to the other four species [zebrafish: 6/48, 12.5%; remaining four species: 36/64, 56.3%; chi square test, $\chi(1) = 22.4$, $p < 0.001$].

No difference among the species was found in the proportion of time spent in the choice areas [one way ANOVA, $F(4, 37) = 0.94$, $p = 0.452$]. In particular, when analyzing the time spent in the choice areas of all individuals, no difference was found between zebrafish and the other species pooled together [independent t-test, $t(110) = 0.84$, $p = 0.400$].

Test

Phase 1: influence of numerical ratio. We found no difference in the accuracy between fish trained with the larger or smaller numerosities as positive (independent t-tests, $p > 0.05$ for both ratios).

No species proved able to discriminate 9 vs. 12 items (**Table 1**). There was no difference in performance among the five species [one way ANOVA, $F(4, 37) = 0.45$, $p = 0.772$]. All species, except angelfish, significantly discriminated 8 vs. 12 items (**Table 1**). A significant difference among the five species was found for this ratio [one way ANOVA $F(4, 37) = 3.30$, $p = 0.021$]. On the whole there was a significant difference between the two numerical ratios [repeated measure ANOVA, Ratio: $F(1, 37) = 9.42$, $p = 0.004$; species: $F(4, 37) = 1.59$, $p = 0.197$; interaction: $F(4, 37) = 0.70$, $p = 0.597$, **Figure 3**].

Phase 2: generalization to small and large numerosities. No species proved able to generalize the learned discrimination to a larger set size, 25 vs. 50 items (**Table 1**). There was no difference in performance among the five species [one way ANOVA, $F(4, 37) = 0.06$, $p = 0.992$]. Three species (redtail splitfin, Siamese fighting fish, and angelfish) significantly generalized the learned discrimination to a smaller set size, 2 vs. 4 items. One species (guppy) yielded a marginally significant result, and one species (zebrafish) was not significant (**Table 1**). However, the trend is similar in all five species, and the difference among them is not significant [one way ANOVA, $F(4, 37) = 0.49$, $p = 0.741$]. A likelihood ratio analysis (see Glover and Dixon, 2004 for details) confirmed that the probability that the five species do not differ is three times larger ($\lambda = 2.98$) than the probability that a difference exists. Overall, the difference in the generalization between the larger and smaller set size was significant [repeated measure ANOVA, $F(1, 37) = 9.84$, $p = 0.003$] with no species variation [$F(4, 37) = 0.23$, $p = 0.919$; interaction: $F(4, 37) = 0.06$, $p = 0.911$, **Figure 3**].

We found no difference in the accuracy between fish trained with the larger or smaller numerosities as positive [2 vs. 4, independent t-test, $t(40) = 1.34$, $p = 0.187$; 25 vs. 50, independent t-test, $t(40) = 0.22$, $p = 0.826$].

EXPERIMENT 2

SUBJECTS, APPARATUS, STIMULI, AND PROCEDURE

Twenty fish (10 *D. rerio* and 10 *X. eiseni*) were tested. Both species were observed in a discrimination between two black geometric figures in a white background (filled triangle vs. empty circle). For

Table 1 | Performance of the five species in the numerical contrasts presented during test phase.

Species	8 vs. 12	9 vs. 12	2 vs. 4	25 vs. 50
Redtail splitfin	$t(9) = 3.25$, $p = 0.010$*	$t(9) = 1.26$, $p = 0.239$	$t(9) = 3.12$, $p = 0.012$*	$t(9) = 0.18$, $p = 0.861$
Guppy	$t(7) = 2.86$, $p = 0.024$*	$t(7) = 0.21$, $p = 0.842$	$t(7) = 2.02$, $p = 0.083$	$t(7) = 0.05$, $p = 0.961$
Zebrafish	$t(5) = 6.10$, $p = 0.002$*	$t(5) = 0.56$, $p = 0.597$	$t(5) = 1.55$, $p = 0.181$	$t(5) = 0.42$, $p = 0.690$
Siamese fighting fish	$t(9) = 3.95$, $p = 0.003$*	$t(9) = 0.79$, $p = 0.453$	$t(9) = 3.42$, $p = 0.008$*	$t(9) = 0.40$, $p = 0.698$
Angelfish	$t(7) = 0.79$, $p = 0.458$	$t(7) = 0.87$, $p = 0.414$	$t(7) = 2.50$, $p = 0.041$*	$t(7) = 0.76$, $p = 0.942$

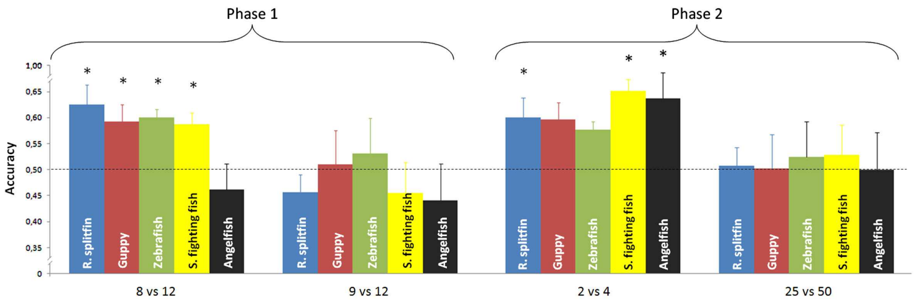

FIGURE 3 | Numerical contrasts were plotted against the accuracy of the five species. Most of the species significantly discriminated 8 vs. 12 and spontaneously generalized to smaller numerosities (2 vs. 4). All species failed to discriminate 9 vs. 12 or generalize to larger numerosities (25 vs. 50). Asterisks denote a significant departure from chance level ($p < 0.05$). Bars represent the standard error.

each species, half of the subjects were reinforced to the triangle, and half to the circle. The same figures were presented during all trials (both training and probe trials). The apparatus was identical to that of experiment 1. The procedure also was the same, with the exception that the experiment ended after the four probe trials of the training phase.

RESULTS

We found no difference in the accuracy between fish trained with the triangle or circle as positive (independent t-tests, $p > 0.05$ for both species). Redtail splitfin significantly discriminated between the two figures [mean ± SD: 0.594 ± 0.06, one sample t-test, $t(9) = 4.65$, $p = 0.001$], while zebrafish did not [0.471 ± 0.08, one sample t-test, $t(9) = 1.08$, $p = 0.307$]. A significant difference between the two species was found [independent t-test, $t(18) = 3.70$, $p = 0.002$, **Figure 4**]. No difference in the accuracy was found between fish trained in numerical discrimination (training of phase 1) and those trained to discriminate geometric figures [independent t-test for unequal cases redtail splifin: $t(24) = 0.807$, $p = 0.428$; zebrafish: $t(56) = 0.005$, $p = 0.996$].

DISCUSSION

The present paper represents the first attempt to compare numerical abilities in teleost fish using the same methodology. Subjects of five teleost species first were trained to discriminate two sets of geometrical figures using an easy 0.50 numerical ratio (5 vs. 10 and 6 vs. 12) and then observed in non-reinforced probe trials in which the numerical ratios or total set size varied. Overall, similarities were far greater than differences. Fish trained with the larger or smaller numerosities as positive showed equal accuracy in all species. When we made the discrimination more difficult by increasing the numerical ratio, we observed a similar pattern of performance in all fish, with no species being able to discriminate the 0.75 ratio (9 vs. 12), but four out of five species being able to discriminate the 0.67 ratio (8 vs. 12). The pattern of generalization of the numerical rule to a different set size was also very similar in the different species. Fish generalized the learned discrimination to a smaller set size (2 vs. 4), showing no substantial inter-specific difference, while no species was able to generalize to a larger set size (25 vs. 50). These data, together with results recently reported in another teleost species tested in the same apparatus, *Gambusia holbrooki* (Agrillo et al., 2012b), point toward the existence of similar numerical discrimination among fish.

In all, we observed three main inter-specific differences. First, the proportion of subjects that reached the criterion in the training phase was similar among species, with the exception of zebrafish, which showed a fourfold smaller proportion of fish reaching the criterion. This difference might be ascribed to two reasons: (a) a specific deficit of zebrafish regarding numerical skills, or (b) a more general inability of this species in discrimination learning. The results of experiment 2 support the latter hypothesis. When trained to learn simple shape discrimination, a filled triangle from an empty circle, zebrafish performed much worse than the control species, redtail splitfin. In recent years, a few works have been published regarding the possibility of training visual discrimination in zebrafish. In most cases, the required discrimination was even more simple than this, i.e., to distinguish a red wall from other non-colored ones (Sison and Gerlai, 2010), or implied a much larger number of trials (Braubach et al., 2009). To our knowledge,

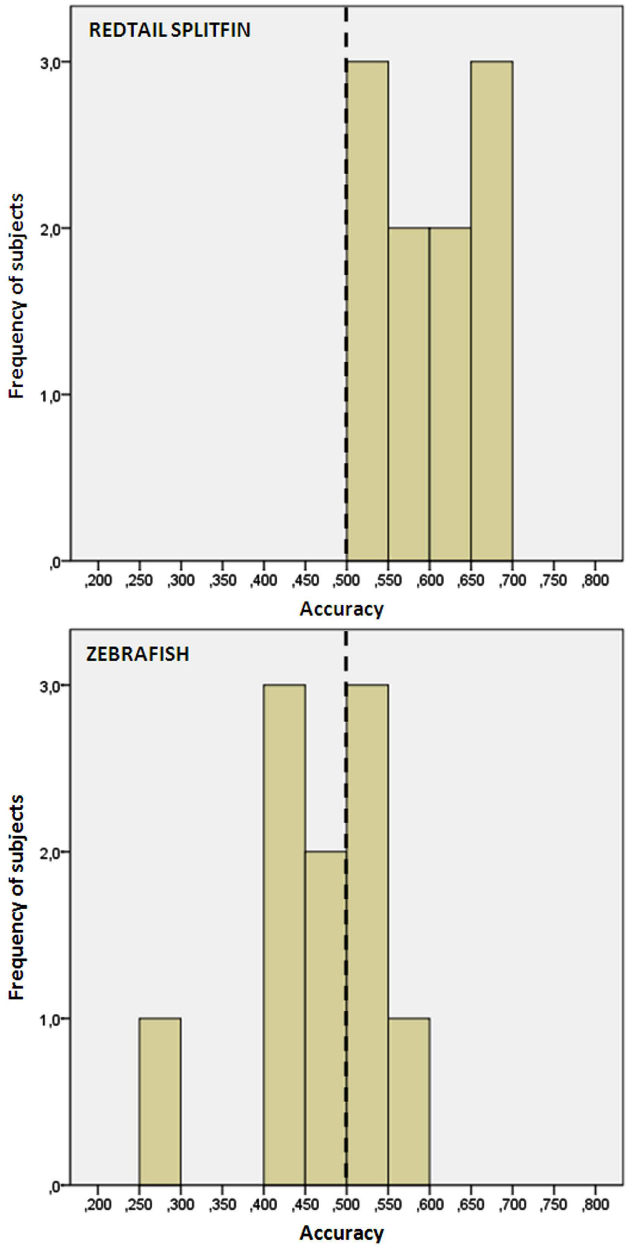

FIGURE 4 | Frequency distribution of the preference score of zebrafish and redtail splitfin in the shape discrimination task of experiment 2. Redtail splitfin significantly preferred the reinforced stimulus, while the performance of zebrafish is indistinguishable from random choice.

there are no data that allow a direct comparison between zebrafish and other teleosts in the same procedure. It therefore remains to be seen whether the difference between zebrafish and other species is specific to the method we used in this study or extends to other learning tasks. It is important to note that the few zebrafish reaching the criterion were similar in performance to the other four species in both phase 1 and 2, reinforcing the hypothesis that the low performance of zebrafish primarily resulted from a low learning performance in this species.

Different learning performance might in turn be explained with species-specific characteristics, such as neophobia. Consistent differences in behavior between individuals in a population, especially in the shy-bold continuum, have been reported in a variety of organisms, including many fish species (Dall et al., 2004; Sih et al., 2004); it has been termed "animal personalities" or "coping styles." In many conditions, these different coping styles may affect the speed of acquiring a task (Sneddon, 2003; Kurvers et al., 2010; Amy et al., 2012). One might argue for instance that a shy species may have explored the experimental tank less than a bold species, thus having less time to associate the proximity to the positive stimulus with food reinforcement. However, this is not the case in our experiment, as we found that the proportion of time spent in the two choice areas by zebrafish was the same as other species.

The second difference among the species was observed in phase 1. Unlike the other four species, angelfish seem to be unable to discriminate 8 vs. 12. Such a result is puzzling and even surprising if we consider that angelfish tested with another paradigm (spontaneous shoal choice) showed the same or even better performance than mosquitofish and guppies in large number discrimination (Agrillo et al., 2008, 2012a; Gómez-Laplaza and Gerlai, 2011a). *P. scalare* is larger species and, in order to match as far as possible the five species in size, we had to test sub-adult angelfish. This factor could potentially account the differences observed in this species. However we believe this is an unlikely explanation for the differences observed in this experiment, as other studies have shown that numerical abilities of very young fish are not much dissimilar from those observed in the adults (Bisazza et al., 2010). It is worth noting that, although the subjects of the five species had comparable body length, the morphological characteristics of angelfish differ from those of the other species tested: in angelfish the longitudinal axis is shortened, and the body is laterally compressed with extended dorsal and anal fins and we cannot exclude that water depth used in experimental tanks was not entirely suitable for this species.

The difficulty to understand the exact nature of angelfish peculiarity highlights one of the main problems of comparative studies: the strength of using the same methodology for testing different species may become a methodological weakness. Different species show different adaptations to their different ecological niches and, therefore, housing and testing requirements could be different in the lab; some species might be affected by such daily handling more than some others, or have perceptual or motivational characteristics that potentially render the tests more dissimilar across different species than initially planned. To assess whether the apparent inability of angelfish to discriminate the 0.67 ratio is simply an artifact of the methodology adopted, replication studies using different methods are needed (Agrillo and Miletto Petrazzini, 2012).

A third possible inter-specific difference was observed in phase 2 in which the generalization to small numbers was fully significant only for three species. The trend is, however, similar for the five species, and the likelihood ratio analyses indicated that the lack of difference among the species was 2.98 times more likely than the alternative hypothesis. One may argue that results of phase 2 might be affected by potential carry-over effects from phase 1, as all subjects performed the experiments in the same order (generalization

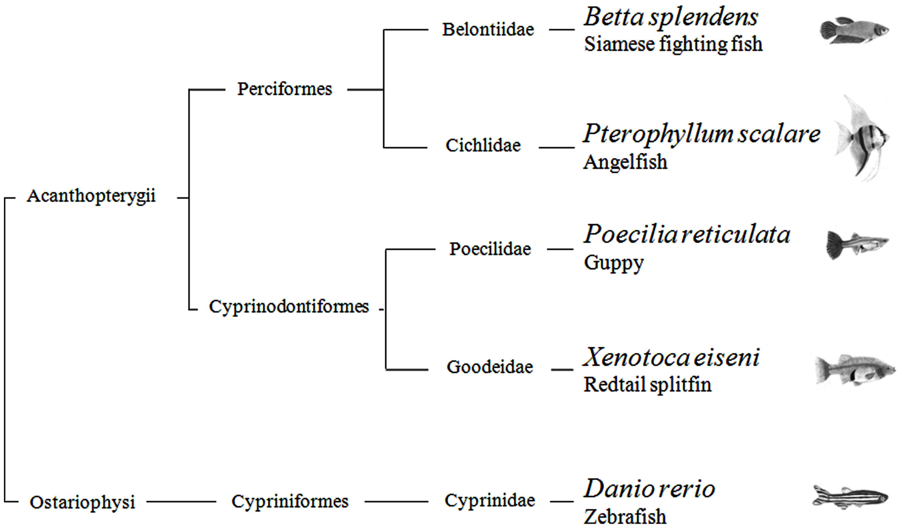

FIGURE 5 | Phylogenetic relationship of the five teleost species used in the study.

to different numerical ratios firstly and generalization to different total numerosities secondly). However, it is worth noting that in the whole experiment 1 fish were trained only in a 0.50 ratio and were exposed to more difficult ratios without receiving any reinforcement.

In summary, with the possible exception of the angelfish results in one of four generalization tests, this study provides scarce evidence that quantification systems differ across teleosts. There is current debate regarding non-verbal numerical systems. Some scholars argue that they are the same in all vertebrates, inherited from a common ancestor; others believe that each species has evolved its mechanisms in relation to the constraints imposed by the nervous system and the ecological problems faced in the environment. From a phylogenetic point of view, the five species studied here are distantly related. According to recent estimates, the Ostariophysi (**Figure 5**), the group to which zebrafish belongs, and the Acanthopterygii, the group which comprises the other four species, diverged more than 250 million years ago (Steinke et al., 2006). They also encompass a broad spectrum of ecological adaptations. For example, some species live in open areas and others densely vegetated shallow waters, some are highly gregarious and other basically solitary, some care their young and other provide no form of parental care. The finding of so few inter-specific differences seems more in accord with the existence of ancient quantification systems inherited from a common ancestor. On the other hand, the species have been compared in a single context, and they may reveal larger differences if studied in wider spectrum of domains.

The observation made in this study that fish can easily generalize to sets of reduced numerosity but not to sets of enlarged numerosity deserves consideration. The failure to generalize the numerical rule learned in 5 vs. 10 and 6 vs. 12 in contrast to 25 vs. 50 items is particularly surprising considering that previous studies (Agrillo et al., 2010, 2012b) showed that mosquitofish can successfully generalize to even larger numerosities, such as 100 vs. 200, provided that they receive some reinforced trials on these new stimuli. One could argue that during training, fish may have learned to choose a precise numerosity instead of learning a number rule (i.e., choose the larger/smaller quantity), and later they preferred the quantity closest to that previously reinforced. For example, a fish trained to choose 12 over 6 items during 25 vs. 50 probe trials might prefer 25 items because it is the closest to the reinforced numerosity. In this case, however, we would expect the same phenomenon to occur during the generalization to smaller numerosities, which did not happen. In addition, we expect an opposite performance depending on whether fish have been trained toward the smaller or the larger numerosity. Yet, no difference was found between these two conditions, thus excluding the possibility that the direction of the training might have interfered with the direction of the variation of total set size.

We can only speculate about the meaning of this result. In nature, some items in a set may partially hide each other or temporarily disappear behind objects, thus reducing the visible total set size even if their composition is constant. For example, during the comparison of 5 vs. 10 conspecifics, fish might be required to continue the enumerating process when the perceived numerosity is reduced, for example when only 4 vs. 8 fish are visible. In this sense, the cognitive systems of these species might have been selected to generalize the numerical rule to another contrast with a reduced total set size. In contrast, it is physically implausible that groups of objects increase their numerosity without altering their composition. In other words, while 2 vs. 4 would appear as another version of the 5 vs.10 task, the shift from 5 vs. 10 to 25 vs. 50 items might appear to fish as a novel task, preventing generalization of the same numerical rule from smaller to larger numbers. It will be a challenging task to determine whether other vertebrate species show the same generalization pattern.

As a last remark, we would like to note one important implication of the findings from experiment 2. While the results of the training phase in experiment 1 would superficially suggest cross-species differences in numerical abilities, the difference observed between redtail splitfin and zebrafish in another type of discrimination showed the true nature of zebrafish low performance. When investigating the existence of differences between experimental groups in one cognitive domain, it is always important to include control tests done in other domains to exclude the possibility that the observed differences depend on concomitant factors, such as personality, motivation, or attention differences. This is routinely performed in other disciplines (i.e., cognitive psychology), but still rarely adopted in comparative psychology studies.

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Memory for multiple cache locations and prey quantities in a food-hoarding songbird

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Most animals can discriminate between pairs of numbers that are each less than four without training. However, North Island robins (*Petroica longipes*), a food-hoarding songbird endemic to New Zealand, can discriminate between quantities of items as high as eight without training. Here we investigate whether robins are capable of other complex quantity discrimination tasks. We test whether their ability to discriminate between small quantities declines with (1) the number of cache sites containing prey rewards and (2) the length of time separating cache creation and retrieval (retention interval). Results showed that subjects generally performed above-chance expectations. They were equally able to discriminate between different combinations of prey quantities that were hidden from view in 2, 3, and 4 cache sites from between 1, 10, and 60 s. Overall results indicate that North Island robins can process complex quantity information involving more than two discrete quantities of items for up to 1 min long retention intervals without training.

Keywords: New Zealand robin, number, field experiment, cache, memory

INTRODUCTION

Numerical processing has been demonstrated in a wide range of animal species (for a review see Brannon, 2005; Reznikova, 2007; Reznikova and Ryabko, 2011) from beetles (Carazo et al., 2009) to bears (Vonk and Beran, 2012). Small numbers of less than four are dealt with innately by most non-human species (Trick and Pylyshyn, 1994; Hauser et al., 2000; Feigenson et al., 2004). Larger number discriminations and advanced numerical processing have been shown in some highly trained lab animals (Beran, 2001; Pepperberg, 2006; Tomonaga, 2008), but also appear to be displayed naturally to some extent by wild or free-ranging animals in the absence of training (Lyon, 2003; Hunt et al., 2008; Low et al., 2009; White et al., 2009; Garland et al., 2012).

Food-hoarding animals may provide a unique window into the evolution of numerical competency in animals. Successful food-hoarding often requires accurate memory of the number of cache sites an animal has created, the number of items in each site, whether some or all of those items have been retrieved, and in some cases how long the items have been stored. New Zealand robins are unique in that they almost exclusively hoard insects that have been hunted and then paralyzed or killed and sometimes dismembered (Powlesland, 1980; Menzies and Burns, 2008). Robins then cache their prey in (and pilfer from) multiple caches containing small numbers of items throughout their territory (Powlesland, 1980; Menzies and Burns, 2008). This unusual combination of behavioral traits – caching highly perishable food items for only 1–3 days, storing food in multiple groups of small quantities, and a high rate of pilferage from conspecifics – could provide ideal conditions for advanced quantity discrimination to evolve.

Food-hoarding is employed by many avian species when faced with a surplus of food. However, in order for food-hoarding to be selectively advantageous, the hoarder must have a better chance of retrieving food stores than other animals (Andersson and Krebs, 1978; Smith and Reichman, 1984). An accurate memory for cache locations provides an important recovery advantage (Tomback, 1980; Sherry et al., 1981; Vander Wall, 1982; Kamil and Balda, 1985). Many scatter-hoarding species can accurately remember the locations of caches and outperform closely related, non-storing species in spatial memory tasks (Balda and Kamil, 1989; Bednekoff et al., 1997; Pravosudov and Clayton, 2002). This suggests that food-hoarding species often evolve cognitive specializations to remember large numbers of spatial coordinates associated with their cache sites. However, animals that create caches do not have exclusive access to their retrieval. Many species are known to pilfer caches made by other species (Burns and van Horik, 2007).

Accurate discrimination between sites containing variable numbers of items may be important when pilfering from caches; especially those located close together such as in the present study. Obtaining the highest available reward would make pilfering a more viable strategy if there is the possibility of aggressive repercussions from the owner of the cache. Robins preferentially select for cache sites containing more mealworms over those with fewer in the present study, as well as in Hunt et al. (2008) and Garland et al. (2012), strongly suggesting that the birds were actively avoiding these sites in favor of the sites containing the larger number of mealworms, which were selected at above-chance levels. Appropriate use of observational spatial memory (OSM) requires that an individual observe caching behavior from a distance in order to avoid alerting the cacher to the pilferer's intentions. Such a distance would also minimize the visibility of minute size and volume differences in such items (which are often already minimized by the cacher dismembering and breaking larger prey into pieces), perhaps selecting for pilferage prioritizing based on cache size as a primary cue rather than prey size or volume. Making such observations would require an individual to maintain an accurate representation of the number of items observed being hidden in several different locations. Prioritizing the pilfering of the cache containing the largest quantity of prey would allow a pilferer to maximize energetic rewards gained during short temporal opportunities while the cacher is not in the vicinity. Because cache pilferers may face reprisals from food hoarders, the capacity to remember the number of items and locations where other animals have stored food could be selective advantageous.

The energy costs associated with food-hoarding mean that it is not surprising that some individuals adopt a "cheat" strategy by pilfering caches made by others. The result of the obvious incentive to steal is that strategies have evolved that allow individuals to conduct more accurate cache theft. After observing a conspecific caching, a pilferer can attempt to immediately steal or re-cache the food items. This is potentially dangerous however as the owner of the cache is likely to still be in the vicinity and may react aggressively if the thief is discovered. Because of this a less risky method is to observe and remember the location of a cache site and to return later when the owner is less likely to be around. This form of memory is referred to as OSM and has been identified as an important and advantageous cognitive ability for food pilfering (Bednekoff and Balda, 1996a,b; Scheid and Bugnyar, 2008). The ability to employ OSM when stealing cached food from others reduces the incidence of potentially dangerous aggressive encounters and may provide a means for subordinate individuals to compete indirectly for food without the need to physically displace dominant individuals.

Black-capped chickadees (*Parus atricapillus*) display excellent spatial memory in recovering their own caches (Baker et al., 1988; Hitchcock and Sherry, 1990). Despite this, black-capped chickadees showed no recovery benefit from observing another individual caching compared to recovering caches made in its absence (Baker et al., 1988; Hitchcock and Sherry, 1995). To date OSM has been demonstrated to varying degrees only in corvid species such as Pinyon jays (*Gymnorhinus cyanocephalus*), Mexican jays (*Aphelocoma ultramarina*), Clark's nutcrackers (*Nucifraga columbiana*), scrub-jays (*Aphelocoma coerulescens*), jackdaws (*Corvus monedula*), and ravens (*C. corax*; Bednekoff and Balda, 1996a,b; Bednekoff et al., 1997; Bugnyar and Kotrschal, 2002; Scheid and Bugnyar, 2008). It has been hypothesized that OSM "could have evolved either as a consequence of extreme cache dependence, as a consequence of caching in flocks, or may have required the combination of these traits" (Bednekoff and Balda, 1996a, p. 824). Further research has produced mixed results in this area. Follow-up studies by Bednekoff and Balda (1996b) found that social Mexican jays (*A. ultramarina*) had a greater accuracy of recovery for caches that they had observed others making than more solitary Clark's nutcrackers (*N. columbiana*). However, conversely, a similar study by Scheid and Bugnyar (2008) found that less social but more caching specialized ravens recovered other individual's caches more accurately than social foraging, low-frequency caching jackdaw. In this instance the less social, but more cache-dependent species performed better than the socially cohesive species that cache only at low densities. Despite the differences in recovery ability both species were able to recover caches that they had observed another individual of the same species make. Black-capped chickadees, in contrast, gained no recovery benefit from observing caching behavior in a conspecific. Bednekoff and Balda concluded that enhanced spatial memory and social living are not both requisites for the evolution of OSM.

North Island robins (*Petroica longipes*) are not highly cache-dependent and rely on caching as an external mechanism for dealing with short-term temporal resource fluctuations (Menzies and Burns, 2008). When they do cache, North Island robins tend to maintain only a few active cache sites at any one time and will also reuse the same locations during subsequent caching bouts (Alexander et al., 2005). Robins are not social or flock foragers and are strictly monogamous (Higgins and Peter, 2002; Taylor et al., 2008), spending most of their lives in mate-pairs. Pairs usually form long-term associations and reside on permanent territories (Flack, 1976; Powlesland, 1980; Ardern et al., 1997; Armstrong et al., 2000). Although both members of the pair cooperate to raise young in the breeding season, males are competitively dominant to females and aggressively monopolize food sources year-round (Steer and Burns, 2008). Numerosity experiments involving a human demonstrator hiding mealworms (Hunt et al., 2008; Garland et al., 2012) showed that robins are capable of accurately locating food items that they have watched an individual of another species hide. This attentiveness to the actions of others suggested that New Zealand robins may be able to display OSM under experimental conditions. Like many animals that are endemic to isolated islands, New Zealand robins are fearless of humans (Alexander et al., 2005; Menzies and Burns, 2008). Their lack of anti-predatory behaviors toward humans facilitates the study of their cognitive abilities in the field. Wild birds can be approached and observed at very close distances (2–3 m).

New Zealand robins appear to possess a highly advanced quantity discrimination ability (Hunt et al., 2008; Garland et al., 2012). Wild birds were able to discriminate between hidden caches with unusually high accuracy far beyond a typical limit of four items in the absence of training. In violation of expectancy trials, they also searched for longer when some of the prey items they saw being cached were hidden from view before they were allowed to retrieve them. These results suggest that they could possess other sophisticated cognitive processes to enhance the likelihood of successful cache retrieval. While abstract numerical representation is yet uninvestigated in this species, the present experiment attempts to further investigate differential responses to quantitative discrimination of physical prey items under varying conditions, where stimuli such as visual access, time lag, and number of hiding places are all manipulated experimentally in a natural setting. It is hoped that this will provide a complementary example of an ecologically salient counterpart to similar, more abstract numerical processing tasks that lab-trained corvids have already proven to be capable of.

In this study, we sought to better understand OSM and prey quantity in a small passerine by conducting a series of experiments on a color-banded, wild population of North Island robins. Variable numbers of prey items were stored in a different number of artificial caches (2–4) in full view of subjects. Cache sites were then obscured from view for variable lengths of time (1–60 s). This experimental protocol was then repeated for different total numbers of stored prey (1–4). Results were then analyzed statistically to determine whether robins were capable of accurately choosing between multiple quantity comparisons that were obscured from view for variable lengths of time.

MATERIALS AND METHODS

This experiment was conducted at Zealandia, a 225 ha fragment of regenerating native bush located close to central Wellington, New Zealand (41° 18′ S, 174° 44′ E). Ten adult, male birds (18+ months of age) were used as subjects in all trials. All were uniquely color-banded for accurate identification.

This experiment was conducted using apparatuses similar to those used by Hunt et al. (2008). Each apparatus was constructed from a tree branch containing 2, 3, or 4 artificial depressions (manually drilled) that served as artificial cache sites (see **Figure 1**). Depressions were 3 cm long, 2 cm deep and were covered by a leather flap attached at one side by a screw swivel to conceal the contents from view. When wild birds forage naturally, they spend the majority of time searching for ground-dwelling invertebrates on the forest floor by turning-over dead leaves with their bill. Because leather flaps were similar in size, shape, and color to fallen leaves on the forest floor, all subjects learned to remove the flaps and retrieve the contents below with little or no training. Familiarization trials consisted of allowing birds to watch prey items being loaded into wells and covered. The birds were then permitted to access prey by allowing them to learn how to turn the leather flaps on the swivel. No comparisons were presented in familiarization trials, which served only to familiarize the bird with pulling the leather flap in the same manner as they overturn leaves. Once birds were able to pull flap to reveal contents, test trials commenced.

Three different variables were manipulated using a three factor, fully crossed design: quantity of mealworms (1v0, 1v2, 1v3), number of caches (2, 3, and 4), and retention interval (0, 10, and 60 s). This created a 3 × 3 × 3 design in which all 27 treatment combinations in the three conditions were repeated four times for each of the 10 color-marked individuals, yielding a total of 1080 trials.

FIGURE 1 | A robin makes his choice by pulling a flap attached to the apparatus and retrieving the contents.

For variable 1, the robins observed 1, 2, or 3 mealworms (*Tenebrio molitor* larvae) being placed in one artificial cache site. Additionally, a variable reward system was used in trials where 2 or 3 mealworms were hidden – an additional mealworm was placed in another cache site to test whether birds could discriminate between two non-zero values of reward. The number of artificial cache sites (variable 2) that robins could choose from was fixed-factor with three levels (2, 3, or 4 cache sites). This factor was included in the experiment to test whether the capacity of birds to choose the larger value declines as a function of the number of choice-locations present (i.e., cache sites). Retention interval (variable 3) or the period of time artificial prey was concealed from view was also fixed-factor with three levels: 0 s (i.e., the bird was allowed immediate access to the cache sites once the leather flaps had been closed), 10, and 60 s.

Memory traces decay over time and longer periods between caching and recovery or pilfering would be expected to lead to a corresponding decrease in success rate either through a reduction in memory accuracy or an increase in search errors. The retention intervals in these experiments were deliberately kept short as the study was designed as a test of OSM, rather than to determine how these memories decrease with time. In addition, the retention intervals in this study were constrained by the difficulties of working with a free-ranging population of birds. In the prolonged absence of visual stimulus (i.e., view of the mealworms or cache site) the robins lose interest and are more likely to abandon the experiment before a choice is made.

To homogenize potential learning effects, the order in which each treatment combination was conducted was assigned randomly. Trials were conducted between July and December 2010. The birds used in the experiment were located by spot-mapping along a series of tracks traversing the valley. Once the bird was located the experimental apparatus was placed on the track and trials began once the bird had approached within 2 m of the apparatus. The artificial cache sites were initially presented with the leather flaps open so the bird was able to see they were empty. Mealworms were then held up individually and displayed to the bird before being placed sequentially into the cache site (at a rate of approximately 5 s per item) and the leather flaps closed following Hunt et al. (2008). For trials where there was a variable reward, the order in which the sets of mealworms (i.e., larger number vs. smaller number) were placed in the cache sites was also randomized to control for potential order preferences. Once a choice was made, and prey was retrieved, the apparatus was removed from the experimental arena, giving birds the opportunity to retrieve from only a single cache.

In trials with a 0 s retention interval the experimenter then immediately stepped back 2 m and the robin was allowed to select and open one cache site. A cache was considered "selected" if the bird actively removed the leather flap from a well. The birds were allowed to retrieve any mealworms in the cache they had chosen, and not differentially reinforced for correct or incorrect responses outside of the differing quantities retrieved in the task itself. The same procedure was used in trials with retention intervals of 10 and 60 s, however after the leather flaps were closed the whole apparatus was covered with an opaque sheet. After the appropriate retention interval (10 or 60 s) the visual barrier (a cloth sheet) was removed and the experimenter stepped back and the trial proceeded as above.

A "successful" choice was defined as a trial in which the bird selected and removed the leather flap from the cache site containing the largest number of mealworms on the first attempt. A mean success rate was calculated as a percentage of successful choices for each treatment condition across the four replicates per individual bird, rendering individual birds as the unit of replication. If birds select cache sites at random, then the chance any particular site would be selected varies as a function of the total number of sites available. When there are two sites the likelihood of "success" by chance is 50%, compared to 33% when there are three sites presented and 25% when there are four sites.

To test whether birds performed above-chance expectations, in each treatment combination, the proportion of trials where birds chose the well with the highest number of mealworms was calculated for each bird. If birds chose sites randomly, the average of these values should be statistically indistinguishable from $1/y$, where y is the number of cache sites available in each particular trial. To test whether birds performed above-chance expectations (i.e., the observed rates of "success" were unusually high), we conducted separate, single-sample t-tests for each treatment combination. In each test, we tested whether the average rates of "success" differed from randomized expectations $(1/y)$. Separate tests were conducted for each treatment combination and $n = 10$ for all.

To test whether performances differed between retention intervals and the number of cache sites, separate linear mixed models were conducted for each condition. The number of cache sites and retention interval were considered fixed factors, each with three levels. Because all 10 birds were included in each treatment combination, "individual" was included in the model as a random factor. If the proportion of trials where the highest quantity of prey was chosen (i.e., success rate) was used as the dependent variable, a significant effect of number of cache sites would be observed even when birds were to choose cache sites at random. This effect due to varying number of cache sites arises mathematically from lower average chances of success in trials with more cache sites. To remove this confounding effect from analyses, the fraction of "successful" trials observed for each bird was subtracted from chance expectations $(1/y)$ prior to analyses. All analyses were conducted in IBM Corp (2011) and data conformed to assumptions without transformation.

RESULTS

This experiment tested for non-random decision making with regards to selecting the larger presented number of mealworms. Each level of the two independent variables (number of cache sites and retention interval) was tested against chance expectation (**Figure 2**) for each of the three conditions. All different levels of number of cache sites (2, 3, or 4 sites) were significantly above-chance across all three conditions ($P \leq 0.021$; **Figure 2**). All retention intervals (0, 10, and 60 s) were also significantly above-chance across the three conditions ($P < 0.017$ for all trials). This strongly suggests that North Island robins are capable of displaying OSM across at least short time intervals.

Robins chose the cache site containing the higher quantity of prey in 67% of trials. More specifically, across the 27 treatment combinations in the three conditions, the average "success" rate was higher than chance expectations in 18 trials (i.e., $P < 0.05$, **Table 1**). Two trials approached significance ($0.05 < P < 0.10$) and seven trials did not approach statistical significance ($P > 0.10$).

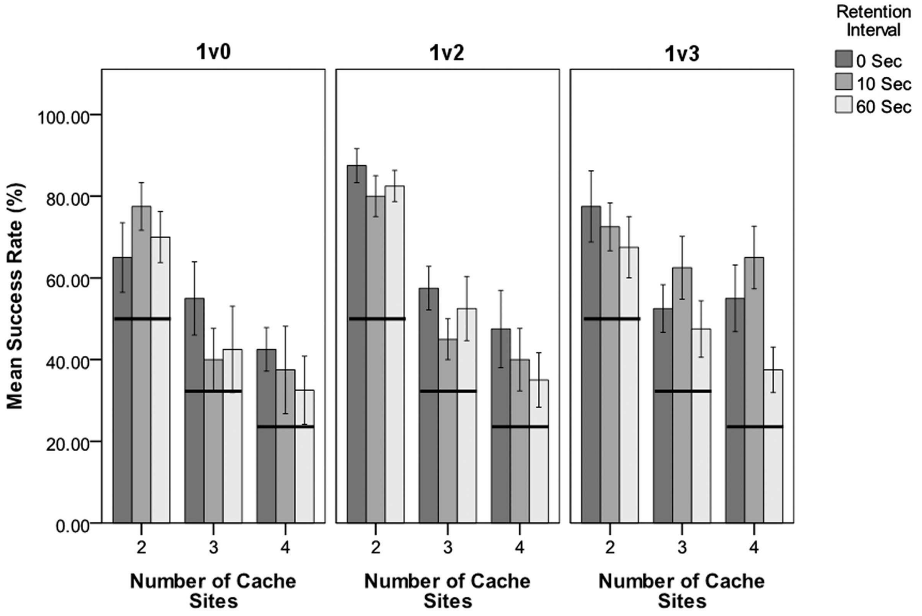

FIGURE 2 | The success rate for each combination of independent variables for the three conditions. Y-axis shows the success rate as a percentage of "correct" choices (i.e., where the largest number of mealworms was selected). X-axis shows number of cache sites with bars grouped according to retention interval (0, 10, and 60 s). Indicates the percentage of successes expected by chance for each cache level. Error bars ± 1 standard error.

Table 1 | Single-sample *t*-tests for all combinations of variables.

Trial	Mealworms	Cache sites	Time	Mean	*T*	*P*
1	1v0	2	0	65.00	1.765	0.111
2	1v0	2	10	77.50	4.714	0.001
3	1v0	2	60	70.00	3.207	0.011
4	1v0	3	0	55.00	2.451	0.037
5	1v0	3	10	40.00	0.917	0.383
6	1v0	3	60	42.50	0.898	0.392
7	1v0	4	0	42.50	3.280	0.010
8	1v0	4	10	37.50	1.168	0.273
9	1v0	4	60	32.50	0.896	0.394
10	1v2	2	0	87.50	9.000	0.000
11	1v2	2	10	80.00	6.000	0.000
12	1v2	2	60	82.50	8.510	0.000
13	1v2	3	0	57.50	4.592	0.001
14	1v2	3	10	45.00	2.400	0.040
15	1v2	3	60	52.50	2.480	0.035
16	1v2	4	0	47.50	2.377	0.041
17	1v2	4	10	40.00	1.964	0.081
18	1v2	4	60	35.00	1.500	0.168
19	1v3	2	0	77.50	3.161	0.012
20	1v3	2	10	72.50	3.857	0.004
21	1v3	2	60	67.50	2.333	0.045
22	1v3	3	0	52.50	3.343	0.009
23	1v3	3	10	62.50	3.840	0.004
24	1v3	3	60	47.50	2.095	0.066
25	1v3	4	0	55.00	3.674	0.005
26	1v3	4	10	65.00	5.237	0.001
27	1v3	4	60	37.50	2.236	0.052

"Success" rates were never below chance expectations. Additional *t*-tests were used to assess whether the robins selected the lower of the variable reward (i.e., the cache site containing only one mealworm) at a level that differed from chance. Trials where the cache site with only one mealworm was selected were significantly below chance level ($P < 0.005$; 1v2, $T = -5.84$; 1v3, $T = -6.87$). Robins did not preferentially select the smaller quantity of mealworms. Birds performed similarly regardless of retention interval and number of cache sites. Birds performed better (i.e., higher chances of success) when they were faced with fewer cache sites. A single-sample *t*-test across all 27 trails for whether the distribution of *t*-values listed in **Table 1** differ significantly from a mean of zero shows significant difference ($t = 8.194$, $\mathrm{df} = 26$, $P < 0.001$), providing evidence that robins consistently chose sites with more items at above-chance expectations across all trials. If robins chose cache sites at random, then the resulting *t*-values for each trial would form a distribution that would not differ from a mean of zero, whereas if they consistently choice sites with few items the mean *t*-value would be significantly negative.

In trials where only a single mealworm was presented, neither the number of cache sites nor the retention interval were significant predictors of success. Both the interaction between number of cache sites and retention interval and the random factor "individual" were also non-significant (**Table 2**).

Table 2 | Results for general linear model analyses of variables 1v0 (top), 1v2 (middle), and 1v3 (bottom).

	SS	df	MS	*F*	*P*
1v0 MEALWORMS					
Individual	3090.278	9	343.364	0.405	0.903
Cache sites (Cs)	1335.556	2	667.778	0.865	0.438
Retention interval (Ri)	513.889	2	256.944	0.342	0.715
Cs × Ri	2069.444	4	517.361	0.766	0.554
1v2 MEALWORMS					
Individual	46013.611	1	46013.611	89.138	0.313
Cache sites (Cs)	4645.833	9	516.204	1.570	0.004
Retention interval (Ri)	5293.889	2	2646.944	7.573	0.189
Cs × Ri	1430.556	2	715.278	1.828	0.896
1v3 MEALWORMS					
Individual	50646.944	1	50646.944	135.337	0.567
Cache sites (Cs)	3368.056	9	374.228	0.964	0.637
Retention interval (Ri)	668.889	2	334.444	0.462	0.003
Cs × Ri	3930.556	2	1965.278	8.035	0.601

SS, sums-of-squares; df, degrees of freedom; MS, mean squares; F, F-ratio; P, type-one error rates are shown.

In trials where two mealworms were presented in one cache (1v2), number of cache sites was significant in determining the likelihood of a successful choice. Within these trials, those involving two cache sites had a higher likelihood of success compared to three or four cache sites (**Figure 2**). Retention interval, individual, and the interaction between number of cache sites and retention interval were all non-significant for this experiment (**Table 2**).

In trials where three mealworms were presented in one cache (1v3), number of cache sites was not a significant predictor of success, however retention interval was significant. Within these trials, those with a 60 s retention interval result in a lower rate of success than trials with a retention interval of either 0 or 10 s. Neither Individual nor the interaction term were significant (**Table 2**).

There were differences in success rate between the three quantity comparisons, suggesting that the number of mealworms offered as a reward affected the bird's average success rate. In trials where the robins were offered only one mealworm there was a significantly lower success rate than in the other two experiments where the birds were offered two mealworms ($T = -2.03$, $P = 0.46$) or three mealworms ($T = -2.37$, $P = 0.20$). Trials with two or three mealworms did not differ significantly from each other ($T = -0.32$, $P = 0.75$). This may be indicative of a differing response to a higher number of null sets (empty caches) in these trials.

DISCUSSION

Results detailed here provide significant evidence that North Island robins are capable of utilizing OSM, at least over short time periods, when faced with variable cache numbers and prey quantities. Overall, they performed at above-chance expectation; however some treatment combinations were not above-chance (**Table 1**), but generally success decreased in a directional fashion as the complexity of the treatment increased. Treatments with a larger number of artificial cache sites would be expected to construe more of a memory challenge, as the birds must discriminate between a larger number of possible locations. Similarly, longer time frames are likely to reduce success rates as a result of temporal memory decay. When viewed in light of previous work on quantity discrimination in New Zealand robins (Hunt et al., 2008; Garland et al., 2012), it appears that this species may have evolved specialized abilities that facilitate the retrieval and pilferage of cached food.

To date OSM has not been demonstrated in a non-corvid avian species (Emery and Clayton, 2004). This study presents the first instance of another avian order with this cognitive ability. This finding is interesting, not only because it represents an incidence of parallel evolution of a cognitive trait, but also because New Zealand robins do not display many of the ecological traits that have been hypothesized as mechanisms behind the evolution of OSM in other species. Both sociality and high cache dependence have been posited as potential drivers in the evolution of OSM (Bednekoff and Balda, 1996a,b; Scheid and Bugnyar, 2008). New Zealand robins do not cache in high volumes (Alexander et al., 2005; Burns and van Horik, 2007; Menzies and Burns, 2008) and are not cache-dependent for winter survival (Menzies and Burns, 2008; Steer and Burns, 2008). Additionally robins are not highly social and so have limited opportunities to interact with conspecifics, and thus gain experience in social interactions. Despite not possessing either of these hypothetically important traits, robins show OSM over short time intervals, suggesting other pressures may have been influential in the evolution of this cognitive adaptation.

Intra-pair competition for resources may have been a driving force behind the evolution of OSM in North Island robins. Intrapair resource competition in robins is intensive, especially during the winter (Steer and Burns, 2008; Menzies and Burns, 2010). Although they cooperate to raise young in the summer, intersexual relationships are decidedly antagonistic in winter (Alexander et al., 2005; Burns and Steer, 2006; Burns, 2009) with males being aggressive and competitively dominant over food resources. Individuals pilfer their mate's caches (van Horik and Burns, 2007) and both sexes frequently re-cache both prey from their own or their mate's caches (Steer and Burns, 2008).

Kamil and Gould (2008) note that there is a negative relationship between the cognitive demands of a cache recovery strategy and resistance of the strategy to competitors for the caches. Under conditions of high cache loss, increased cognitive abilities may be favored despite the large metabolic costs such cognitive abilities incur. The high level of cache loss and reciprocal cache pilferage in robins may have provided the necessary conditions for OSM to evolve, possibly driven by intraspecies sexual competition. Advances in OSM ability in one sex would likely be also conferred on the other sex over time, and an evolutionary "arms race" for better pilfering systems to reduce the impact of cache loss from pilfering could arise. Close social interactions between members of a pair may also provide the necessary social experiences for OSM to develop.

Given that New Zealand robins do not fulfill the hypothesized ethological confines for OSM: sociality and high levels of cache dependence, their memory abilities as displayed in this study appear to be more sophisticated than we had initially anticipated. This is surprising, as pilot studies had shown the birds performing at close to chance level when presented with three cache sites. Future work aimed at identifying the limits of their memory and quantitative ability would need to adopt longer retention intervals and larger numbers of cache sites. While a larger range of quantity comparisons investigated ratio and numerical distance effects in previous studies (Hunt et al., 2008; Garland et al., 2012), looking more in-depth at ratio and prey size/volume and the role it plays in decision making when more than two caches are present is also a salient aim for continued research with this species.

This study also included the use of a variable reward to test for not only OSM ability, but also to investigate the robins' ability to make quantity judgments regarding pilfering activity. This is a novel feature of this study, as it shows that North Island robins are capable of sophisticated decision making regarding cache selection, even when required to rely on memory. The number of mealworms presented had an effect on the accuracy with which the robins were able to locate the hidden prey. Trials where the birds were only offered one mealworm had the lowest average success rate, whereas trials involving three prey items, had the highest average success rate. One thing to note is that in presenting a single quantity of worms (one worm) in the same number of caches, the nature of the task in these trials is somewhat different than the two conditions where two different quantities (1v2 and 1v3) were presented; the cognitive demand is on locating an item in an array of empty wells rather than discriminating quantities of prey. The difference in response may reflect the added complexity of including a higher number of null sets, or empty caches, present in trials where only a single mealworm was displayed. While a zero-like concept has been demonstrated in some animals (Pepperberg and Gordon, 2005; Merritt et al., 2009), no experimentation specifically focusing on null sets has been done with North Island robins to date. Without further research it is not possible to say definitively what the reason behind this number discrepancy is. Certainly, a number of additional factors could have played a role: increased motivation resulting from increased food reward, or a higher chance of momentary distraction influencing outcome when only one worm is dropped, for example. Both of these influences were minimized by halting trials if the bird appeared to not be watching the demonstration, only conducting a trial when the bird was less than 2 m away, and holding each worm in clear view prior to being placed in the artificial cache.

Hunt et al. (2008) conducted a series of experiments with robins that accounted for the potential confounding effects of the amount of time taken to fill each cache site with different numbers of prey items as well as for the volume of items in the trial. Neither of these factors were found to be significant in his study, meaning the robin's ability to choose larger quantities is not related to either of these variables. While these factors are not ruled out as influencing the results of the present study, there is no indication that their influence should differ between these studies, as the methods and nature of the prey retrieval task are essentially the same.

Trials with one vs. two mealworms comprised the only group of trials where there was a significant difference in success rate between the number of sites. In this instance it was the two-site trials that had the higher success rate (**Figure 2**), i.e., the less complex treatments. However trials involving three or four cache sites still produced above-chance success rates. The number of cache sites selected for these experiments was based on the average number of individual cache sites that a robin might generally maintain at any one time, which has been observed as one to three different cache sites (van Horik and Burns, 2007) within view of an observing experimenter, when presented with a overabundance of prey. The fact that number of cache sites was non-significant in two of the three conditions here shows that robins are capable of distinguishing between a larger number of locations than the maximum of four sites used in this study. This suggests that robin's possess the ability to track more locations than they may typically utilize for their own caching needs. Increased memory load can cause an increase in interference in memory retrieval. Being able to recall more separate locations than the robins require for their own caching needs would be a useful memory component for OSM. It would allow an individual to monitor the locations of caches belonging to others without the risk of displacing memories for their own cache sites.

The effect of retention interval is difficult to interpret from this study as retention interval was significant only in trials that offered a maximum of three mealworm prey items in a single cache. Within this condition, the longest 60 s trials had a lower success rate than the 0 or 10 s trials, which did not differ significantly from each other. While lower success rates for the longest trials may suggest that accuracy decreases somewhat over a period of 60 s, this still appears to be within the memory capabilities of North Island robins. It should be noted however that the 0 s trials were also methodologically different from the longer retention intervals as they did not involve the cache sites being occluded from view. In this respect the 0 s trials were not a test of memory and so are not directly comparable to the other retention intervals. A decrease in accuracy over comparatively short periods should be predicted by current knowledge of robin caching behavior. Cache recovery by robins is usually on the same day that the cache is created, and always within 3 days (Powlesland, 1980). Pilfering on the other hand usually occurs over shorter intervals of less than 30 min (van Horik and Burns, 2007), and often within a few minutes of caches being created.

The retention intervals used in this study are significantly shorter than those of the corvid and parid studies that currently make up the majority of the literature on OSM. Parid studies used retention intervals ranging from 6 min to 2 h (Baker et al., 1988), while corvid studies covered a wide range of intervals, from 5 min to 7 days (Bednekoff and Balda, 1996a,b; Bugnyar and Kotrschal, 2002). However these species are predominantly long-term hoarders that rely on cached food for significant proportions of their winter energy requirements. The shorter retention intervals used in this study were more ecologically relevant for robins given the time periods over which most of their cache recovery and pilfering activities take place. It should be noted however that Scheid and Bugnyar (2008) also used a 1 min retention interval for ravens and jackdaws. Of the current literature in the observational memory area, Scheid and Bugnyar's study is methodologically closest to the study presented here. Short retention intervals were used, along with small numbers of artificial cache sites (between 2 and 10) and the birds observed a human experimenter hiding food items rather than a conspecific.

Bugnyar and Kotrschal (2002) also noted that the ravens used in their study began pilfering attempts between 1 and 2 min after watching the caching event. This suggests that even in ravens, a species shown to possess accurate and flexible OSM abilities (Heinrich and Pepper, 1998; Bugnyar and Heinrich, 2006; Scheid and Bugnyar, 2008), pilfering is still conducted soon after witnessing caching. In situations where there is a large amount of food available, pilfering soon after the caching event may be advantageous as it is likely that, after creating one cache, the storer will continue to create more caches in different locations for as long as the food source persists. During this period of caching the individual may be distracted from monitoring the first cache it created, thereby allowing a window where pilfering can safely occur. Robins cache in a highly complex temperate rainforest, as opposed to in more open environments. This provides many opportunities for a potential thief to be out of sight and thus able to re-cache items with a reduced risk of being noticed. This would be expected to reduce the incentive to develop longer-term pilfering strategies as short-term approaches may be equally effective, without the need for more advanced cognitive abilities.

Possibly because robins do not risk high levels of cache theft from individuals (either con- or hetero-specific) other than their mates, and they benefit genetically from having a healthy mate, this species may be able to tolerate higher levels of pilferage than flock foraging species where kinship is low and there is no direct benefit from cache loss. The presence of other individuals (either the study bird's mate or another individual) was not recorded in this study and it is possible that this may have impacted on the birds' cache retrieval decisions.

Robins provide a new avian model: small passerines that nevertheless are capable of displaying sophisticated cognitive abilities. While many of the robins' cognitive processes may not be as complex as those displayed by corvids or parrots, they may provide an interesting intermediate. Studies on robins could be used to shed light on the conditions necessary for these advanced cognitive abilities to evolve. New Zealand robins do not display either high levels of sociality or cache dependence, the two traits hypothesized to be mechanisms leading to OSM evolution in corvids. This suggests that there are alternative pressures that could drive the evolution and development of this trait, at least in North Island robins. Intensive intra-pair competition for resources, characterized by high levels of reciprocal cache theft can be proposed as a possible mechanism leading to advanced cognitive traits that improve pilfering strategies. Comparatively little is known about the extent to which non-human animals are capable of identifying inequalities that involve more than two quantities of items. The results from this study indicate that New Zealand robins appear to successfully choose a larger quantity of mealworms when confronted with multiple possible obscured caches and delays in access, but that the accuracy with which they do so is not necessarily related to each of these features in a predictable linear way. These initial findings lay the groundwork for continued research into the myriad of influences that may play a role in avian cognition and cache strategy for this small songbird.

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Quantity judgments in the context of risk/reward decision making in striped field mice: first “count,” then hunt

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We simulated the situation of risky hunting in the striped field mouse *Apodemus agrarius* in order to examine whether these animals are able to make a choice between small and large quantities of live prey (ants). In the first (preliminary) experiment we investigated to what extent mice were interested in ants as a live prey and how their hunting activity depended on the quantity of these edible but rather aggressive insects. We placed mice one by one into arenas together with ant groups of different quantities, from 10 to 60. Surprisingly, animals, both wild-caught and laboratory-reared, displayed rather skilled predatory attacks: mice killed and ate from 0.37 ± 003 to 4 ± 0.5 ants per minute. However, there was a threshold number of ants in the arenas when rodents expressed signs of discomfort and started to panic, likely because ants bit them. This threshold corresponds to the dynamic density (about 400 individuals per m^2 per min) in the vicinity of anthills and ants' routes in natural environment. In the second experiment mice had to choose between different quantities of ants placed in two transparent tunnels. Ants here served both as food items and as a source of danger. As far as we know, this is the first experimental paradigm based on evaluation of quantity judgments in the context of risk/reward decision making where the animals face a trade-off between the hedonistic value of the prey and the danger it presents. We found that when mice have to choose between 5 vs. 15, 5 vs. 30, and 10 vs. 30 ants, they always tend to prefer the smaller quantity, thus displaying the capacity for distinguishing more from less in order to ensure comfortable hunting. The results of this study are ecologically relevant as they reflect situations and challenges faced by free-living small rodents.

Keywords: quantity judgments, cognition, behavioral ecology, rodents, ants, risky hunting, feeding patches, decision making

INTRODUCTION

Recent behavioral studies have given rise to a growing body of evidence that members of many species, from insects, fish and salamanders to rodents, dogs, cats, horses, dolphins, elephants, and primates, can judge about proportions and numbers of things, sounds, time intervals, smells, and so on. In this field of experimental animal cognition different levels of numerical competence have been revealed, from the ability to discriminate between clearly distinct quantities (relative numerousness judgments) to exact “counting” and arithmetic operations (see: Reznikova and Ryabko, 2011, for a detailed review). In nature, being able to perceive quantities is helpful in many situations, such as tracking predators, selecting the best foraging grounds or the best chance to mate. For example, beetles *Tenebrio molitor* (Carazo et al., 2009, 2012) and meadow voles *Microtus pennsylvanicus* (Ferkin et al., 2005) demonstrated the ability to discriminate between “more or less smells” left by competitive males within the limit of four; honey bees can “count” landmarks within the same limit (Chittka and Geiger, 1995; Dacke and Srinivasan, 2008); female lions can judge about the number of possible intruders by “counting” unfamiliar roars also within the limit of four (McComb et al., 1994); spotted hyenas react with increasing vigilance to calls produced by one, two and three unknown intruders (Benson-Amram et al., 2011); fish use number estimation in order to join a greater shoal (Agrillo et al., 2008, 2011; Gòmez-Laplaza and Gerlai, 2011); North Island robins New Zeland robins (*Petroica australis*) use quantity judgments when retrieving and pilfering cashed food (Hunt et al., 2008; Armstrong et al., 2012); and ants of several species are able to estimate numbers of encounters with members of other colonies on their feeding territories (Reznikova, 1999; Gordon, 2010).

Different kinds of cognitive processes, including numerical discrimination, can be understood in terms of the ways in which species are cognitively adapted to their different ecological niches. Questions remain regarding the taxonomy of the development and organization of numerical information, and its relationship to other domains in human and non-human minds (Davis and Pérusse, 1988; Beran, 2008, 2012; Cantlon, 2012). Experiments on ants (Reznikova, 2007, 2008; Reznikova and Ryabko, 2011) and newly hatched domestic chicks that displayed the ability to perform very simple arithmetic operations (Vallortigara et al., 2010) enable researchers to appreciate core components of animals' numerical cognition. It is likely that some non-human animals possess a higher potential in numerical abilities than we had previously assumed. We are still far from understanding how these capacities evolved and to what extent they are adaptive, and more comparative studies in the context of animals' day-to-day ecological problems are needed.

In this study we focused on the capacity of small rodents for choosing between small and large quantities of live prey, both edible and dangerous, in simulated feeding patches. We simulated a paradoxical natural situation where animals could prefer to "go for less" instead of "going for more," as is typically the case with spontaneous choice tasks. In behavioral ecology, theories of optimal foraging (MacArthur and Pianka, 1966; Pyke et al., 1977; Stephens and Krebs, 1986) predict that animals "go for more," because they evolve foraging strategies that maximize their net energy gain when foraging. The ability to distinguish between quantities and to choose the larger one may be widespread in the animal kingdom. In experiments many species demonstrated discrimination between different quantities of food items basing on the "go for more" strategy. For example, great apes (Call, 2000; Hanus and Call, 2007), monkeys (Hauser et al., 2000; Uller et al., 2003; Evans et al., 2009), elephants *Elephas maximus* (Irie-Sugimoto et al., 2009; Perdue et al., 2012), domestic dogs *Canis lupus familiaris* (Ward and Smuts, 2007), coyotes *Canis latrans* (Baker et al., 2011), wolves *Canis lupus* (Utrata et al., 2012), sea lions *Otaria flavescens* (Abramson et al., 2011), salamanders *Plethodon cinereus* (Uller et al., 2003), and some other species, when presented with two alternatives each comprised of different numbers of food items, prefer the larger quantity. However, when dealing with uncertainty in the environment, animals cannot simply "go for more." There are some experimental studies in which members of different species are required to choose between foraging options when risk is generated by variability in the amount of reward or by variability in delay to reward (Kacelnik and Bateson, 1996; Heilbronner et al., 2008; Beran et al., 2009, 2012). In nature animals can face even more risky situations when foraging on prey that differ in their dangerousness. Under such circumstances consumers must be sensitive to the relation between quantity of prey and their potential for injury. For example, in grasshopper mice (*Onychomys spp*; Rowe and Rowe, 2006) and meerkats (*Suricata suricatta*; Thornton, 2008) feeding on neurotoxic scorpions, predators should benefit from assessing the risks posed by prey. We suggest that in such situations animals can distinguish between quantities of dangerous food items and make their decision cautiously basing on risk/reward evaluation. In order to test this hypothesis, we simulated ant-hunting in the striped field mouse *Apodemus agrarius*. This is a common dwelling, agile and exploratory species whose cognitive abilities have, to the best of our knowledge, never been studied. Our intuition about the ability of mice to judge encounters with differing quantities of ants in their feeding territories in order to decide to hunt or flee from numerous biting (but edible) insects is based on our previous studies of relations of *A. agrarius* with red wood ants (*Formica* s.str.) as hunters and mass prey (Panteleeva et al., 2011; Panteleeva and Vygonyailova, 2012). We found that red wood ants and rodents share areas in forest habitats. Within their large feeding territories red wood ants create "black holes" in the habitat, i.e., areas that are highly perilous for other species, both invertebrates and small vertebrates, where intruders can be killed or at least injured. The most risky areas are in the vicinities of anthills and ants' foraging routes (Reznikova and Dorosheva, 2004). Surprisingly, inter-relations between red wood ants and small rodents have not been investigated before. We found that ants have high hedonistic value for striped field mice: in our laboratory experiments rodents always tried to eat as much ants as they could, although they have enough food in their home cages, including proteins (Panteleeva et al., 2011). At the same time, when performing ant hunting, mice face a sophisticated foraging challenge: they cannot simply decide to "go for more" because when their number increase, red wood ants become more and more dangerous for small rodents. We suggested that striped field mice could estimate what is for them the critical level of the dynamic density of ants (individuals per m^2 per min) in order to hunt comfortably. So, we considered ant-hunting in wild-caught mice as a good model for studying quantity discrimination in an ecological context.

In order to investigate the potential cognitive mechanisms of decision-making in wild-caught field mice, we simulated feeding patches in two experiments in which mice dealt with different quantities of natural stimuli. In the first (preliminary) experiment we investigated to what extent mice were interested in ants as a live prey and how their hunting activity depended on the quantity of edible but rather aggressive insects. We placed mice, both wild-captured and their progeny, one by one into arenas together with ant groups of different quantities, from 10 to 60 individuals, and recorded the behavior of the mice. In the second experiment mice had to choose between different quantities of live prey that served both as food items and as a source of danger. We presented mice with pairs of transparent tunnels with different quantities of live ants inside (5 vs. 15, 5 vs. 30, 10 vs. 30, in different sessions). The tunnels were devised so that mice were able to enter, kill and eat ants there and then leave, whereas ants were locked up. As far as we know, this is the first experimental paradigm based on evaluation of quantity judgments in the context of risk/reward decision making in a simulated ecologically relevant situation where the animals face a trade-off between the hedonistic value of the prey and the danger it presents.

EXPERIMENT 1. PREDATORY BEHAVIOR OF MICE TOWARD ANTS WITH RESPECT TO THEIR QUANTITY

SUBJECTS AND HOUSING

The experiment was conducted in 2009, 2010, and 2012 in the laboratory on striped field mice *A. agrarius*. These mice do not form aggregations during active periods of their annual life cycle, and adults live solitary (Wolff and Sherman, 2007). We used 25 striped field mice (12 females and 13 males), from which 4 (2 males and 2 females) were captured in a mixed-pine forest near Novosibirsk, and 20 were born in the laboratory, being progeny of the wild-caught mice. These "naïve" mice were from 2 to 12 months of age when they were tested. All animals were housed singly in clear plastic cages (40 × 30 × 20 cm) that contained cotton nesting material. Laboratory-born mice were weaned between 25 and 35 days of age, housed with littermates until 40 days of age, and thereafter housed singly in cages. All mice were fed each day with mixed seeds, fruits, and dried shrimps, and they had *ad libitum* access to water. When they were taken into experimental set-ups, mice always had enough food in their home feeders, so they were not hungry. However, as it has been revealed earlier (Panteleeva et al., 2011), ants are rather attractive for them as a prey. Animals voluntarily participated in experiments and readily entered the plastic cup that we used in our manipulations with them.

We used red wood ants as live prey: *Formica polyctena* in 2009 and *F. aquilonia* in 2010 and 2012. These are closely related species which even form common two-species nests (Korcsiñska et al., 2010). It is worth noting that red wood ants do not display considerable variability in size, that is, in our experiments mice were presented with live prey items of approximately the same size. Ants were taken from the same forest with mice and were housed in groups of about 1000 individuals in artificial nests on separate arenas (60 × 50 cm), where they received water, carbohydrate and protein food *ad libitum*.

PROCEDURE

In the first part of the experiment conducted in 2009, we investigated the process of ant hunting in striped field mice. We placed each mouse into a separate round arena (40 cm in diameter, 20 cm high) containing 10 ants. The arena was covered with a transparent lid in order to prevent animals from getting out. Both ants and rodents could freely move in the arena. In each trial a mouse was placed in the arena 2 min after ants. Video recordings were made during 10 min, using a camera Sony Handycam DCR DVD408. Each mouse was tested 3 times, with the interval 3 days between trials. To analyze ethograms from video records, we used the Observer XT 7.0 (version: 7.0.214, Noldus Information Technology). In total, we analyzed 6 h of video by the second, for 9 laboratory-reared and 4 field-caught mice (39 trials).

In the second part of the experiment conducted in 2010 and 2012 we examined mice' predatory behavior toward different quantities of ants. The apparatus and video recording were the same as in the first part, as well as the analysis of ethograms. We tested 20 laboratory-reared and 3 field-caught mice (12 males and 11 females), 3 times each, with different numbers of ants placed in the arena: 10 ants (35 trials in 2012), 20 ants (25 trials in 2010), 30 ants (30 trials in 2010), 40 ants (20 trials in 2010 and 34 trials in 2012), and 60 (29 trials in 2012). Note that numbers of trials are not always multiples of 3 because 28 trials in which mice did not display any activity toward ants were excluded. We tested each animal for 10 min per trial with 10, 20, and 30 ants, 5 min per trial with 40 ants, and 3 min per trial with 60 ants. We used different intervals for different quantities of ants because it could be traumatic for mice to spend more time in the arena with biting ants. Appropriate interval lengths were established in auxiliary trials, in which the trial was stopped when mice displayed distinct signs of discomfort such as jumping, shaking legs, rubbing eyes, and so on. Intervals between trials in this part of the experiment were from 5 to 24 h for each animal, so that mice had sufficient time to rest. In sum, 206 trials were recorded. We examined the number of killed ants, the number of eaten ants, and the details of mice' behavior, including attacks toward insects and signs of dismay (jumps and "freezing" when an animal stayed motionless with its legs and tail hidden and the head ducked). We defined the efficiency of attacks as the proportion of successful attacks (that is, attacks in which the ant was killed) in the total number of attacks toward ants.

In order to establish the correspondence between numbers of ants placed in our arena and the dynamic density of ants in different parts of their feeding territory in nature, we made auxiliary recordings in the field: a wire frame of the same shape and size as the bottom of the arena was placed on plots chosen in different parts of the ant feeding territory, and we counted all ants captured within the boundaries of the frame during 1 min. In total, 71 of such recordings were made. It turned out that 10 ants placed on the arena corresponds to the dynamic density of ants of about 80 individuals per m^2 per min, which is characteristic for the periphery of an ants' feeding territory. The value of 60 ants placed in the arena corresponds to the dynamic density of ants about 400 individuals per m^2 per min, which is characteristic for the vicinity of ant routes and anthills (Reznikova and Dorosheva, 2004).

RESULTS

Ant hunting in striped field mice

In the first part of the experiment subjects demonstrated predatory behavior toward ants in 33 out of 39 tests. The latency time, that is, the time from the first encounter with an ant until the first attack, lasted from 14 s to 8 min. It is worth noting that ants displayed aggressive behavior toward mice (see: Dorosheva et al., 2011 for a detailed description of signs of aggression in ants): they exhibited aggressive postures, bit rodents on the legs and splashed acid toward their eyes (**Figure 1**). Mice displayed agitation when damaged by ants, such as twitching, jumping, and rubbing their eyes, and they contacted each insect many times before making their final attack. We recorded 3.48 ± 0.95 contacts with ants per minute which included orienting the body to face the ants, touching insects with the nose, and probing bites that did not end with killing. Mice made a final attack by quickly getting a better grip with their teeth, and then killed and ate the ant holding it in their paws. Rodents thoroughly collected all fallen fragments of insects including legs and even antennae, and ate them. Mice killed 0.37 ± 0.03 ants per minute; thus, their hunting appeared to be quite active, taking into account that they had to cope with the biting prey.

FIGURE 1 | An ant exhibits the aggressive posture and splash acid toward mouse's eyes. Photo by Yu. Danilov.

Reactions of striped field mice to different quantities of ants

Being presented with different quantities of ants in arenas, mice actively hunted until no ants remained. The number of killed and eaten ants increased with the number of insects (from 10 to 40) placed in the arena (**Figure 2**). Mice killed up to 4.0 ± 0.50 ants per minute. The efficiency of attacks, that is, the proportion between killed and attacked insects, increased with the number of ants placed in the arena. In 2009–2010 the efficiency of attacks was 11.44 ± 1.34% in trials with 10 ants, 16.83 ± 2.35%, 25.25 ± 3.58%, and 36.26 ± 3.60 in trials with 20, 30, and 40 ants correspondingly. In 2012 the efficiency of attacks was 6.14 ± 0.57%, 17.86 ± 1.80%, and 21.92 ± 2.32 in trials with 10, 40, and 60 ants correspondingly. However, successfully attacking and killing ants did not always lead to mice eating them. **Figure 2** shows that when finding themselves in the arena with 30, 40, and 60 ants, mice killed significantly more ants than they were able to eat. It possibly means that mice kill ants in self defence in situations when there are too many aggressive insects around. Indeed, it can hardly be considered comfortable hunting when ants' number in the arena increases up to 40 and 60, and thus becomes comparable with their number in the vicinity of foraging routes and ant-hills in nature. Mice suffered from bites and displayed more and more signs of discomfort such as jumping and freezing; they sharply jumped trying to shake ants off their legs. The number of signs of discomfort significantly increased with the increase in the number of ants placed in the arena. When 40 ants were placed in the arena, mice mainly switched from jumping to freezing (**Figure 2**). Only when they had brought the number of ants down to an acceptable level were mice able to start collecting killed insects and eat them. Surprisingly, they were able to eat up to all 40 ants during 5 min trials. These data enabled us to conclude that, although ants' attractiveness as prey is rather stable for mice, they have to choose feeding patches with relatively small quantities of active ants in order not to suffer from their bites too much. The next experiment ("Experiment 2") was aimed at examining whether rodents can use quantity information to make a decision where to hunt ants.

EXPERIMENT 2. DISTINGUISHING BETWEEN QUANTITIES OF AGGRESSIVE ANTS: HUNT OR FLEE?

SUBJECTS AND HOUSING

The experiment was conducted in 2011. We used 16 striped field mice (9 males and 7 females), of 4–15 months of age, that were first and second generation descendants of those captured in a mixed-pine forest near Novosibirsk. Mice were housed and fed as it was described in the section "Experiment 1." As before, animals voluntarily participated in experiments and readily entered the plastic cup that we used in our manipulations with them.

APPARATUS, STIMULI, AND PROCEDURE

In order to simulate "feeding patches" with different dynamic densities of active ants, we recycled transparent plastic 0.3 L water

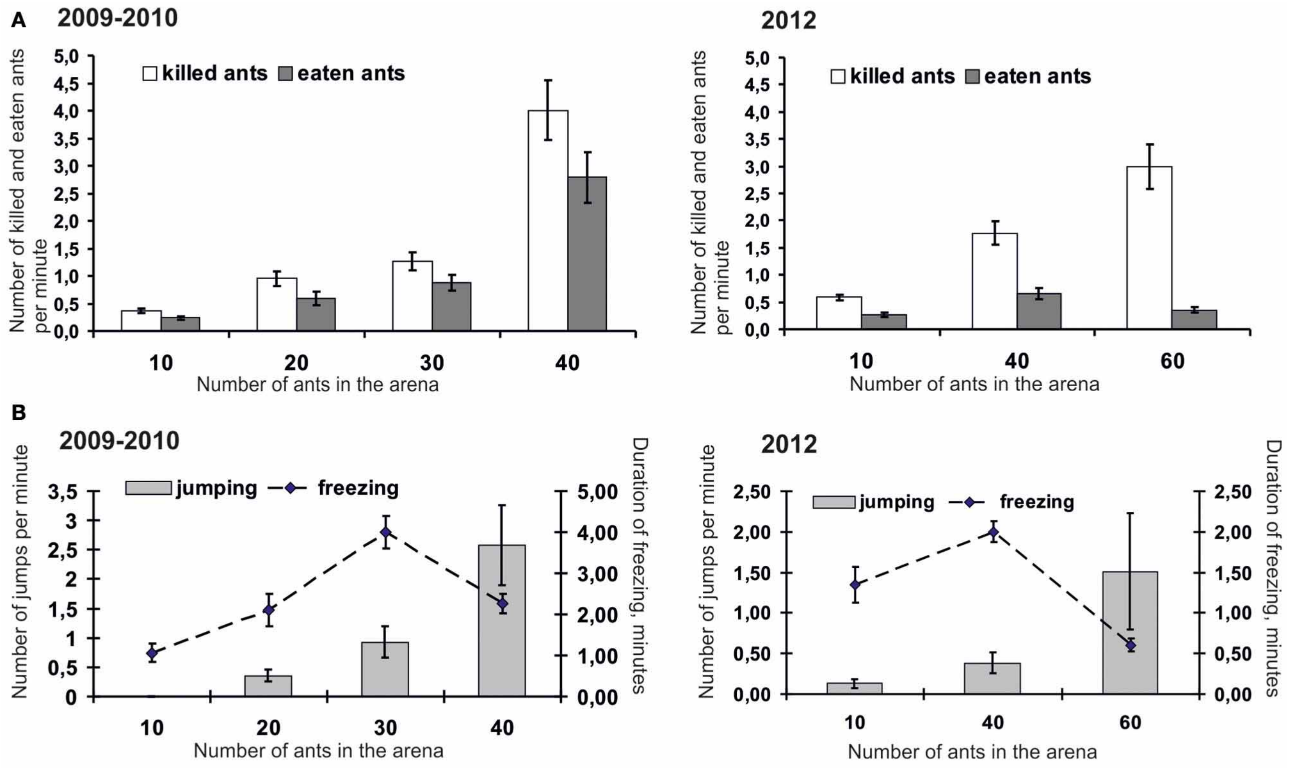

FIGURE 2 | Number of ants killed and eaten by mice (A), and number of signs of dismay in mice (B) placed in the arena together with different number of ants (Mean ± SE). Note for the two left graphs: data with 10 ants were obtained in 2009, and the rest were obtained in 2010.

bottles in order to make tunnels containing different quantities of live ants that were actively moving inside. These tunnels were presented in such a way that mice could enter them from the bottom side; the bottom was cut off and replaced by an elastic plastic lid with crosswise narrow slits that allowed a mouse to pass in and out by applying its own weight, and did not allow ants to either enter or leave, as they were lightweight and could not press through narrow slits in the elastic lid. Mice were tested one by one in a rectangular container (25 × 35 cm, and 21 cm high) with two tunnels attached to its sides (**Figure 3**). So, mice were able to enter, kill and eat ants in the tunnel, and then leave, whereas ants were locked up. The subject could see and compare the contents of the two tunnels at the same time. We relied on free hunting behavior of mice that had no previous training history of ant hunting in the containers.

Before being tested with ants, each mouse passed through the training phase of the experiment, being presented with a small piece of cheese inside each tunnel. At this stage there were no ants inside the tunnels. The training phase lasted for each subject until it began to inspect tunnels voluntarily immediately after finding itself in a center of the experimental container. It took usually not more than three training trials for each animal, and after that all of them actively chose containers with ants inside.

During the main course of the experiment animals could freely move in the experimental container (10 min per trial). In order to avoid positional learning (left or right), we changed positions of the tunnels after each trial, so the animals could rely only on the different quantity of ants inside the tunnels. Both tunnels were kept stationary during each trial. As the main characteristic of mice' behavior in the artificial "feeding patches" we recorded all choices of tunnels by each animal during each 10-min trial. We considered a response to be the choice of a tunnel if an animal entered the tunnel completely (including its tail). As supplementary characteristics, we also considered the time duration spent by an animal inside a tunnel, and, separately, all cases when a mouse touched the entrance with its nose or front paws. We considered touching of the entrance as a sign of exploratory activity of mice toward the tunnels.

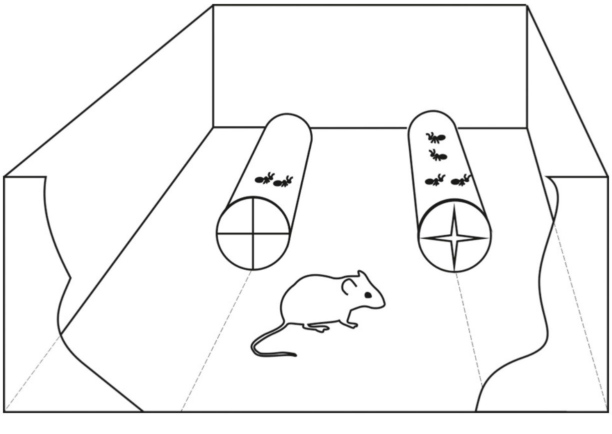

FIGURE 3 | Experimental setting used: tunnels contain different number of live ants. It is shown in the right tunnel how crosswise slits allow a mouse to pass in and out by applying its own weight. Note that in reality mice had to choose between 5 and 15 ants (and so on, see the text), and never between 2 and 4.

In different conditions the tunnels contained different numbers of live ants: condition 1: 5 vs. 15 (14 mice were tested); condition 2: 5 vs. 30 (16 mice were tested); condition 3: 10 vs. 30 (14 mice). It is worth noting that, although numbers of ants placed in the container in several cases were the same as in the open arena (for example, 10 and 30), situations differed considerably. Ants were locked within a small volume of 0.3 L where they could move freely in 3-dimensional space, so, when entering a bottle containing ants, a mouse must have felt less comfortable than in the open arena. Each mouse was tested three times with 2 days interval between the trials, and we summarized the data obtained in three trials. The total number of trials was 132, totaling 22 h of duration.

STATISTICAL ANALYSIS

As the main characteristic of mice' behavior in simulated feeding patches, we compared the number of choices the mice made between the two containers during trials. To test whether the mice' choices for one of the tunnels deviated from the chance level we applied Pearson's chi-squared test (χ^2). To test whether the mice' exploratory activity was higher toward one of the tunnels, we compared numbers of mice' contacts with the lids of the tunnels applying Pearson's chi-squared test (χ^2). To test whether the mice spent significantly more time in one of the tunnels during trials, we applied the Wilcoxon signed-rank test.

RESULTS

We compared tunnel exploration by rodents across conditions. Striped field mice appeared to choose significantly more frequently the tunnels containing fewer ants (**Figure 4**). In condition 1 (5 vs. 15 ants) all mice in sum chose the tunnel containing 5 ants 131 times, whereas the tunnel with 15 ants they chose 16 times ($\chi^2 = 89.97$, $P < 0.01$). In condition 2 (5 vs. 30 ants) mice chose the tunnel containing 5 ants 131 times, and the tunnel with 30 ants they chose 16 times ($\chi^2 = 89.97$, $P < 0.01$). In condition 3 (10 vs. 30 ants) the mice chose the tunnel containing 10 ants 90 times, whereas the tunnel with 30 ants they chose 21 times ($\chi^2 = 42.89$, $P < 0.01$). Taking into account that we tested 16 mice altogether, these proportions mean that, on average, during the first two sessions mice chose the tunnel containing more ants only once, and the number of "go for more" choices during the third session was 1.7 per mouse. Numbers of mice' contacts with the lids significantly differed in conditions 1 and 2 between the smaller quantity and the larger quantity ($\chi^2 = 10.00$, $P < 0.01$ и $\chi^2 = 32.26$, $P < 0.01$, correspondingly). It is important to note that in all three conditions the mice spent significantly more time in the tunnels containing fewer ants (Wilcoxon signed-rank test: session B1: $T = 0.00$, $Z = 5.37$, $P = 0.00$; session B2: $T = 3.00$, $Z = 5.11$, $P = 0.00$; session B3: $T = 1.00$, $Z = 4.76$, $P = 0.00$). During condition 1 the mice spent in total 65.65 min in the tunnel containing 5 ants, and 0.95 min in the tunnel with 15 ants; during session 2 and 3 these values were correspondingly 65.87 vs. 3.83 min, and 39.05 vs. 1.33 min.

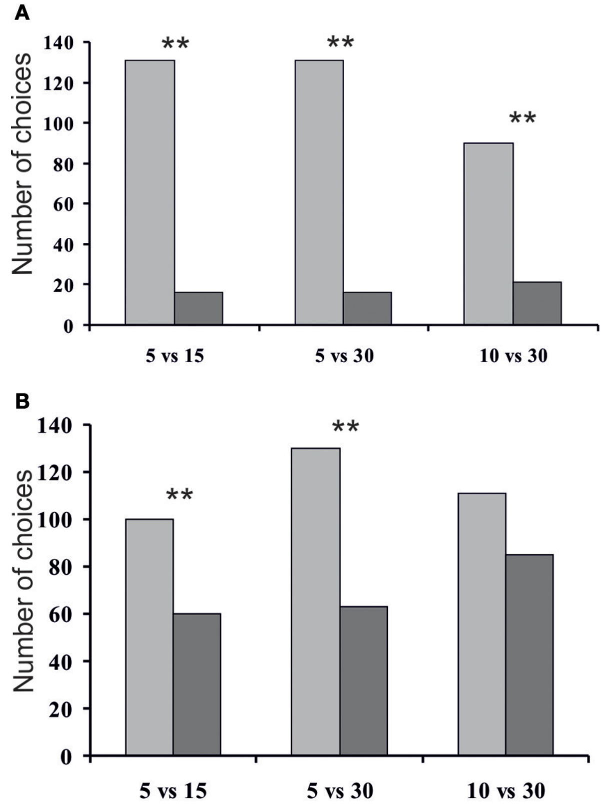

FIGURE 4 | Total number of choices of the tunnels by mice (A) and total number of all cases when mice touched the entrance of the tunnels (B) ($P < 0.01$ Pearson's chi-squared test).**

Behaviorally, mice caught ants in the tunnel that contained less ants, killed and ate the insects, then quietly left the tunnel and after a short time went back to hunt again. In contrast, they jumped out of the tunnel containing many ants, and rarely visited it again. In either case, these behaviors were independent of the position of the tunnel (right or left).

DISCUSSION

We developed a naturalistic test of quantity judgments in striped field mice basing on their free hunting behavior, that is, on cognitive abilities that are spontaneously present in the species. Instead of working, as is typically the case, with laboratory strains of rodents (Capaldi and Miller, 1988; Janus et al., 2009), we tested wild-caught striped field mice and their progeny in situations nearest to their vital environmental problems, that is, in simulated feeding patches. To test the hypothesis about the ability of mice to apply the "go for less" strategy in order to ensure comfortable hunting of dangerous prey, we presented mice with a spontaneous choice task in which they were forced to choose between different amounts of ants.

It is worth noting that this is the first study of ant hunting in Muridae, even though insect predation has been described in this family. While nearly every rodent species is to some degree an omnivore (Landry, 1970), the degree of carnivory has been, as far as we know, poorly estimated for Muridae. It is known that striped field mice, although they eat mainly seeds and plants, include a great deal of insects in their diet (Babiñska-Werka, 1981); however, details of insect hunting were not studied in this species. In our previous studies (Panteleeva et al., 2011) we revealed that red wood ants are always attractive as a prey even for replete rodents. The reasons are not entirely clear yet. The high hedonistic value of ants makes mice not only catch and eat them but also collect and eat all fragments of those insects including legs and even antennae. This can perhaps be explained by the high concentration of glucose in their bodies and on their covers (see: Jilková et al., 2012), as well as by the accumulation of certain microelements by them (see: Frouz and Jilková, 2008) as well as proteins. That striped field mice demonstrate stable and active predatory behavior toward aggressive (but edible) red wood ants enabled us to study quantity judgments in the context of risk/reward decision making.

In "Experiment 1" we examined mice' reactions toward different quantities of ants in order to reveal how many ants a mouse can catch without suffering from bites too much. In our study both field-caught and naïve mice displayed rather skilled predatory attacks, and their efficiency of hunting was comparable with that of specialized predators. At the same time, ant hunting appeared to be risky for striped field mice, as they suffered from bites and displayed more uncomfortable reactions when they encountered more ants as opposed to less ants. In our experiments we observed behaviors, including turning to face the ants, touching insects with the nose, and probing bites that did not end with killing, each of which can be considered an element of risk assessment in striped field mice, analogous to those described in grasshopper mice toward dangerous prey (Rowe and Rowe, 2006). The limit of dynamic density (individuals per m^2 per min) of ants that allows mice to hunt comfortably appeared to be about 80 individuals per m^2 per min which corresponds to the level of dynamic density in peripheral parts of ants' feeding territories in nature, that is, far away from ant-hills and foraging routes. In sum, ant hunting can serve as a good model for investigating cognitive mechanisms of risk/reward decision making in small rodents.

In "Experiment 2" mice had to choose between 5 vs. 15, 5 vs. 30, and 10 vs. 30 ants placed in two transparent tunnels. The subject could see and compare the content of the two tunnels at the same time. Animals could freely enter the tunnels and hunt there, and so ants served both as food items and as a source of danger. In this situation striped field mice displayed the clear tendency to "go for less" in all three trial types, thus displaying the capacity for distinguishing more from less in order to ensure comfortable hunting. Additional experiments should be conducted to examine what level of accuracy animals can achieve when distinguishing between tunnels containing different quantities of ants, and when they might "go for more" instead of "go for less." It is also important to note that based on the results of the experiment conducted, we cannot determine the preferred sensory modality used by striped field mice to make their decision. In our experiments mice could estimate quantities of moving visual objects, but they also could use the amount of smell and (or) the patter of ant feet within tunnels as cues. Additional experiments are needed with non-transparent tunnels in which ants would be invisible for mice. However, even if mice in our experiment use cues of different modalities, our results show that they can estimate proportions of edible but dangerous objects and make the decision to hunt or flee based on distinguishing between quantities, possibly evaluating not only moving visual objects but also smells and sounds. These results are ecologically relevant as they reflect situations and challenges faced by free-living small rodents when they have to estimate the frequency of encounters with dangerous prey. It would be interesting to go deeper in studying quantity judgments in "wild" rodent species and test their ability to distinguish between numbers or other quantities of arbitrary stimuli.

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Evidence for a numerosity category that is based on abstract qualities of "few" vs. "many" in the bottlenose dolphin (*Tursiops truncatus*)

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A previous study (Kilian et al., 2003) had demonstrated that bottlenose dolphins can discriminate visual stimuli differing in numerosity. The aim of the present study was twofold: first, we sought to determine if dolphins are able to use a numerical category based on "few" vs. "many" when discriminating stimuli according to the number of their constituent patterns. Second, we aimed to extend the previously demonstrated range of numbers, thereby testing the limits of the numerical abilities of bottlenose dolphins. To this end, one adult bottlenose dolphin learned to discriminate between two simultaneously presented stimuli which varied in the number of elements they contained. After initial training, several confounding parameters were excluded to render it likely that discrimination performance indeed depended on numerosity. Subsequently, the animal was tested with new stimuli of intermediate as well as higher numbers of elements. Once discrimination had been achieved, a reversal-training on a subset of stimuli was initiated. Afterward, the subject generalized the reversal successful to new and unreinforced stimuli. Our results reveal two main findings: firstly, our data strongly suggest a magnitude and a distance effect. Thus, coding of numerical information in dolphins might follow logarithmic scaling as postulated by the Weber-Fechner law. Secondly, after learning a reversal of contingencies, the dolphin generalized the reversal successful to new and unreinforced stimuli. Thus, within the limits of a study that was conducted with a single individual, our results suggest that dolphins are able to learn and use a numerical category that is based on abstract qualities of "few" vs. "many."

Keywords: cetacea, numerosity, reversal learning, categorization, Weber-Fechner law

INTRODUCTION

The visual world comes in a bewildering variety of shapes and colors. Since it is impossible to learn the relevant properties of each object one by one, humans and other animals have developed the ability to group stimuli along several dimensions (e.g., Herrnstein and Loveland, 1964; Delius et al., 2000; Makino and Jitsumori, 2007). Usually, members of a category are grouped on the basis of physical similarities. Behaviorally, a category is defined by an ability to generalize within a class of stimuli and to discriminate between classes (Keller and Schoenfeld, 1950), as well as to extrapolate the categorical knowledge to new members of the stimulus class (Wasserman et al., 1988). To date, a large number of demonstrations of successful categorizations in non-human animals have been published. However, in most of these studies performance could simply be based on "categorization by rote" (Vaughan and Greene, 1984; Yamazaki et al., 2007) without requiring an understanding of the abstract relation between the categorized stimuli.

Some methods have been proposed to be critical for proving the establishment of a flexible and abstract relation between stimulus classes (e.g., Astley and Wasserman, 1998). One important technique is the discrimination reversal procedure. It was first proposed by Lea (1984) in order to show concept discriminations, and has since been used in a variety of experiments (e.g., Vaughan, 1988; Von Fersen and Lea, 1990; Delius et al., 1995, 2000), including one which tested a dolphin with auditory stimuli (von Fersen and Delius, 2000). Using a discrimination reversal procedure permits testing whether the subject associates all members of a category even if these members have no common physical property. In a standard reversal procedure, the subject is first trained to discriminate between members from two different categories in a simultaneous discrimination task. After mastering the discrimination, the trained contingencies are reversed in a subset of the employed stimuli. Thus, responses which previously led to reinforcement are now punished, and vice versa. After again reaching discrimination criterion, the new contingency is tested with the remaining members of a group. If the subject spontaneously transposes the reversed contingency to these remaining patterns, it is likely that the animal is able to categorize the members dependent on associations within a category.

Kilian et al. (2003) have previously reported a bottlenose dolphin to be able to discriminate among visual patterns differing in numerosity, i.e., a stimulus property defined by the number of discriminable elements contained in the stimulus. Although it is very likely that dolphins were able to use numerosity to discriminate between different patterns in this experiment, it is not clear if they indeed used a more abstract category based on "few" vs. "many." Therefore, the present experiment was designed to test for the presence of such an abstract relation when performing a numerical discrimination task. Additionally, we aimed to extend the previously demonstrated range of numbers (1–6) to a larger range (1–10) in order to define the limit of a bottlenose dolphin's numerical discrimination abilities.

MATERIALS AND METHODS

The subject of the present study was an experimentally naive male bottlenose dolphin. At the start of the investigation "Blue" was 10-years old and from birth on almost blind on his right eye. He was housed together with four other bottlenose dolphins in a 13.5 m × 28 m outdoor pool of 4.5 m depth in Marineland Majorca (Spain). The experiments took place in an adjacent pool of 4.45 m × 5.70 m × 1.80 m ($w \times l \times d$) in which he was separated from the others during each session.

GENERAL PROCEDURE

The animal had to discriminate between simultaneously displayed stimuli representing "few" and "many" elements (**Figure 1A**). The stimuli consisted of 25cm × 25 cm white PVC boards with black items stuck onto them. Each stimulus was inserted in a square-shaped window located on a white painted wooden panel of 1 m^2. A push with the dolphin's beak could flip the stimulus backward (**Figure 1B**). The stimuli were positioned to the left and to the right of the experimenter. The distance between the two panels was 1.50 m. During the discrimination process the experimenter was hidden from the subject's view by means of a plastic curtain. Each trial started with the animal being positioned at the tip of a 2.50 m target, above water level, and facing the apparatus (**Figure 1A**). After positioning the animal, the experimenter revealed the covered stimuli and 4 s later indicated by a short whistle that the subject had to leave the target to touch one of the displayed stimuli with its rostrum. Only responses which tipped either stimulus backward were recorded. Correct responses were followed by a continuous whistle blow and reinforced with fish. Incorrect choices were indicated by non-continuous whistle blows and directly followed by correction trials. The position of the correct stimulus (left or right) was alternated quasi-randomly (Gellermann, 1933). The subject was presented with one to two daily sessions of 20 trials each. The only exceptions were the very first presentations of new number pairs, for which a session consisted of 10 trials only to minimize frustration. Criterion was reached after achieving 85% correct performance within a given session.

PRE-TEST AND HABITUATION PHASE

Prior to starting the actual experiment, "Blue" received some habituation training with the apparatus. He learned to be sent and wait at the target until the starting signal was given, and then to swim back and touch one of the two white panels. During five sessions of 20 trials each, he was rewarded irrespective of the side the panel he touched was on. This was done to test for a possible side preference. Subsequently, Blue was tested for a possible preference for "few" or "many" items, again in five sessions of 20 trials. To this end, the panels containing few or many items were alternated quasi-randomly, and "Blue" was rewarded after each choice irrespective of which stimulus he had chosen.

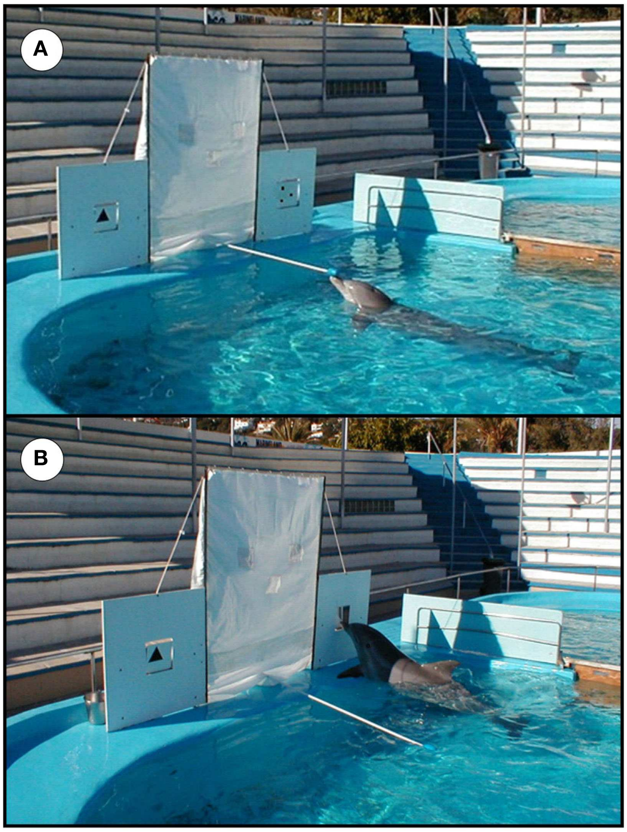

FIGURE 1 | (A) Overview of the testing situation with the apparatus, the stationing device, and the position of the dolphin facing the revealed stimuli; **(B)** Blue touching one of the displayed stimuli with his rostrum.

EXPERIMENT 1

TRAINING PHASE

During training sessions, the animal learned to discriminate 1 vs. 5 and was rewarded for choosing the stimuli which contained more elements. The stimuli consisted of black circles ($r = 2.4$ cm). After reaching 85% correct performance, this stimulus pair was used to habituate "Blue" to unreinforced trials (catch trials). Subsequently, he was trained with the following number pairs: 1 vs. 4, 1 vs. 3, and 1 vs. 2. After successful performance, the animal was also trained with stimulus pairs varying in surface, shape, and element patterns, whereby two different conditions were conducted for the variable "surface": (1) single items with the same surface, and (2) items having the same overall surface. For "shape," the initial circles were substituted for triangles. In order to create different "patterns," the elements were organized in different arrangements (**Figure 2A**). For each condition (surface, shape, and pattern), five sessions were run, each of which included six catch trials. We did not balance or

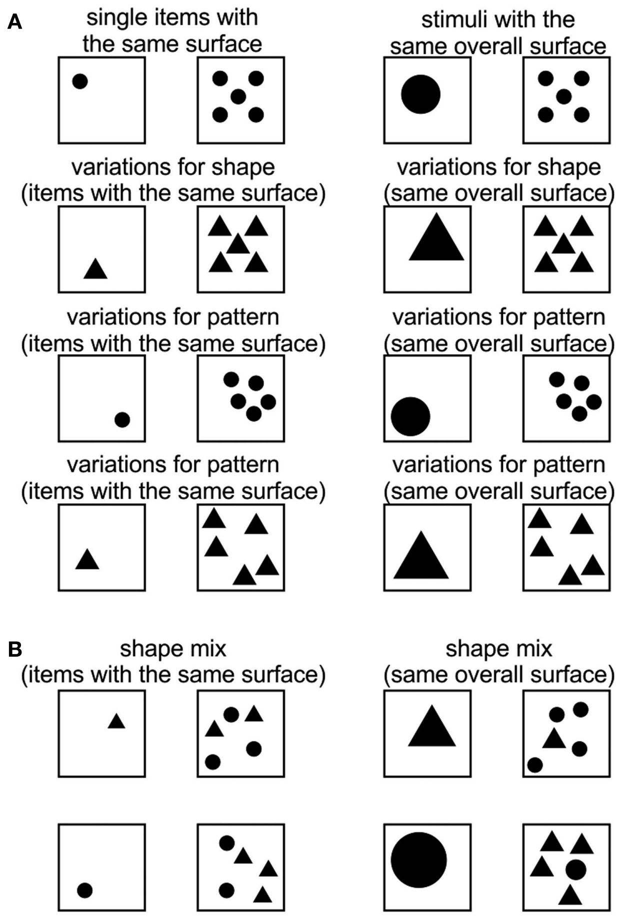

FIGURE 2 | (A) Examples of the stimulus pair 1 vs. 5 with variations of surface, size, shape, and pattern of elements. Similar conditions were also used for 1 vs. 4, 1 vs. 3, and 1 vs. 2; **(B)** examples of control stimuli for 1 vs. 5. Similar conditions were presented for 1 vs. 4, 1 vs. 3, and 1 vs. 2.

systematically vary the perimeter of the stimuli, but ensured that in our stimulus set, the overall perimeter was sometimes longer or shorter on the rewarded panel. For example, the perimeters of a single triangle vs. two circles were 27.57 and 30.16 cm, respectively, in one set of panels and 39 and 30.16 cm, respectively, in another.

CONTROL PHASE

During control sessions, new stimulus pairs were introduced, mixing the shapes of the elements (circle, triangle, square) for the two panels representing "few" and "many." Furthermore, variations of up to 100% regarding the size of the elements were introduced (**Figure 2B**). In a given session, 16 familiar stimulus pairs were mixed with four novel pairs which were never reinforced (catch trials). Moreover, two familiar stimulus pairs were also not reinforced in order to prevent novelty to be exclusively associated with no reward. During this procedure, "Blue" was only confronted with the familiar number combinations of the training phase (1 vs. 5, 1 vs. 4, 1 vs. 3, and 1 vs. 2). He always had to choose the panel containing more elements. These elements could be either circles or triangles or squares, and the total surface of the elements could be the same, smaller, or bigger than for the panel representing "few" elements. In total, 10 sessions were run and 40 new unreinforced stimuli pairs were introduced. Criterion was reached after 85% correct performance had been achieved.

TESTING PHASE

During the testing phase, new number pairs with new numerosities (2 vs. 5, 3 vs. 5, 2 vs. 4, 2 vs. 3, 3 vs. 4, 4 vs. 5, 5 vs. 6, 5 vs. 7, 5 vs. 9, and 5 vs. 10) were introduced, mixed with training and control stimuli, and tested without feedback (catch trials). As in the control phase, a session consisted of four new number combinations and 16 familiar stimuli of which two were also not reinforced. For each new number pair, five sessions were conducted, and again, variations concerning the shape, size, and pattern were presented. In this phase, we also used outlined and filled elements. In addition, different shapes and sizes were mixed on one panel. Accuracy criterion was again set to 85% correct answers during one session.

RESULTS OF EXPERIMENT 1

Pre-test

Blue showed a clear preference for the left side, choosing left in 70% of trials. When being confronted with panels showing "few" or "many" items that alternated between left and right, he continued to swim left, this time even in 96% of cases. No spontaneous preference for "few" (52%) or "many" elements (48%) could be detected.

Training phase

For the first training pair (1 vs. 5), the subject needed 13 sessions to reach criterion. His performance remained stable even after introducing catch trials. For the following training pairs (1 vs. 4, 1 vs. 3, 1 vs. 2), criterion was already reached in the first session. Performance levels remained constant also for pattern, shape, and size variations (**Figure 3**).

Control phase

Blue's performance for variations of shape, pattern, and surface size was above the criterion level for all conditions (**Figure 4**).

Testing phase

Blue's performance for the new and untrained stimuli (**Figure 5**) 2 vs. 5 was 90%. For 2 vs. 4, he reached 95%, and for 3 vs. 5, 2 vs. 3, 3 vs. 4, and 4 vs. 5 85%. For the combinations 5 vs. 6 (65%), 5 vs. 7 (50%), and 5 vs. 9 (70%), Blue failed to reach criterion. For 5 vs. 10, the criterion was (85%; **Figure 6**).

DISCUSSION OF EXPERIMENT 1

The aim of the first experiment was two replicate the results of Kilian et al. (2003), and to test if the numerical range of the previous study (1–6) can be extended to 1–10. Our results clearly replicate Kilian et al. (2003) and demonstrate that numerical competence is in the reach of bottlenose dolphins. Our results are largely in line with a previous study (Mitchell et al., 1985) which showed that a dolphin could choose correctly among the number of fish on a scale from 0 to 5. However, in the study by Mitchell et al. (1985), numerosity was confounded by the amount of food, and the subject could just have perceived the objects as representing hedonic values rather than members of an ordinal series.

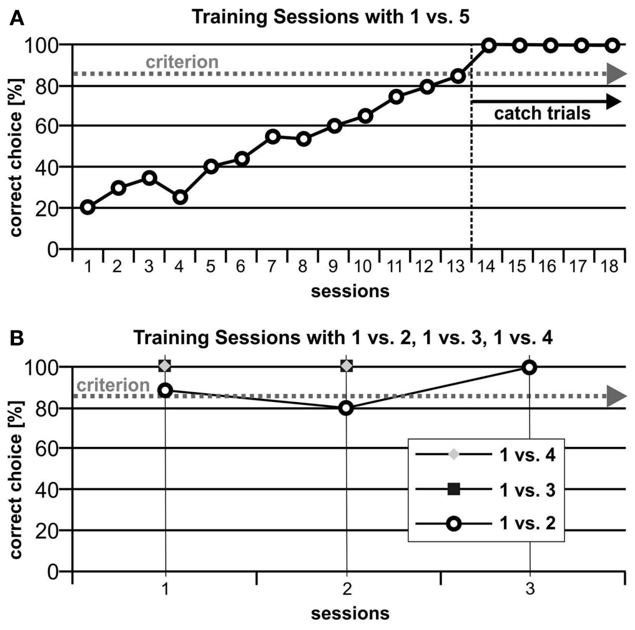

FIGURE 3 | (A) For the first stimulus pair 1:5, the subject needed 13 sessions to reach criterion. His performance remained stable even after the introduction of catch trials. **(B)** For the following numerosities, criterion was already reached in the first sessions.

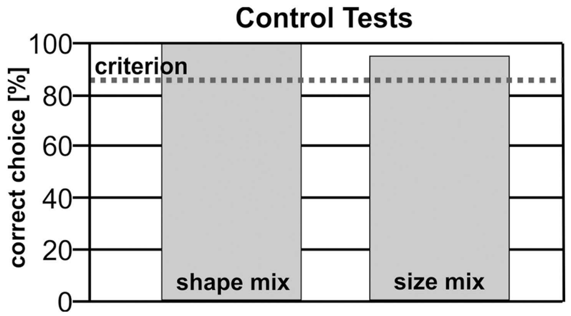

FIGURE 4 | The results of the control phase show that the animal could transfer the learned performance to new and unreinforced stimuli.

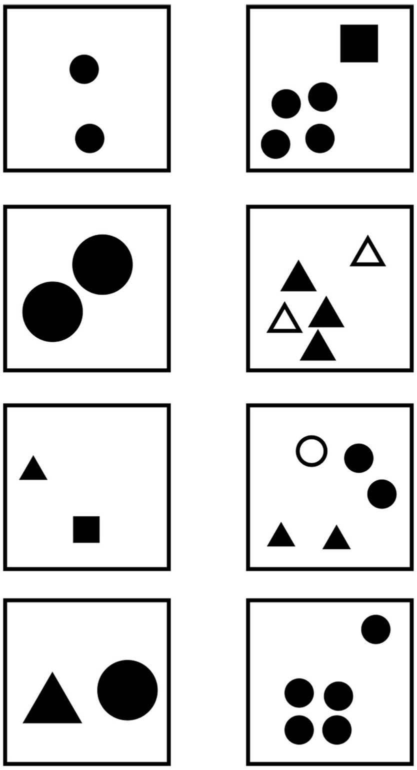

FIGURE 5 | Examples for the testing stimuli 2 vs. 5. Similar variations were prepared for the stimuli 3 vs. 5, 3 vs. 5, 2 vs. 4, 2 vs. 3, 3 vs. 4, 4 vs. 5, 5 vs. 6, 5 vs. 7, 5 vs. 9, and 5 vs. 10.

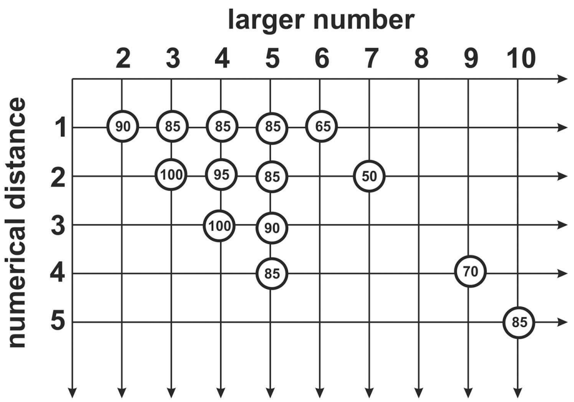

FIGURE 6 | The figure indicates the larger number within each pair as well as the difference between this pair of stimuli. The number within the circles indicates the achieved performance of Blue. The data show that Blue had more difficulties in discriminating higher numerosities with small differences between the two numbers.

At the beginning of the experiments, Blue demonstrated a preference for the left side, possibly due to his right eye being almost blind. A tendency to shift to the sighted side is well known under monocular vision (Ulrich et al., 1999). Blue's side preference disappeared after being rewarded for selecting the "many" patterns. Overall, Blue's performance did not appear to be influenced by confounding stimuli like surface, shape, and element patterns. The importance of controlling these factors has been described in several studies on numerical abilities using various species like dolphins (Kilian et al., 2003), pigeons (Emmerton et al., 1997; Xia et al., 2001), monkeys (Cantlon and Brannon, 2007), newborn chicks (Rugani et al., 2011), and human infants (Strauss and Curtis, 1981; Clearfield and Mix, 1999, 2001). These results suggest that, if available, animals including humans may rely on variables that are simpler and therefore less effortful than numerosity (Davis and Memmott, 1982; Beran, 2007). Consequently, Davis and Pérusse (1988) argued that numerosity is the last cognitive resort if other means fail. Along with data from other species

(Brannon and Terrace, 1998; Boysen and Hallberg, 2000; Brannon, 2006; Cantlon and Brannon, 2007; Vallortigara et al., 2010), our data clearly argue against this notion, since Blue seemed to spontaneously use numerosity even though other cues were initially available.

This interpretation could also explain why Blue was so rapidly able to generalize to other numerical examples during the control phase without loss of performance (**Figure 4**). Similar results regarding a transfer to heterogeneous stimulus sets were also found for other animals such as pigeons (Emmerton et al., 1997), a gray parrot (Pepperberg, 1987), a Californian Sea lion (Dieckmann, 1999), rhesus monkeys (Brannon and Terrace, 1998), rats (Suzuki and Kobayashi, 2000), and hooded crows (Smirnova et al., 2000). In the very beginning of the task, Blue could have relied on a strategy to avoid 1. However, the fact that he worked above threshold when being confronted with panels that did not contain the element "1" renders it likely that Blue grasped numerosity as the essence of the task very early on. At least at the present state of analysis of a single subject, our results indicate that for dolphins, numerosity could be a cue that is available before experimental onset (Hauser et al., 2002; Hyde, 2011). In this sense, Blue could reveal a "number sense" (Dehaene et al., 1998).

This last interpretation contrasts with the data of Kilian et al. (2003) who reported Noah, their subject, to completely rely on non-numerical cues in the beginning of the experiment. Although the difference between Blue and Noah could be ascribed to inter-individual differences, other interpretations are also conceivable. Kilian et al. (2003) used three dimensional stimuli consisting of diverse objects in different numbers hanging into water. Noah had to swim from a distance of 10 m and indicate his choice by touching one of the objects. Thus, Noah was confronted with stimuli which provided cues that could be discerned by visual and auditory senses. Additionally, Noah could utilize motion parallax, shape and depth cues, whereas Blue could only use two dimensional vision. It is possible that the comparably more frugal stimulus repertoire of the present study made the spontaneous use of numerosity cues more likely. Thus, dolphins appear to be able to apply a concept of numerosity very early on when encountering stimuli if other cues are less salient. Similar results were obtained by Beran (2007) who tested the influence of non-numerical cues in rhesus monkeys, and by Agrillo et al. (2009) who studied mosquito fish in a 2 vs. 3 object discrimination task, also probing the influence of non-numerical parameters.

Within the limitations of a study conducted with a single animal, the present data suggest that bottlenose dolphins are able to categorize numerosities up to 10. The next experiment was designed as a reversal task in order to test if Blue was able to process a more abstract relation of "few" vs. "many." According to some authors (Lea, 1984), successful transfer of reversed contingencies to items that were never reversed requires the existence of intra-categorical associations and could even be seen as evidence for a true numerosity concept.

EXPERIMENT 2

REVERSAL PHASE

To evaluate whether Blue indeed had acquired associative bonds between single numerical elements, the animal was confronted with a reversed S+, thus having to decide in favor of the panel with the "few" element. For this purpose, Blue was successively trained with only two numerical combinations: 1 vs. 4 and 1 vs. 5. Blue was already familiar with these numerical combinations from the initial training phase, but this time, reinforcement was delivered after choosing the panel with "1." After reaching the criterion of 85% correct performance, catch trials with other numerical combinations (1 vs. 3, 2 vs. 3, 3 vs. 4, 3 vs. 6) were intermixed with the two training pairs. The procedure of this phase was the same as described for the test phase. Note that because of poor performance of the number pairing 3 vs. 4 (see Results), the subject received additional training sessions with the training pair 1 vs. 4 and 1 vs. 5 before the combination 3 vs. 6 was tested.

RESULTS

Blue needed eleven sessions to reach criterion for the first reversal stimuli 1 vs. 5. The performance after the introduction of catch trials initially dropped to 80%, but recovered in the next session and remained constant for the following sessions. Blue reached the criterion for the reversal stimuli 1 vs. 4 already in the second session, and the animal's performance was constant after the introduction of catch trials (**Figure 7**).

Over five sessions, Blue reached 100% correct answers for 1 vs. 3. For the combination 2 vs. 3, he reached 85%, whereby the first four catch trials of the first session were correct. For the stimulus pairing 3 vs. 4, he failed to reach criterion (75% correct performance). For the last number combination 3 vs. 6, Blue reached 90% correct performance (**Figure 8**).

DISCUSSION OF EXPERIMENT 2

The second experiment was designed to test if Blue had already acquired strong intra-categorical associations. As argued by several authors (Lea, 1984; Herrnstein, 1990), members of a category or concept are bound together independent of their perceptual similarities. Thus, contingencies applied to one stimulus of a class should be transferred to all other members. Indeed, Blue was highly successful in this transfer. His performance dropped to 75% only for 3 vs. 4, possibly due to the operations of the analog

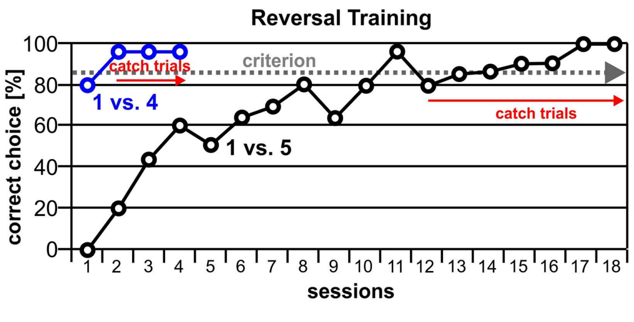

FIGURE 7 | Blue reached the criterion for the first reversal-training of 1 vs. 5 (85% correct choices) after 11 sessions, and in the following session the introduction of catch trials started. In the next session, performance dropped to 80% but recovered quickly. For the subsequently introduced training pair 1 vs. 4, criterion was already reached in the second session, and performance remained constant even after the introduction of catch trials.

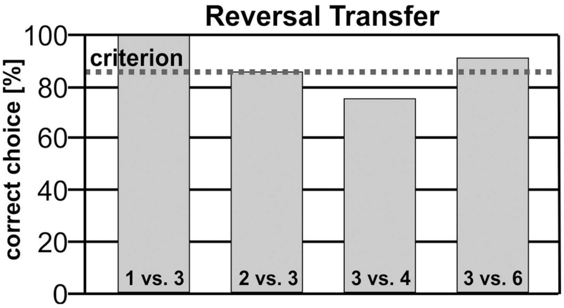

FIGURE 8 | Blue's performance for the reversal contingencies 1 vs. 3, 2 vs. 3, 3 vs. 4, and 3 vs. 6. Only for the stimuli pair 3 vs. 4 did Blue's performance not reach criterion (75%), albeit his acquisition clearly was above chance level.

magnitude system that is subject to a ratio limit in accordance with the Weber-Fechner law (Fechner, 1888; Agrillo et al., 2012). Thus, a simple stimulus generalization can be excluded, since Blue could base his decision only on abstract qualities (few/more). As a further control, we had used new stimuli for the reversal transfer, with a different arrangement of items compared to the first part of the experiment. The possibility that Blue based his decisions on a response outcome is also unlikely, as all new stimuli were introduced by catch trials. Thus, we can also exclude new learning by feedback.

Taken together, the dolphin of the present study demonstrated its capacity to reverse all numerical comparisons after being trained for reversal with only two numerical distinctions. Our results contrast with the results of other authors who reported the necessity of large amounts of training stimuli in non-human animals for developing an abstract concept (Roitblat and von Fersen, 1992; Zentall et al., 2002; Fabre-Thorpe, 2003). Independent of this, we are inclined to conclude that an abstract representation of "few" vs. "many" is within the reach of dolphins.

GENERAL DISCUSSION

In the present work, we examined whether a bottlenose dolphin could rely on a numerical understanding of "few" vs. "many." Similar to Kilian et al. (2003), we carefully excluded several confounding factors, i.e., that the subject was cued by physical properties of the stimuli other than numerosity. Blue immediately transferred learned contingencies to novel numerical combinations. Data suggest that he likely made the use of a parallel subitizing and an analog magnitude system. Moreover, he was able to reverse the remaining stimulus sets after being exposed to only two number pairings without being taught to do so. Such immediate reversal of performance strongly suggests an abstract understanding of "few" vs. "more" and could even be considered as evidence for a numerosity concept (Lea, 1984). Bottlenose dolphins often aggregate in "super – alliances." Here, subgroups of males join temporally in order to get numerical advantage over another group to gain access to a receptive female (Hauser, 2000; Connor et al., 2001). Thus, an understanding of magnitude could be of advantage to dolphins living in the wild. In the following, we will discuss the present data in a more general framework.

For magnitudes up to three, Blue could readily discriminate between numerosities that differed by one. Beyond that, his performance started to deteriorate and was just at criterion in experiment 1 or slightly below in experiment 2. This is typical for a "parallel" or subitizing system that only works for small sets up to 3 or 4. Usually, reaction time curves of human subjects that having to judge the number of dots within briefly flashed displays show a monotonic increase with an increase in dot numbers. However, the slopes of these curves display a distinct change at around 3–4 items, for which a fast subitizing process is thought to be succeeded by a true counting mechanism (Trick and Pylyshyn, 1993; Lemer et al., 2003). Below 4, subjects usually accurately discriminate dot numbers despite only brief presentation times and when the ratio of the two numbers is smaller than 1:2.

When being confronted with numerosities beyond 3 or 4, animals seem to process numerical comparisons logarithmically. Indeed, Nieder and Miller (2003) showed that in monkeys, the coding of numerical information follows logarithmic scaling as postulated by the Weber-Fechner law. Thus, with pairings of higher numbers but constant absolute difference, the relative difference becomes smaller and is therefore more difficult to discriminate. Numerous investigations in human infants (Strauss and Curtis, 1981; Xu and Spelke, 2000), human adults (Xu, 2003; Piazza et al., 2004; Hyde and Spelke, 2008; Cordes and Brannon, 2009; Schmitt and Fischer, 2011), human adults with few number words (see citation inside of Brannon, 2006), other primates (Thomas et al., 1980; Boysen, 1993; Boysen and Hallberg, 2000; Smith et al., 2003; Brannon, 2006; Jordan and Brannon, 2006; van Marle et al., 2006; Addessi et al., 2007; Beran, 2007; Cantlon and Brannon, 2007; Hanus and Call, 2007; Nieder and Merten, 2007; Beran et al., 2008), pigeons (Scarf et al., 2012), New Zealand robins (Hunt et al., 2008), and domestic chicks (Rugani et al., 2008) show similar results. Agrillo et al. (2012) observed this distinction in comparable ways in undergraduate students and guppies, and argued for the existence of two numerical systems that have a long phylogenetic history. However, the existence of two systems is not undisputed. Some authors present evidence that most experimental data can be explained by a single magnitude system (Nieder, 2005; Nieder and Merten, 2007). Alternatively, subitizing could mainly occur in studies in which subjects use behavioral discriminations by accessing implicit representations of the number of objects (Hauser et al., 2000).

We set out to study if numerosity in dolphins is represented as a flexible and abstract category representing the more or the less of a magnitude. To this end, we employed the partial reversal procedure in which only a subset of numerosities is reversed and the remainders are subsequently tested. According to Lea (1984) and Herrnstein (1990), successful partial reversal can signal the presence of a numerosity concept. Indeed, Blue successfully switched his choices after single reversal learning. Thus, within the limits a study conducted with only a single individual, we are inclined to believe that bottlenose dolphins can flexible represent numerosity as an abstract magnitude system. This result is similar to another dolphin study in which two dolphins were shown to categorize "same" vs. "different" for different visual objects (Mercado et al., 2000). Numerical competence at a level similar to Blue has previously also been shown for monkeys and parrots (Matsuzawa, 1985;

Pepperberg, 1987). A successful mastery of abstract category use in monkeys was described by Bovet and Vauclair (2001). In this study, animals had to judge two objects as same or different and afterward transfer their learned skills to new objects which belonged to two functional categories (food/non-food). Other examples are provided by flexible token use in capuchin monkeys as described by Addessi et al. (2007), or by achievement of abstract relations like "inside-outside" (Herrnstein et al., 1989). The parallel results of cognitive capacities of dolphins and primates, other mammals and birds despite their different evolutionary history and ecology reveal that vertebrates uses the same basic and evolutionary old processes when flexibly dealing with categories (Mercado et al., 2000). Results like these argue in favor of a continuous evolutionary process of cognitive competences, an evolutionary process for which humans represent an integral part of the overall pattern (Vauclair, 2002; Pepperberg and Gordon, 2005; Diester and Nieder, 2007).

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A shared system of representation governing quantity discrimination in canids

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One way to investigate the evolution of cognition is to compare the abilities of phylogenetically related species. The domestic dog (*Canis lupus familiaris*), for example, still shares cognitive abilities with the coyote (*Canis latrans*). Both of these canids possess the ability to make psychophysical "less/more" discriminations of food based on quantity. Like many other species including humans, this ability is mediated by Weber's Law: discrimination of continuous quantities is dependent on the ratio between the two quantities. As two simultaneously presented quantities of food become more similar, choice of the large or small option becomes random in both dogs and coyotes. It remains unknown, however, whether these closely related species within the same family – one domesticated, and one wild – make such quantitative comparisons with comparable accuracy. Has domestication honed or diminished this quantitative ability? Might different selective and ecological pressures facing coyotes drive them to be more or less able to accurately represent and discriminate food quantity than domesticated dogs? This study is an effort to elucidate this question concerning the evolution of non-verbal quantitative cognition. Here, we tested the quantitative discrimination ability of 16 domesticated dogs. Each animal was given nine trials in which two different quantities of food were simultaneously displayed to them. The domesticated dogs' performance on this task was then compared directly to the data from 16 coyotes' performance on this same task reported by Baker et al. (2011). The quantitative discrimination abilities between the two species were strikingly similar. Domesticated dogs demonstrated similar quantitative sensitivity as coyotes, suggesting that domestication may not have significantly altered the psychophysical discrimination abilities of canids. Instead, this study provides further evidence for similar non-verbal quantitative abilities across multiple species.

Keywords: Weber's law, canid, quantity discrimination

INTRODUCTION

Recent findings (Baker et al., 2011) add coyotes (*Canis latrans*) to the list of known species capable of making psychophysical discriminations of continuous quantities (e.g., see Brannon and Roitman, 2003; Brannon et al., 2010 for review of other species that share similar abilities). Shared among the discrimination abilities of these species is an adherence to Weber's Law, which states that the ability to discriminate one continuous quantity from another is mediated by the ratio between the two quantities. As this difference approaches a 1:1 ratio (e.g., as the to-be-compared sets are more similar in quantity/have a larger ratio), discrimination becomes more difficult for non-human animals and humans.

Since such findings are common to a wide range of species and methodological approaches, it has been hypothesized that all species may in fact possess an approximate representation of continuous quantities (e.g., Gibbon, 1977; Gallistel, 1989). In humans, looking time paradigms have revealed approximate representations of numerosity in infants (e.g., Wynn, 1998; Spelke, 2000; Xu and Spelke, 2000; Jordan and Brannon, 2006a; Jordan et al., 2008), while explicit choice paradigms demonstrate maintained adherence to Weber's Law in these representations throughout childhood and adulthood (e.g., Moyer and Landauer, 1967; Jordan and Brannon, 2006b, 2009; Halberda et al., 2008, 2012; Jordan and Baker, 2011). Variations on such experimental approaches used in humans have demonstrated similar abilities in orangutans (Call, 2000), rhesus macaques (Jordan and Brannon, 2006b,c), chimpanzees (Rumbaugh et al., 1987; Beran, 2004, 2010), and other primates (see Brannon et al., 2010 for review). Similar abilities exist in species ranging from newborn chicks (Rugani et al., 2009), rats (Meck and Church, 1983), dogs (Ward and Smuts, 2007), birds (Pepperberg, 1987; Al Aïn et al., 2009), dolphins (Kilian et al., 2003), raccoons (Davis, 1984), insects (van Hateren et al., 1990), amphibians (Krusche et al., 2010), fish (Gòmez-Laplaza and Gerlai, 2011), elephants (Perdue et al., 2012), and many others (see Brannon and Roitman, 2003; Jordan and Brannon, 2009; Brannon et al., 2010; for review).

Such consistent replication of findings across research groups, designs, and species suggests a highly conserved non-verbal system of representation. Moreover, given the ubiquity of approximate quantitative abilities across species, it is likely that such representations are evolutionarily valuable. However, the biological niche filled by various species may also have honed this ability to different degrees, perhaps depending on each species' need to discriminate quantity. Purposeful domestication, for example, has been shown to affect various aspects of animals' behavior. Research comparing foraging behaviors between the "wild type" red jungle fowl (*Gallus gallus*) and the domesticated White Leghorn chicken have identified differences that researchers believe may have arisen as a direct result of domestication (Lindqvist et al., 2009). It is hypothesized that when food supplies across generations become stable as a result of purposeful domestication, an animal's need to exert effort for high quality and quantity foods is diminished. As a result, the foraging behaviors seen across these two species are markedly altered (Lindqvist et al., 2009).

The domestication process between red jungle fowl and White Leghorn chicken is thought to have occurred over the last 8000 years (Fumihito et al., 1994). Comparatively, domestication between two canids, dogs and wolves, is thought to have occurred over the last 30,000 years (Germonpré et al., 2009). In this time, domesticated and wild canids have experienced significant cognitive divergence. For example, differences between these species of canids in social cognition – namely, differences in animals' responses to communicative cues from humans – have been shown between domestic dogs and wolves (*Canis lupus*; e.g., Hare et al., 2010). It is possible that similar effects of domestication may have differentially shaped quantitative discrimination abilities between coyotes (*C. latrans*) and domestic dogs (*Canis lupus familiaris*). That is, while the quantitative discrimination capacities of both species adhere to Weber's Law, the ratio needed to detect the larger food option may differ between the two species. Perhaps, much like the changes in social cognition, domestication brings with it differential abilities to perceive the quantity of or base decisions on the quantity of food options. Alternatively, these two species of canids may show similar abilities for quantitative representation, despite their different ecological niches. The current experiment is an effort to address this question. Direct intra-family comparisons, such as that between coyotes (*C. latrans*) and domestic dogs (*Canis lupus familiaris*) offer a unique look at the effect of domestication on quantitative discrimination abilities.

The procedure used by Baker et al. (2011) to show that coyotes can compare and discriminate different quantities was similar to that of Ward and Smuts (2007), who had previously demonstrated that domestic dogs discriminate quantity and that this ability is mediated by Weber's Law. In both studies, two different quantities of food were prepared out of the animals' view, after which both options became visible to the animals as they decided which food option to choose and consume. While Baker et al. (2011) showed that coyotes discriminated between different quantities of food and that these discriminations were mediated by Weber's Law, they did not directly compare the acuity of this quantitative ability with the acuity of domestic dogs. The current experiment makes this comparison by testing dogs with a similar procedure as was used by Baker et al. (2011) to test coyotes. Comparing these data collected by the same research group, we hypothesize that domesticated canines will show similar quantitative discrimination abilities as coyotes.

To answer such questions, here we replicate the Baker et al. (2011) coyote study in domestic dogs. Next, we subject these new data from domestic dogs to direct comparison with the data from coyotes reported by Baker et al. (2011), in order to identify whether quantitative discrimination abilities differ within divergent members of a single biological family – one of which has been domesticated.

MATERIALS AND METHODS

FACILITIES AND EXPERIMENTAL ANIMALS

This study was conducted at each animal's home environment in Cache County, UT, USA. All domestic dogs were tested in an indoor or outdoor open space of approximately $6' \times 6'$. All sessions were videotaped for later review. To be eligible to participate in the study, an animal had to show willingness to approach the researcher for food. Sixteen domestic dogs of various breeds met this criterion and participated in this study.

FOOD MAKE-UP AND FOOD PREPARATION

Pup Peroni© dog treats were used in the current experiment. Each *Pup Peroni*© stick was cut into eight equal-sized pieces approximately $1/4'' \times 1/4''$. Since each animal was fed regularly, this was considered a high-value "treat" food given in addition to its daily food intake; therefore, the size of the treat pieces were small in order to prevent satiation before the end of the experimental session.

PROCEDURE

All animals were tested individually. Each animal experienced eight ratio comparisons, and one olfactory control (1:6 ratio comparison) identical to that used by Baker et al. (2011) to determine whether animals were discriminating quantity based on smell alone, for a total of nine trials per session. Each animal experienced one session of testing. The animal's owner was present for each trial and kept the animal seated at the beginning of each trial by kneeling behind his/her dog and holding it by its collar. This allowed the animal to remain centered while a food quantity was placed on each side. In order to prevent possible non-verbal cues, the owners were asked to close their eyes during each trial.

To begin each trial, the experimenter sat on the ground approximately 3 feet in front of the animal, while the owner sat behind the dog and held it in place in the manner described above. Once the owner had closed his/her eyes, the researcher obtained the appropriate amount of treats for that trial's quantitative comparisons and placed one quantity in each hand. The side placement of the large option was pseudo-randomized. The treats were kept in a cloth bag that was easily accessible by the experimenter, yet kept the treats out of the animal's view. Both quantities were then removed from the bag and placed on the ground covered by the experimenter's hands; the experimenter then removed her hands simultaneously from the two piles, ensuring they were uncovered at the same time. The treats in each pile were placed close together on the ground so that all pieces could be viewed by the animal and were not obstructed by other pieces piling atop each other. Once the dog had looked at both food options, the experimenter instructed the owner to release it so that it could make its choice. A choice was defined as the animal directly sniffing and/or attempting to retrieve a treat from a pile. Once a food choice was made, the experimenter covered and removed the pile not chosen. Thus, no animal retrieved food from the unchosen pile. An animal was considered to have failed to make a choice if it did not approach the researcher within a minute from the start of a trial.

Each animal received all nine quantitative contrasts used with coyotes by Baker et al. (2011) within a session, which included: 1:4; 1:3; 2:5; 1:2; 2:4; 3:5; 2:3; 3:4; and a 1:6 olfactory control trial. Left-right side presentation of the larger quantity for all ratio comparisons was pseudo-counterbalanced and randomized within and across animals. Order of ratio presentation was also randomized within session; as a result, roughly two-thirds of the animals (68.75%) began testing with small ratio comparisons (1:4, 1:3, 2:5, or 1:2). No animal began testing with the olfactory control trial. On the olfactory control trial, the experimenter placed both food options on the ground but did not reveal them visually to the dog, instead keeping them covered with his/her hands. The owner was instructed to release the dog, and a choice was defined as approaching one of the researcher's hands within 5′ or less; all dogs actually sniffed the chosen hand as well. Once a choice had been made, the food pile was visually revealed to the animal, and the animal was allowed to eat it. Choosing the large and small food quantities with equal frequency on the olfactory control trial would indicate that the dogs were not discriminating different quantities of food by smell alone.

DATA ANALYSIS

We hypothesized that, as found in previous studies such as Ward and Smuts (2007) and Baker et al. (2011), animals would choose the larger quantity of food more often than the smaller quantity. We also predicted that accuracy of choice, or percentage of times that the animal chose the larger quantity over the smaller quantity, would improve as the ratio between food choices decreased. Statistical tests of these hypotheses were conducted using R® (R Core Team, 2012), Prism®, and Excel® version 10.

First, binomial tests were used to determine if animals chose the larger quantity more often than the smaller quantity. To test whether animals' ability to choose the larger quantity of food changed as a function of the ratio between large and small food quantities, binary logistic regression was employed (Agresti, 1996). Finally, to determine whether animals' choice behavior exhibited scalar variability, linear regression analysis was used. For all parametric statistics, the assumptions of homogeneity of variance and normality were met.

RESULTS

An alpha level of 0.05 was used for all analyses. Significantly more dogs (12 of 16) chose the larger food quantity more often than the smaller food quantity overall, across all trials (binomial sign test, $p = 0.027$). **Table 1** shows the individual animal average performance across all ratios. No significant difference was found between the number of dogs more often choosing the large (7 of 16) vs. the small food quantity in the olfactory control trial (binomial sign test, $p = 0.175$), suggesting that the dogs were not discriminating between quantities of food based on olfactory cues alone.

In order to identify the influence of ratio on dogs' food option choice, data were subjected to binary logistic regression. As predicted, this model significantly predicted dogs' food choice behavior ($\chi^2 = 4.21$, $p = 0.04$, *Cox and Snell pseudo-*$R^2 = 0.03$), indicating that the ratio between food option does influence animals' choice behavior. Moreover, as predicted, linear regression analysis identified significant scalar variability in animals' choice; variability was significantly lower for small compared to large ratio comparisons [$F(1, 7) = 7.87$, $p < 0.001$, $R^2 = 0.9$].

Table 1 | Average percentage of times choosing the large option across all ratios for each individual dog and coyote.

Animal	Dogs	Coyotes
1	37.5	12.5
2	37.5	37.5
3	50	37.5
4	50	50
5	62.5	50
6	62.5	50
7	62.5	62.5
8	62.5	62.5
9	62.5	62.5
10	62.5	62.5
11	62.5	62.5
12	75	75
13	75	75
14	75	75
15	87.5	75
16	87.5	100
Species average	63.28	59.37

Coyote data were collected by Baker et al. (2011).

Similar to Baker et al. (2011) findings in coyotes, we also did not identify any learning effects across trials. Animals that began testing sessions on trials with small ratio (e.g., 1:4, 1:3, 2:5, or 1:2) comparisons succeeded on a similar percentage of small ratio trials compared to animals that began testing sessions on trials with large ratio comparisons [e.g., 2:4; 3:5; 2:3; 3:4; $t(15) = 0.44$, $p = 0.66$]. Similarly, there was no significant difference in the percentage of large ratio trials correct between animals that began testing on small compared to large ratio trials [$t(15) = 1.19$, $p = 0.24$]. A laterality bias (i.e., an animal always chooses the right or left food option) was not observed within any animal.

COMPARISON WITH COYOTES

In order to compare the relative quantitative discrimination abilities of dogs and coyotes, the new data collected in dogs reported above were directly compared with the data from coyotes reported by Baker et al. (2011). First, we used an independent sample t-test to compare the percentage of trials in which each animal chose the larger food option across species. The results of this comparison indicate that the difference in percentage of trials in which the larger option was chosen between dogs ($\bar{x} = 63.28\%$, SD = 14.76 %) and coyotes ($\bar{x} = 59.38\%$, SD = 20.15%) was not statistically significant, $t(30) = 0.62$, $p = 0.53$.

Figure 1 shows the proportion of dogs in the current study that chose the larger food quantity as a function of ratio between large and small food choices. Data previously collected in the analogous task by Baker et al. (2011) in coyotes are overlaid onto this

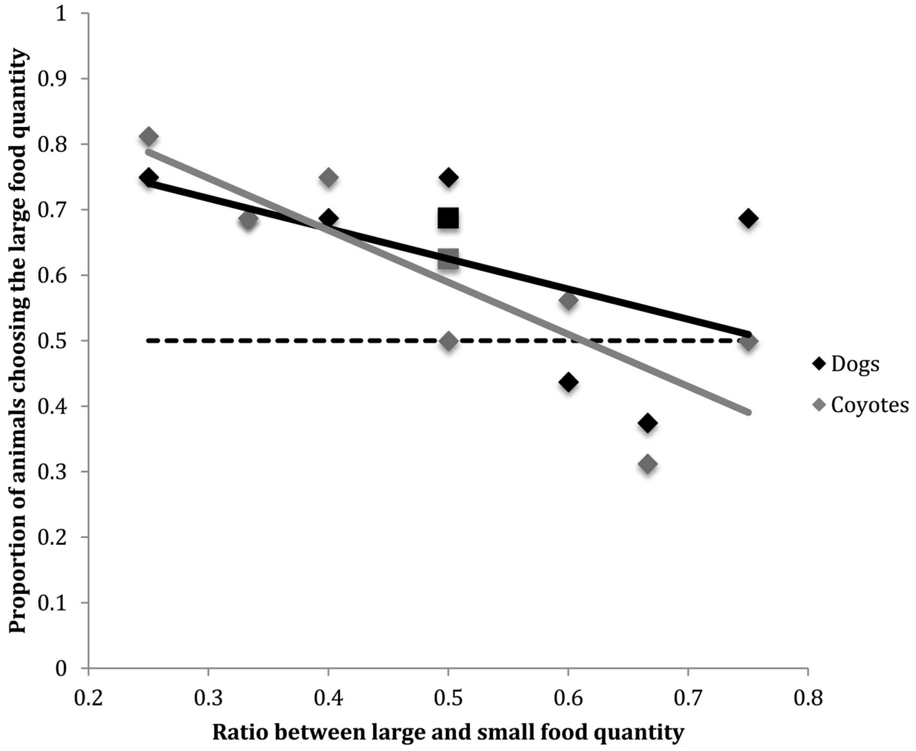

FIGURE 1 | Proportion of dogs vs. coyotes choosing the larger food quantity as a function of the ratio between large and small food quantities. Solid lines indicate regression lines (i.e., slopes) for both canid species. Horizontal dashed line indicates chance performance (50%). The negatively sloped regression lines indicate that dog and coyote quantitative choice behavior becomes more random as the ratio between food options approaches 1:1. Coyote data were collected by Baker et al. (2011). The squares displayed at the 0.5 food quantity ratio comparison along the *x*-axis indicate the proportion of animals selecting the larger food quantity when the comparison was 2 vs. 4 food items. The diamonds displayed at the 0.5 food quantity ratio comparison along the *x*-axis indicate the proportion of animals selecting the larger food quantity when the comparison was 1 vs. 2 food items.

figure. The slopes produced by the two species are not significantly different [$F(1, 13) = 0.48$, $p = 0.49$]. The superimposition of the psychophysical functions for these two species suggests that dogs and coyotes may share a similar system of quantity representation.

DISCUSSION

As predicted, here we show that domestic dogs' ability to discriminate visual quantities of food items is strikingly similar to their non-domesticated counterparts, the coyote. By using an experimental procedure similar to Baker et al. (2011), we show that domestic dogs' and coyotes' quantitative choice behavior adheres to Weber's Law: discrimination of large vs. small quantities is mediated by the ratio between the two options. Furthermore, quantitative behavior in neither species is mediated by olfactory clues alone. By directly comparing current results in dogs with those of Baker et al. (2011) in coyotes, we find no statistical differences between the two data sets.

Data thus support our hypothesis that the two species exhibit similar quantitative discrimination abilities. These findings further support the claim that certain psychophysical abilities such as ratio-dependent quantitative representation are shared across many species (see Brannon et al., 2010 for review). Results also suggest that such abilities may remain fundamentally unchanged through canid domestication.

While we did not conduct any such analyses here, further tests of possible behavioral differences exhibited by coyotes compared to domestic dogs while foraging could theoretically still reveal differences in quantitative foraging behavior. For example, it remains unknown how testing in the presence of another animal (e.g., competitor or subordinate) may affect quantitative choices in the two species. It is also unknown if there are canid species differences in willingness to exert extended effort due to depletion in food quantity, such as was found between bumblebees (*Bombus impatiens*) and honeybees (*Apis mellifera*; Townsend-Mehler et al., 2011). In this study, bumblebees were willing to change foraging strategy and travel far distances in response to food depletion, though honeybees were not. Thus, there may also be differences in the ways in which species "weight" different quantitative variables in their foraging behavior. Further, it is unknown whether coyotes' abilities to remember various quantitative comparisons when they are not visible (e.g., in working memory) are comparable to those of dogs found in such studies as Ward and Smuts (2007). It remains possible that the domestication process affected performance on such other quantitative tasks. However, comparative tests of psychophysical discriminations such as those reported here suggest that such abilities may be stable across domestication. Moreover, the ubiquitous nature of such abilities across species further supports the idea of a shared system for non-verbal magnitude representation across many non-human and human organisms.

In addition to providing a comparison to the coyotes tested in Baker et al. (2011), current results provide an approximate replication of Ward and Smuts (2007). There were some small but nevertheless important procedural differences between Ward and Smuts (2007) and the results reported here; for example, the dogs used in Ward and Smuts (2007) were tested in a single testing room environment that was devoid of distractions, while the dogs used in the current study were tested at their own homes. Importantly, despite such environmental differences, similar results were obtained; this contrasts with other recent tests of canine choice behavior in lab vs. open-air environments, where differences in dogs' choice behavior based on referential emotions displayed by the experimenter have specifically been found (Buttelmann and Tomasello, 2012; though breed also was confounded with testing environment in these conditions). Thus, our replication will do well to justify future research endeavors, which intend to test canid quantitative discrimination abilities in a naturalistic environment. Unfortunately, such replication studies are not currently common in comparative psychology, yet they can provide useful convergent evidence (e.g., Agrillo and Petrazzini, 2012; Irie and Hasegawa, 2012; Perdue et al., 2012).

Our results, however, are not without limitations. For example, because stimulus size and number were positively correlated in the current design, we are unable to discern potential numerical discrimination abilities from potential size/surface area discrimination abilities. Such issues have confounded similar studies of relative quantity judgments in other species of the carnivore order as well (e.g., South American sea lions, Abramson et al., 2011). Future studies on comparative numerical cognition in carnivores, perhaps using a non-food stimulus, should further address this issue by removing the correlation between number and size, as has recently been accomplished in American black bears (Vonk and Beran, 2012). Furthermore, future studies could include a greater number of trials per ratio comparison, enabling for example assessments of functions for individual animals. Because each animal in the current study was only presented with each quantitative contrast once, we were not able to determine consistency of individual choice behavior within each ratio comparison. In the future, it will also be necessary to compare domesticated and non-domesticated canids on their abilities to discriminate quantities that are not both visible sets available at the time of the decision. For example, animals could be tested with items or sets presented sequentially into opaque containers or covered out of sight, so that they would have to hold the quantities perceived in memory and make a final comparison (e.g., Beran et al., 2008; Evans et al., 2009). Such a test may perhaps be more relevant to certain species than others based on their ecology.

Finally, there was in this experiment the potential for experimenters to unintentionally cue the dogs, as the experimenter watched the dogs approach and knew which choice was the larger food quantity. Current data suggest that dogs were not using any such unintentional cues, especially data from the olfactory control trial. On this trial, the dogs' performance was not above chance, even though this was a very easy comparison (1 vs. 6). Similarly, the dogs did not reach 100% accuracy on all visual trials – even though the experimenter always knew which side held the larger food item – suggesting lack of use of any unintentional human cues. Moreover, as reported by Buttelmann and Tomasello (2012), domestic dogs do not modify their choice behavior when humans display non-meaningful emotional expressions in the direction of one of two choices. The experimenter in the current study remained emotionally neutral throughout all trials. Nevertheless, in the future a more "blind" protocol to make sure the experimenter is not signaling or otherwise cuing the dogs to which option contained the larger amount of food would be useful.

In conclusion, our results demonstrate that domestic dogs possess similar abilities to discriminate visual quantities of food items as non-domesticated coyotes. These results suggest that domestication may not significantly affect quantitative discrimination of visually presented food items. Future studies are needed to further elucidate such issues and to investigate performance across related species in discriminating and basing decisions on other quantitative properties such as number, space, and time. Because such abilities have been shown to exist across many species, it would be interesting to identify whether they, too, maintain relative consistency across the domestication process or whether they are altered in a way not observed here. Consistency across such related species may support our claim that ratio-dependent, approximate quantitative abilities may be shared across many species.

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Quantity discrimination in wolves (*Canis lupus*)

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Quantity discrimination has been studied extensively in different non-human animal species. In the current study, we tested 11 hand-raised wolves (*Canis lupus*) in a two-way choice task. We placed a number of food items (one to four) sequentially into two opaque cans and asked the wolves to choose the larger amount. Moreover, we conducted two additional control conditions to rule out non-numerical properties of the presentation that the animals might have used to make the correct choice. Our results showed that wolves are able to make quantitative judgments at the group, but also at the individual level even when alternative strategies such as paying attention to the surface area or time and total amount are ruled out. In contrast to previous canine studies on dogs (*Canis familiaris*) and coyotes (*Canis latrans*), our wolves' performance did not improve with decreasing ratio, referred to as Weber's law. However, further studies using larger quantities than we used in the current set-up are still needed to determine whether and when wolves' quantity discrimination conforms to Weber's law.

Keywords: numerical competence, Weber's law, domestication, wolf

INTRODUCTION

Being able to discriminate between different quantities yields advantages for animals' fitness and survival (Gallistel, 1990). For example, according to the optimal foraging theory, animals optimize their energy intake (Stephens and Krebs, 1986), and studies on different great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*, e.g., Hanus and Call, 2007) have shown that animals prefer the larger quantity of food if they are presented with a choice between two available food amounts. Another context where some rudimentary numerical competence provides an advantage is participation in intergroup conflicts over food, mates, and territory (Parker, 1974). Playback experiments in lions (*Panthera leo*; McComb et al., 1994) and chimpanzees (Wilson et al., 2001) have shown that animals adjust their cooperative behavior to a quantitative estimation of the opponent's strength in comparison to that of their own group (Maynard Smith and Price, 1973; Maynard Smith and Parker, 1976).

In theory, animals can base their decisions in such contexts on the number of items, a quantity assessment, or some correlated perceptual features. While numbers are regarded as the product of counting (one-by-one), continuous (uncountable) quantities are the product of measurements, making the former accurate, and the latter approximate (Gallistel and Gelman, 2000). Moreover, up to a number of four items, the discrimination is also possible without actual counting but instead by relying on pattern recognition (also referred to as subitizing; Gallistel and Gelman, 2000). Finally, independent of number or quantity, the choice for one set of items over another one can be affected by perceptual features such as the size of a food pile or the surface area.

Researchers have used various methods to disentangle whether animals rely on numerical or quantitative information or instead on perceptual features to make their decisions. In particular there are two paradigms which have been used extensively: the two-box spontaneous choice and the violation of expectation paradigm. In the two-box spontaneous choice paradigm, animals are encouraged to choose between two quantities of either simultaneously or sequentially presented food items that can be visible or invisible at the time of choice. If the two sets of items are presented simultaneously, non-human animals may choose based on surface area or other correlated perceptual features rather than numerical properties (but see Brannon and Terrace, 2000 for possible controls). Instead, if the items of each set are consecutively presented and invisible during the choice, the subject never sees the entire content of either set, but instead must modify its representation of each set's content as one item is added after the other. After the animal has done so for both sets, it must then compare the two representations to choose the larger set. Previous studies based on this paradigm affirmed that animals, e.g., northern mockingbirds (*Mimus polyglottos*; Farnsworth and Smolinski, 2006), mosquitofish (*Gambusia holbrooki*; Dadda et al., 2009), non-human primates, such as rhesus monkeys (*Macaca mulatta*; Hauser et al., 2000), or chimpanzees (Beran, 2001, 2004; Beran and Beran, 2004) were able to discriminate different quantities with varying success, depending on factors such as absolute set sizes or ratios between the presented items. The problem with the two-box spontaneous choice paradigm is that while it allows exclusion of perceptually based choice it does not discriminate whether they rely on numerical or quantity information to make their choice since the number of food items is perfectly correlated with the amount of food.

The second task, the violation of expectation paradigm, also requires that animals have some mental representation of the presented items. In this task, the animals are first presented with a certain quantity and then, after it disappears, with a different quantity. If animals perceive the unexpected change, they should look longer than if no change occurred. Several species have more or less successfully solved the tasks, including rhesus monkeys (Hauser et al., 1996), mongoose lemurs (*Eulemur mongoz*; Lewis et al., 2005), cotton-top tamarins (*Saguinus oedipus*; Uller et al., 2001), or mosquitofish (Dadda et al., 2009). Lewis et al. (2005) showed that the lemurs' performances depended on the ratio between the presented sets, e.g., that their judgment and discrimination decreased when the ratio (ratio > 0.5) increased ("Weber's law," in, e.g., Gallistel and Gelman, 2000). However, as shown by the different success rates, the animals might attend to different perceptual properties such as the surface area or pattern of the presented sets, requiring proper controls in order to elucidate the subjects' quantitative skills.

Although in their natural environment both dogs and wolves have been shown to adjust their behavior in intergroup conflicts according to the number of opponents (Harrington and Mech, 1979; Sillero-Zubiri and MacDonald, 1998; Bonanni et al., 2009, 2011), little is known whether they base their choices on quantity judgments or numerical properties in such encounters. To investigate canines' quantitative representations, several studies have been conducted. Two studies on dogs (West and Young, 2002; Ward and Smuts, 2007) and one study on coyotes (Baker et al., 2011) found positive results using the violation of expectancy looking paradigm (West and Young, 2002) as well as the two-box spontaneous choice paradigm (Ward and Smuts, 2007; Baker et al., 2011). The latter two studies showed that dogs and coyotes could discriminate between two small quantities of one to five items, if those were visible at the moment of choice and if the subjects' performances conformed to Weber's law. However, these results have to be considered with caution, due to (1) their use of only three very simple calculations ($1 + 1 = 1$; $1 + 1 = 2$ and $1 + 1 = 3$; West and Young, 2002), (2) decreased numerical competence if the presented quantities were invisible during the choice (Ward and Smuts, 2007; Baker et al., 2011), (3) a small sample size ($n = 2$) in the invisible choice condition in the dog study (Ward and Smuts, 2007). Furthermore, although both dogs and coyotes had to mentally compare both sets in some conditions, the discriminations could still have been based on pattern recognition, the surface area of the presented food, the volume of said food, or a combination of the above, since no controls for such confounding factors were implemented.

To further investigate canines' competence for quantity judgment, we tested whether wolves were able to discriminate presented quantities in a two-way choice task used by Hauser et al. (2000) and adapted by Dorottya Ujfalussy (unpublished manuscript). In our study (1) the food items were placed one-by-one into an opaque container, thereby avoiding the possibility that subjects made a choice based on seeing the complete quantities of the two sets at the moment of choice, and (2) the handling time during which a smaller vs. a larger quantity would be inserted as well as the total amount of items were controlled for by adding additional stones, resulting in equal net quantities of items on both sides. We aimed at testing whether wolves could discriminate between the presented quantities when properly controlling for these perceptual properties.

MATERIALS AND METHODS

No special permission is required in Austria for using animals (wolves) in such cognitive studies. The applicatory committee for research without special permission regarding animals is the "Tierversuchskommission am Bundesministerium für Wissenschaft und Forschung (Austria)."

SUBJECTS

The 11 timber wolves (*Canis lupus*) that participated in this study were born in different facilities in Europe and America (see **Table 1** for details). They were separated from their mothers within the first 10 days of their life, and were hand-raised and socialized at the Wolf Science Center (WSC), Austria. The animals grew up in peer groups and eight of them were introduced to packs of older animals at the age of 5 months. At the time of this study, the 11 wolves were living in three different packs in separate enclosures ($2\,\text{m}^2 \times 8000\,\text{m}^2$ and $1\,\text{m}^2 \times 4000\,\text{m}^2$). The wolves were fed once or twice a week with meat or carcasses; water was available *ad libitum.* Since puppyhood all animals have regularly participated in different cognitive behavioral tests and have been trained on a daily basis. They are rewarded with dog dry food, cheese, or sausage. The training, executed by professional animal trainers, consists of obedience training, including commands such as sit, down, roll-over, or touch and is conducted either in the test building or the testing enclosure in physical separation of the pack. Accordingly, the animals are entirely used to being separated from their pack in order to work with familiar humans.

EXPERIMENTAL SET-UP

The experimental apparatus was placed directly next to the fence outside of the enclosure. It consisted of a wooden table ($170\,\text{cm} \times 40\,\text{cm} \times 60\,\text{cm}$) with two opaque cans ($h = 14\,\text{cm}$, $\varnothing = 8\,\text{cm}$) mounted on top (**Figure 1**); one to the left and one to the right side of a familiar experimenter, who was sitting on a chair behind the table opposite from the fence. The cans were fixed 5 cm from the fence and each 75 cm from the center of the table. The bottom of the cans as well as the table had a hole so that a funnel could be connected directly to each of the cans. Each funnel was further linked to a plastic tube, which led into the enclosure. In this way food that was inserted into a can could slide into the enclosure. To prevent the food from sliding into the enclosure immediately after inserting it into the can, the bottom of the cans could be closed by a plastic bar that the experimenter could remove by sliding it toward herself. Below the table, a curtain, with two holes for the tubes, prevented the wolves from seeing the lower body of the experimenter. Moreover, a visual barrier placed on the table behind the cans prevented the subject from seeing the experimenter's upper body and, therefore, minimized the possible influence of inadvertent cues ("Clever Hans effect"; Pfungst, 1907). The visual barrier had two holes for the experimenter's hands immediately above the cans and a slim hole at the experimenter's eye level, which allowed her to see the cans as well as the animal's choice. During the experiment, the experimenter wore sunglasses so that the wolves could not see their gaze.

Table 1 | Detailed information on the subjects participating in this study.

Subject	Origin	Litter	Pack	Age	Sex	Participation			
						Train	Test	Time	Stone
Kaspar (Ka)	Game park Herberstein, Austria	1	1	3.5	Male	x	x	x	x
Shima (Sh)	Game park Herberstein, Austria	1	1	3.5	Female	x	x	x	x
Aragorn (Ar)	Game park, Herberstein, Austria	1	1	3.5	Male	x	x	x	x
Apache (Ap)	Zoo Basel, Switzerland	2	1	2.5	Male	x	x	x	x
Cherokee (Ch)	Zoo Basel, Switzerland	2	1	2.5	Male	x	x	x	p.p.
Nanuk (Na)	Tripple D Farm, Montana, USA	3	2	2.5	Male	x	x	x	p.p.
Yukon (Yu)	Tripple D Farm, Montana, USA	4	2	2.5	Female	x	x	x	x
Geronimo (Ge)	Tripple D Farm, Montana, USA	4	2	2.5	Male	x	x	x	x
Tatonga (Ta)	Tripple D Farm, Montana, USA	5	2	2.5	Female	x	x	x	x
Kenai (Ke)	Zoo, Canada	6	3	1.5	Male	x	n.p.	n.p.	n.p.
Wapi (Wa)	Zoo, Canada	6	3	1.5	male	x	x	x	x

Participation in the different parts of this study is included as "x" for participating, "p.p." for participating partly and "n.p." for not participating.

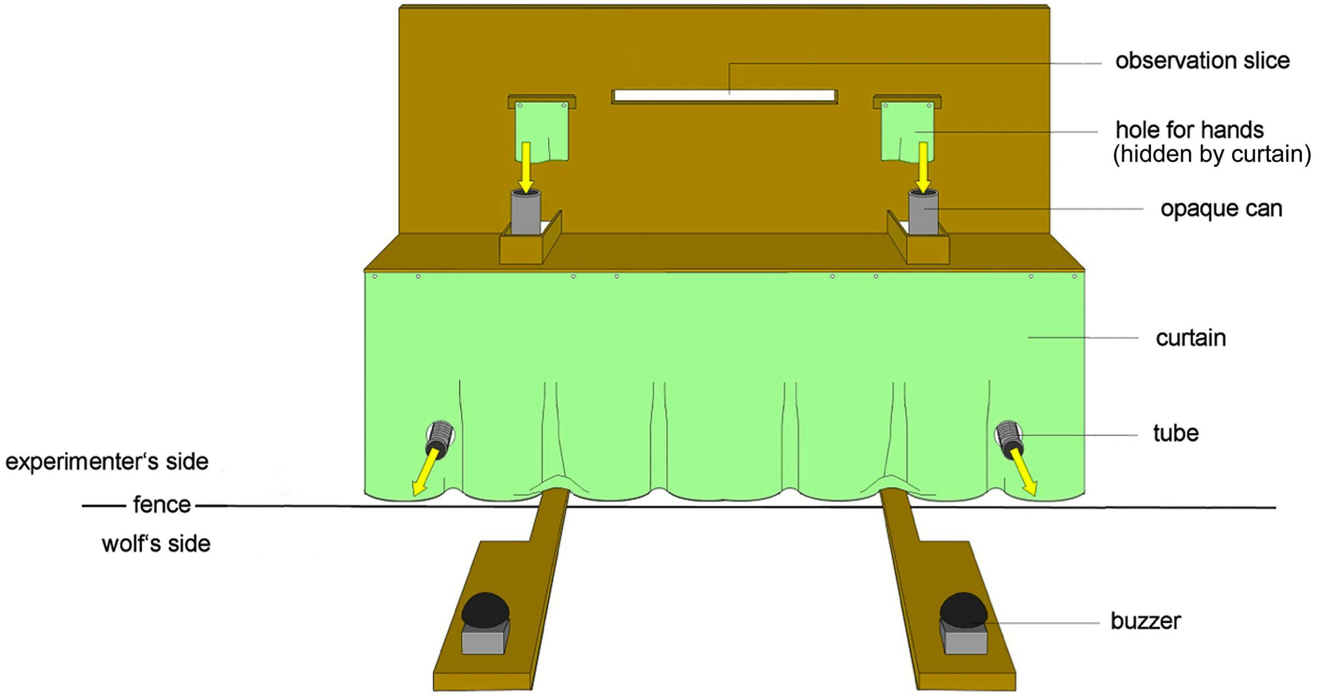

FIGURE 1 | The experimental set-up of the apparatus from the wolf's perspective. The draft shows the table, the buzzer and the opaque cans with the rewarding tubes, which are leading from the air lock into the testing enclosure.

On the wolf's side of the fence, under each tube, a wooden panel was placed with a buzzer fixed on it.

BASIC PROCEDURE

For the experiment, the subject was separated from its pack and moved into the testing enclosure. A trainer was present in the testing enclosure, where the animal could move around freely except during the experimental trials when the trainer was holding it on a collar about 1.5 m in front of the apparatus.

The experiment started after the experimenter had taken her position and picked the required amount of food (and stones) out of a bowl on her side of the table. Both filled, closed hands were inserted into the holes above the cans. We pseudorandomized the side on which the first item was inserted, with the restriction that both sides started equally often and that the same side did not start more than three times consecutively, so as to avoid any potential side preferences. One of the items from the hand (held by two fingers, the other items hidden in the closed palm) was presented in the direction of the wolf. After the wolf looked, the experimenter placed it either onto the table next to the can (*training level 2 + 3 + 5*) or into the opaque can (*training level 4*, *test*, *time control*, *and stone control*). If the wolf was looking in another direction the experimenter called it by name to attract its attention. This procedure (item-by-item) was then repeated until the first hand was empty and shown to the wolf. Then the items from the other hand were placed accordingly. When both empty hands had been shown to the wolf, the experimenter gave a signal to the trainer by saying "go."

Upon the signal, the wolf was released to make its choice. The wolves had been trained to step on the buzzer to provide an acoustic signal in order to clearly indicate their choice. In the test trials, however, a choice was regarded valid when the wolf either (1) used the buzzer, (2) stepped on the wooden panel to which the buzzer was attached to or (3) was touching the fence on the side of the can with its nose for at least 3 s. The variety of choices was necessary to avoid missing or misinterpreting the wolf's first choice by waiting too long for it to use solely the buzzer. In the test and in both controls, the wolf only received the chosen food if the choice was correct, while in the training phase rewarding depended on the level (see below for details). The trainer called the animal back after it was rewarded or saw that it did not get a reward.

Depending on the experimental phase (training, test, controls), the experimenter pulled out the plastic bar after a wolf's correct choice and thus released the reward that slid into the enclosure. If the items were placed on the table, the experimenter picked them up and inserted them into the can from where they could slide into the enclosure. When the wolf chose incorrectly, the experimenter retrieved the items from both sides.

Three professional animal trainers were involved in this experiment shaping the buzzer pressing behavior of each subject during the training phase and handling the wolves during the experiments. During the experiments, the trainers wore a baseball cap and looked down at their feet preventing them from seeing the placement of the food.

Cheese (sort: Gouda; 1 cm × 1 cm × 1 cm) was used to reward the animals to guarantee high motivation to work. For the controls (see below), black stones of comparable size were used. We conducted only one session per day with 1–2 days (test and control phase) elapsing between sessions.

DETAILED PROCEDURES

We conducted a training phase, a testing phase, and two control experiments (time and stone control; **Table 2**).

Training phase

The training phase was conducted to familiarize the animals with the apparatus and the procedure. It consisted of five steps: (1) buzzer training to teach the wolf how to use the experimental apparatus, (2) choosing the larger of two visible quantities (1 vs. 4) presented on the table, (3) discrimination between a visible piece of stone and a visible piece of cheese, (4) same as *step 3*, but now the food and stone were inserted into the opaque cans and thus were invisible during the choice and (5) choosing once again the larger of two visibly presented quantities (1 vs. 4) to assure that the wolves still chose the larger number after training *step 3 and 4.*

In *step 1*, the animals were trained using a clicker (operant conditioning with a secondary reinforcer) and dry dog food to push the buzzer with their paw. No table was present and the rewarding was done by hand. First, only one buzzer was available to train the animals how to operate it with their paws. After the wolves were able to push the buzzer on the command "touch" with the paw 10 times in a row, the second buzzer was introduced. *Step 1* was continued till the wolves could use both buzzers showing no side preference. That is pressing the buzzer on the side the trainer pointed to at least 10 times in a row in one session. The number of trials per day depended on the motivation and concentration of each animal and thus varied between sessions (range: 7–15).

In *step 2*, the wolves were trained to choose the larger of two quantities (four against one) by placing cheese pieces next to the opaque cans on the table in full view of the wolves. To avoid a situation in which the wolves would choose based on other potential factors like side preference or order of placement rather than quantity, we presented the four possible combinations ($R-1$ vs. 4 (= four pieces placed first on the right side, then one piece placed on the left side), $R-4$ vs. 1, $L-1$ vs. 4, $L-4$ vs. 1) in a randomized and predetermined order in each session. In *step 2*, we conducted eight trials per session if each choice was correct. However, if the subject made a mistake, the same combination was repeated until the animal chose the larger reward (correction trials) and thus the number of trials per session increased. The criterion to pass *step 2* was at least nine correct choices in the last 11 trials to assure that

Table 2 | Conditions of the experiment and criteria for the training steps.

Condition	Aim (criterion for each training step)	Items	*N*
Training step 1	Confident buzzer usage (10x sequentially per session)	Dry dog food	11
Training step 2	Making a choice (9/11 trials)	Cheese	11
Training step 3	Discrimination of stone and cheese (6/7 trials)	Cheese, stone	11
Training step 4	Introduction opaque can, stone vs. cheese (6/7 trials)	Cheese, stone	10
Training step 5	Repetition choice for more items (6/7 trials)	Cheese	10
Quantity test	Quantity discrimination	Cheese	10
Time control	Handling time adaption	Cheese, stones	10
Stone control	Dismissal of time and sound factor	Cheese, stones	10 (8)

One of the 11 animals did not reach the criterion of step 4 and, therefore, did not participate in the rest of the experiment. In the stone control 10 animals participated in three of the four sessions and eight of them participated in all four sessions.

the animals made correct choice at least twice in each of the four possible combinations.

In *step 3*, the wolves had to discriminate between one piece of cheese (ch) and one stone (st) that were placed on the table in full view. We conducted seven trials per session and the animals had to choose the cheese at least six times in one session in order to reach criterion. A milder criterion was used than in *step 2* to keep habituation to the presence of the stone at minimum, and thus, to avoid that the wolves learn to base their decision on discrimination of the stimuli instead of using cognitive processes (Stevens et al., 2007).

In *step 4*, we inserted the food and the stone into the opaque cans requiring the wolves to make a choice when neither cheese nor stone were visible. Each session consisted again of seven trials, and the same criterion was used as in *step 3*. In *step 3 and 4*, we always released the selected item into the enclosure to give the animals the opportunity to inspect the stone. The stones were collected by the trainer and handed over to the experimenter at the end of each trial.

Step 5 was similar to *step 2* with the only difference that no correction trials were conducted limiting each session to seven trials. The criterion was set at six correct choices in the last seven trials.

For each step, we counted the number of trials a wolf needed to reach the criterion (including the correction trials in *step 2*).

Testing phase and control experiments

Quantity discrimination test. Using the opaque cans, we tested whether the animals could also discriminate between the six pairs of quantities (1 vs. 2, 1 vs. 3, 1 vs. 4, 2 vs. 4, 2 vs. 3, 3 vs. 4) not tested in the training phase. Depending on the combination, the distance and the ratio between the two presented quantities varied. Randomizing the side and the placing order, each pair can be presented in four different ways resulting in 24 conditions. All of these conditions were repeated twice in a total of eight test sessions of six trials each.

Time and stone control. We conducted two control experiments after the quantity discrimination test to stepwise exclude further factors that might have had an influence on the test performance. Each control experiment consisted of four sessions of six trials each. Both controls contained the following three of the six quantity pairs used in the test: 1 vs. 2, 1 vs. 4, 2 vs. 3. Accordingly, we had a set with a small distance and an intermediate ratio between sets (1 vs. 2), a set containing a large distance and a small ratio between both sets (1 vs. 4) and a set with a large ratio and an intermediate distance (2 vs. 3). The first control was conducted to investigate whether the wolves solved the discrimination task by actually comparing the food quantities or, alternatively, by using the time interval it took to insert the different number of food pieces into the cans (time control). Accordingly, we added stones to the smaller quantity of cheese pieces until both cans contained the same number of items – that is the handling time was the same on both sides (**Figure 2**). However, since the stones were always added last to the side with the fewer pieces of cheese, it was still possible that the animals solved this first control experiment by avoiding the (sound of the) stone(s). To exclude this opportunity we added an extra stone to both sides in the stone control experiment (e.g., 4 vs. 1: one can contained four pieces of cheese and one stone and the other can containing one piece of cheese and four stones; **Figure 3**).

FIGURE 2 | Illustration of the task 4 vs. 1 in *Time control*.

FIGURE 3 | Illustration of the task 4 vs. 1 in *Stone control*.

Each session of the test and both control experiments were followed by a so-called concentration control. The latter consisted of four trials in which only one piece of cheese was inserted into one of the two cans randomizing the sides. This concentration control was conducted to ensure that the animal paid attention to the experiment and did not solely pick a side randomly. All of the participating animals performed without a single mistake in the concentration controls of the test and both control experiments.

DATA ANALYSIS

We first examined whether non-quantity factors influenced the performance of the animals in the testing phase or control experiments by calculating non-linear mixed effect models (nlme) using a binomial distribution. Accordingly, we analyzed whether the wolves' choices for the cans were influenced by the side with the larger quantity of food items ("side_larger quantity), by the order of placing ("order_first" and "order_second"; large amount first or second) or the session ("sess"; 1–8). To test for side bias, bias for side of first presentation and changes in performance across all trials we compared the data to chance level with a one-sample t-test each. Provided those non-quantity factors had no influence, they were excluded from further analyses. In the main analyses we examined if the animals' choice of the larger quantity depended on the ratio of the two numbers presented ("ratio"; 0.25, 0.33, 0.5, 0.66, 0.75). Wolf identity and the sessions were treated as random factors in the models. The data analysis was repeated excluding the combinations (1 vs. 4 and 4 vs. 1), since these were extensively used in the training phase. For investigating the performance of each individual (No. of correct choices) in the test, we additionally conducted a binomial test. When an individual wolf did not choose the larger quantity above chance, we analyzed whether its performance, respectively its success rate ("choice_larger_quantity," correct choice of the side with the larger quantity of cheese), was influenced by the order of placing, side of larger quantity and if it varied across the sessions. The control experiments were analyzed with the same model as the quantity discrimination test.

To control for training effects in all three tests we calculated a nlme using a binomial distribution to investigate whether the performance was influenced by the number of training trials ("train," overall number of trials to complete all training sessions). Treatment ("treatment_test,""treatment_time_control," and "treatment_stone_control"), wolf identity and the sessions were included as random factors. The wolves might have learned also across the test and control trials, predicting an increasing performance ("choice_larger_quantity") from the quantity discrimination test to time control and stone control. We tested this by running a nlme using a Poisson distribution and analyzing whether the choice was influenced by the treatment (*test*, *time control*, *stone control*), the session (1–8), or trial (*test:* 1–6, *time control*, *stone control*: 1–4).

The data were analyzed using the statistical program *R* (version 2.14.1). Results are given for two-tailed tests and alpha was set at 0.05. Trends are reported for $0.1 < p < 0.05$.

RESULTS

TRAINING PHASE

Ten of the 11 wolves participating in this study passed all training steps and were tested in the quantity discrimination test. The subjects needed between 150 and 404 trials to pass the training and proceed to the test phase (**Table 3**). One wolf (Kenai) did not reach the criterion of *step 3* (discrimination of stone vs. cheese, visible) and, therefore, did not proceed to the next step.

TESTING PHASE

Non-quantity factors

The animals' choices in the test were influenced neither by the placing order (large amount first or second; NLMEorder: $t_{394} = -0.07$, $p = 0.93$) nor the session (NLMEsess: $t_{69} = -0.38$; $p = 0.70$). Further on, although the wolves chose the right can more often than the left can if the larger amount of cheese was placed second (NLMEorder: $t_{396} = 2.814$, $p = 0.005$), no side bias occurred (one-sample t-test: $t_9 = -0.64$, $p = 0.53$).

In the time and stone control, we again found no differences in performance across sessions (NLMEsess: time control: $t_{29} = -1.10$; $p = 0.27$; stone control: $t_{27} = 0.76$; $p = 0.45$), and the one-sample t-test revealed no side bias in either control (time control: $t_9 = -0.60$, $p = 0.56$, stone control: $t_9 = 0.11$, $p = 0.91$). While the placing order (large amount first or second) had no significant effect on the animal's choices in the time control (NLMEorder: $t_{196} = 0.19$, $p = 0.84$), it had an influence in the stone control (NLMEside_larger_quantity $_\times$ order: $t_{186} = 2.401$, $p = 0.017$), suggesting that the wolves chose more often the larger quantity if it was placed second. However, in both situations (larger quantity being placed first or second) they chose the larger quantity more often than the smaller one (NLMEside_larger_quantity: placed first: $t_{77} = 2.425$; $p = 0.018$; placed second: $t_{72} = 4.980$; $p < 0.001$).

Quantity discrimination test

Overall the wolves chose the side with the larger quantity above chance in 70.21% of the cases (337 of 480 trials; **Table 3**; one-sample t-test: $t_9 = 8.881$, $p < 0.001$). After excluding the combinations 1 vs. 4 used extensively in the training, we found that the wolves still chose more often the larger quantity in 69% of the cases (276 of 400 trials; one-sample t-test: $t_9 = 8.249$, $p < 0.001$). There was a tendency for improved performance as the ratio between sets got lower (NLME$_{\text{ratio}}$: $t_{471} = -1.71$, $p = 0.08$; **Figure 4**).

At the individual level, nine out of the 10 wolves picked the side with more pieces of cheese above chance. The wolf Nanuk had the most correct choices with 39 of 48 trials choosing the larger quantity (81.25%; binomial test: $p = < 0.001$). One wolf (Kaspar) was not choosing the big amount more often than the small one (binomial test: $p = 0.19$). However, his choice to take the larger quantity depended on whether the larger quantity was placed first or second (NLMEorder: $t_{39} = -2.097$, $p = 0.043$).

Table 3 | Number of trials every subject needed to reach the next step (*step 1–5*) in the training phase.

Subject	*Step 1*	*Step 2*	*Step 3*	*Step 4*	*Step 5*	Overall
Apache	85	14	7	7	113	226
Aragorn	115	16	14	21	166	332
Cherokee	107	11	7	6	131	262
Geronimo	70	7	7	6	90	180
Kaspar	106	12	21	6	145	290
Kenai	72	22	56	n.p.	n.p.	dism.
Nanuk	132	49	7	14	202	404
Shima	91	10	7	6	114	228
Tatonga	99	7	7	21	134	268
Wapi	106	11	21	7	145	290
Yukon	47	15	6	7	75	150

The "n.p." stands for steps in which a subject was not participating because it did not reach the criterion. Not passing a step leads to not proceeding in the quantity discrimination test and being dismissed for the rest of the study (dism.).

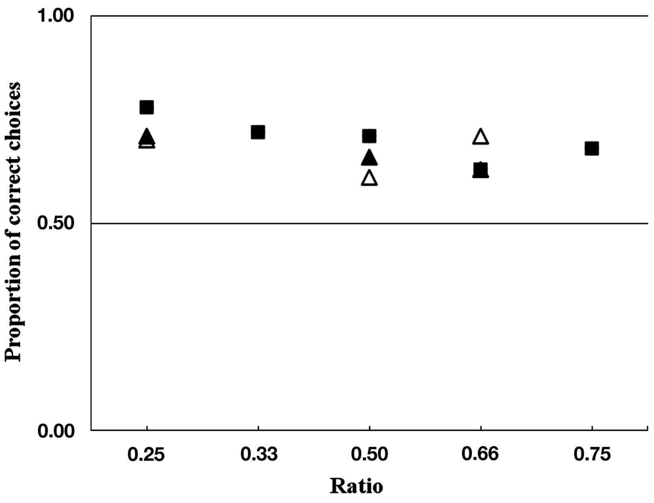

FIGURE 4 | Performance of the wolves across all conditions (■ = quantity test, ▲ = time control, △ = stone control) shown as proportion of correct choices for the given ratios. The ratio 0.33 and 0.75 were only present in the quantity test.

Time control and stone control

With 160 of 240 (66.67%) correct choices in the time control, the group chose more often the side with the larger amount (one-sample t-test: $t_9 = 5.164$, $p = 0.001$). The performance of the wolves was not influenced by the ratio between the two presented sets (NLME$_{\text{ratio\_0.5}}$: $t_{198} = -0.73$, $p = 0.46$; $_{\text{ratio\_0.066}}$: $t_{198} = -1.11$, $p = 0.26$). At the individual level, in the time control two wolves chose more often the side with more pieces of cheese (binomial test: Apache: $p < 0.001$; Aragorn: $p = 0.023$) and two other wolves showed a tendency to do so (binomial test: Geronimo: $p = 0.06$; Yukon: $p = 0.06$).

In the stone control, the wolves chose the larger quantity of cheese in 67.11% of the trials (135 out of 228 trials; one-sample t-test: $t_9 = 4.391$, $p = 0.002$). We found that the wolves made their choice independent from the ratio between the two sets (NLME$_{\text{ratio\_0.5}}$: $t_{187} = -0.13$, $p = 0.17$; $_{\text{ratio\_0.66}}$: $t_{187} = 0.16$, $p = 0.87$; **Figure 4**). At the individual level, three animals chose significantly more often the larger amount of cheese (binomial tests: Apache: $p = 0.002$; Aragorn: $p = 0.023$, Tatonga: $p = 0.007$), and two others showed a tendency for the larger quantity (binomial test: Nanuk: $p = 0.096$; Geronimo: $p = 0.064$).

"TRAINING EFFECT" AND "LEARNING EFFECT"

The number of training trials needed to reach the testing phase did not have any influence on the frequency of choosing the larger quantity (NLMEtrain, $t_8 = 1.02$, $p = 0.33$). This pattern ("Training effect") did not differ between the tests and control sessions (NLMEtrain $\times$ treatment_test: $t_{16} = 1.47$, $p = 0.16$; train $\times$ treatment_control: $t_{16} = 0.42$, $p = 0.67$). Regarding "learning effect" throughout the testing periods, we found that the wolves' performance did not change (NLMEsess: $t_{936} = -1.16$, $p = 0.25$). Furthermore, the wolves' performances did not differ between the test and control sessions (NLMEsess $\times$ treatment_test: $t_{143} = 0.93$, $p = 0.35$; sess $\times$ treatment_control2: $t_{143} = 1.39$, $p = 0.16$; **Figure 5**).

DISCUSSION

We found that the wolves' choices were not influenced by the side and order of placement or the session, suggesting that the wolves based their choice on the representation of two food quantities. Nine of 10 wolves performed significantly above chance also at the individual level. Two additional controls assured that the animals did not use the handling time (time control) or the sound of the stone(s; stone control) as discriminative stimuli by stepwise excluding these factors. In the controls, three animals still chose significantly more often the larger quantity of cheese and two other wolves showed a tendency to do so.

In Ward and Smuts (2007) study, two dogs successfully discriminated two presented quantities even if they were not visible at the time of choice. Baker et al. (2011) showed that coyotes behaved similarly to dogs, but could only discriminate correctly between two quantities if the sets were visible at the moment of choice. Our paradigm of presenting the food items invisibly controlled for some of the confounding properties (volume, surface area, pattern recognition) that were not controlled for in the coyote study. Moreover, by adding the first control situation, we equalized not just the handling time, but also the total amount of items that were inserted into each can, making it much harder for the animals to choose based on properties other than the quantity of food. However, it is theoretically still possible that the animals made their choice based on the total amount of cheese that was added to each can, assuming that they left the inedible stones out from their representation of the total amount of food.

The wolves' performance did not improve with decreasing ratio of the two sets, and thus did not confirm to Weber's law (Gallistel and Gelman, 2000). However, in the testing phase the wolves showed a tendency to improve in discriminating both sets when the ratio was decreasing. In previous studies, two dogs failed to discriminate correctly in the 3 vs. 4 task (ratio = 0.75) and only one of them was able to discriminate 2 vs. 3 (ratio = 0.66; when not visible at the moment of choice; Ward and Smuts, 2007). Moreover, coyotes experienced trouble discriminating the visible sets of 2 vs. 3 and 3 vs. 4 at the group level, whereas they reliably chose the larger of two presented sets when the ratio decreased below 0.5 (e.g., 1 vs. 4., 1 vs. 3, and 2 vs. 5). Those results are in support of Weber's law and suggest that the performance of canines might decrease or even break down for high ratios (ratio > 0.5). On the other hand, theoretically Weber's law is mainly connected to larger set sizes (above four items). That is, it is interesting that these previous canine studies found limitations in the animals' performance for small quantities. The wolves in our study successfully discriminated all combinations above chance, with a slight tendency for being better with sets of a smaller ratio in the test. Interestingly, however, in both controls the set ratio had no influence on the performance. A possible explanation might be that the wolves used the different handling times or the total amount of all items as indices for the larger quantity in the first test condition whereas they could rely only on food quantity in the control conditions. This would mean that instead of benefiting from multiple sources of information, the wolves could profit

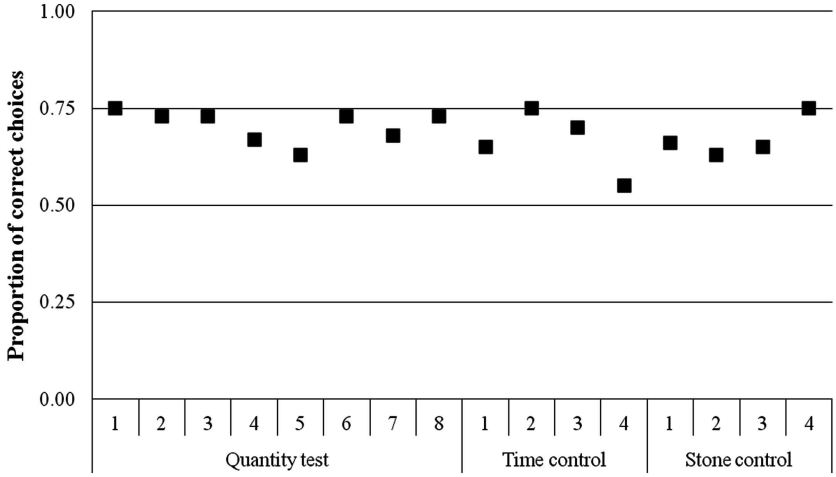

FIGURE 5 | Performance of the wolves given as the proportion of correct choices for every session across the different experimental conditions (Quantity test: 1–8, Time control: 1–4, Stone control: 1–4).

more from clear and unequivocal information provided in the control conditions.

Although the performance of the wolves was not influenced by the set ratio in the control conditions, it is not possible to confirm which model explains the numerical skills of wolves (small quantities: object-file model' (e.g., Kahneman et al., 1992; Hauser et al., 2000; large quantities conforming to Weber's law: accumulator model (e.g., Meck and Church, 1983; Gallistel and Gelman, 2000). To confirm which model would be better suited one would need to demonstrate similar results with higher ratios and larger set sizes (e.g., one to seven pieces of cheese). However, expanding the set size could prove difficult because based on the experience in this study, the wolves' concentration decreased with increasing number of items. In the *stone control* an extra stone was added to both sides and, therefore, the total number of items on each side was increased to five pieces of cheese and stones. Some of the wolves seemed to get over-excited or even frustrated (increased locomotion: strong pulling toward the table or jumping around) because of the longer handling time, which might have an influence on the performance if even bigger numbers are used.

Studies on other species that used a comparably complex method could show that both monkeys (Beran, 2007) and great apes (Hanus and Call, 2007) are able to discriminate quantities that are presented item-by-item depending on the ratio between two sets. In both studies they tested different combinations between one and 10 items and found that the animals' performance decreased with increasing ratio. This is in curious contrast with our results on the wolves. Beran (2007) tested two rhesus monkeys and found that the animals failed in discriminating high ratios (>0.83). Further, both animals failed to discriminate sets of a ratio of 0.6 and only one animal was able to choose the larger quantity when the ratio was 0.75. The latter conforms to our 3 vs. 4 combination that the wolves were able to discriminate above chance. Additionally, Beran (2007) showed that when the total set presentation could not be used as a cue (e.g., by varying the presentation time of smaller and larger sets) then the animals' performance fell to chance level. In contrast to this, in our wolf study, we equalized the duration by the addition of stones, excluding this potential non-numerical influence, and still found that the wolves performed above chance.

Hanus and Call (2007) tested different great apes and showed that after item-by-item presentation, at group level all species except bonobos (but overall only 26% of the subjects) selected the larger quantity in low quantity combinations (up to six) in accordance with Weber's law. However, Hanus and Call (2007) did not conduct any control experiments to exclude non-numerical influences such as duration of handling. Therefore, it can not be excluded that the performance of the subjects relied on these cues, and it is possible that – similarly to the wolves – they would have performed better if they could discriminate the combinations purely based on food quantities.

In summary, our study showed that wolves are able to make quantitative judgments even when alternative strategies such as paying attention to non-numerical properties such as the surface area or time and total amount are ruled out. To determine whether and when their quantity discrimination conforms to Weber's law and to elucidate which model describes the numerical skill of wolves best, studies using larger quantities are needed. Finally, to compare their performance with that of other species, better controlled comparative experiments are necessary.

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Inherently analog quantity representations in olive baboons (*Papio anubis*)

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Strong evidence indicates that non-human primates possess a numerical representation system, but the inherent nature of that system is still debated. Two cognitive mechanisms have been proposed to account for non-human primate numerical performance: (1) a discrete object-file system limited to quantities <4, and (2) an analog system which represents quantities comparatively but is limited by the ratio between two quantities. To test the underlying nature of non-human primate quantification, we asked eight experiment-naive olive baboons (*Papio anubis*) to discriminate between number pairs containing small (<4), large (>4), or span (small vs. large) numbers of food items presented simultaneously or sequentially. The prediction from the object-file hypothesis is that baboons will only accurately choose the larger quantity in small pairs, but not large or span pairs. Conversely, the analog system predicts that baboons will be successful with all numbers, and that success will be dependent on numerical ratio. We found that baboons successfully discriminated all pair types at above chance levels. In addition, performance significantly correlated with the ratio between the numerical values. Although performance was better for simultaneous trials than sequential trials, evidence favoring analog numerical representation emerged from both conditions, and was present even in the first exposure to number pairs. Together, these data favor the interpretation that a single, coherent analog representation system underlies spontaneous quantitative abilities in primates.

Keywords: numerosity, primates, baboons, object-file, analog magnitude

INTRODUCTION

From Euclid, who said, "The laws of nature are but the mathematical thoughts of God," to the modern mathematical scholar Paul Dirac who stated, "If there is a God, he's a great mathematician," great thinkers have often associated abstract numerical thought with the divine. However, in contrast to human intuitions, cognitive science has demonstrated that the seemingly supernatural human capacity for symbolic mathematical thought – responsible for scientific measurement, architectural design, and economic exchange – likely arises from a primitive number representation system (or perhaps systems) that appear in creatures like beasts and babies. Evolutionarily and developmentally primitive numerical systems are well-documented. Non-linguistic infants can reason about small and large numerosities (for reviews on the extensive literature, see Feigenson et al., 2004; Cordes and Brannon, 2008), as can many non-human animals (Primates: e.g., Brannon and Terrace, 1998, 2000; Hauser et al., 2000; Beran and Rumbaugh, 2001; Cantlon and Brannon, 2006, 2007; Other mammals: e.g., Jaakkola et al., 2005; Ward and Smuts, 2007; Uller and Lewis, 2009; Birds: e.g., Pepperberg, 2006; Rugani et al., 2007, 2008, 2010; Amphibians: e.g., Uller et al., 2003; Fish: e.g., Agrillo et al., 2007). However, the precise nature of the representations underlying infant vs. animal quantity judgments has been a subject of discussion in the numerical cognition literature.

Non-linguistic numerical cognition in human infants is hypothesized to involve two different mechanisms: a precise object-file system and an analog magnitude system. The object-file system is thought to be an aspect of working memory, which individuates, enumerates, and tracks objects, and so, is inherently capable of tracking the number of objects (Trick and Pylyshyn, 1993, 1994). As working memory is limited to tracking three or four objects, the signature of the object-file system as a number representation system is the failure of an individual to discriminate between two quantities if at least one of those quantities is larger than three (or four). The analog system also has a set of signatures that can be used to detect its functioning (Dehaene, 1997). Unlike the object-file system, the analog system is (in principle) capable of representing any number. Instead of bearing a capacity limit, the analog system is limited by the ratio of two compared quantities, with crude ratios being more distinguishable than fine ratios. For example, two numbers that have a crude ratio, such as 1 and 4 (0.25 ratio) will be easily discriminated, while two numbers with a fine ratio, such as 3 and 4 (0.75 ratio), may not be discriminated. The magnitudes are psychologically spaced either logarithmically or linearly with scalar variability, and because of this, the numerical ratio (and not the absolute numerical value) is the critical variable that determines whether two quantities can be discriminated in the analog system (e.g., Gallistel and Gelman, 1992; Cantlon et al., 2009). The proportion difference in quantity needed to successfully discriminate between two quantities is called the Weber fraction. In summary, the analog system is limited by ratio but provides a larger range of numerical values that can be represented whereas the object-file system is precise, but limited to representing only very small quantities.

The existences of the object-file system and the analog system are not controversial. The role of the object-file system in tracking objects is well established. The relevant research questions are if, when, and how the object-file system is spontaneously recruited to represent quantity. Infants appear to use both an analog and an object-file system to compare quantities spontaneously. With small numbers of objects (<4), infants are capable of making correct numerical judgments no matter the ratio between sets (Feigenson et al., 2002; Feigenson and Carey, 2003). In contrast, when infants judge larger sets, accurate discrimination is a function of ratio (Xu and Spelke, 2000; Xu, 2003; Lipton and Spelke, 2004; Xu and Arriaga, 2007). Most importantly, studies have found that when infants and toddlers are required to compare a small vs. large set on a given trial, their performance is random (Feigenson and Carey, 2005; Le Corre and Carey, 2007; but see Cordes and Brannon, 2009; Cantlon et al., 2010). Researchers argue that the comparison of a small and large value cannot be completed because each numerical system handles just one type of number (small or large) and the two systems do not communicate (Feigenson et al., 2002; Feigenson and Carey, 2003). The finding of failures of infants to compare small and large numbers is taken as further evidence of the presence of two distinct numerical systems.

The pattern of success and failure observed in infants is not observed in adults. When adults are asked to judge quantities while their verbal abilities are occupied by an articulatory suppression task, their number discrimination behavior exhibits the ratio signature of the analog system for small and large numbers alike (Whalen et al., 1999; Cordes et al., 2001; Barth et al., 2003; Beran et al., 2006). Adults can successfully discriminate small (<4) from large (>3) sets in the same comparison, unlike infants. Likely, the analog system is the primary non-linguistic number representation system in adults, although the object-file mechanism might be recruited for quantitative judgments under limited conditions (Trick and Pylyshyn, 1993, 1994). Current evidence suggests that the adult pattern of predominantly analog numerical representation emerges by at least 3 or 4 years of age (Halberda and Feigenson, 2008; Cantlon et al., 2010).

The data from human infants and adults raise the question of whether the "two systems" view of quantity development also characterized the evolution of numerical cognition. Comparative studies of numerical cognition with non-human animals have yielded mixed results on the fundamental nature of number cognition in non-humans. In one study, Hauser et al. (2000) presented experiment-naive rhesus macaques with differing quantities of apple slices dropped sequentially into two boxes. The macaques chose the box with the larger amount in 1 vs. 2, 2 vs. 3, 3 vs. 4, and 3 vs. 5 contrasts, but failed with larger numbers such as 4 vs. 5 and span contrasts such as 3 vs. 8. Given these data, these researchers concluded that only the object-file system is spontaneously available to rhesus macaques, a position that was supported by subsequent testing with the same population (Hauser and Carey, 2003; Barner et al., 2008; Wood et al., 2008). However, the majority of other non-human number studies have not upheld these results. For instance, Beran (2007) found evidence of the analog system in rhesus macaques with a joystick task that was highly similar to Hauser's design. Subjects watched as an image of a hand appeared to drop between 1 and 10 blocks into two boxes onscreen. Macaques succeeded at choosing the box with the larger quantity of blocks at above chance levels with both small and large set sizes, with success on each contrast being a function of numerical ratio. In critical test trials, Beran's macaques also succeeded when contrasts involved one small set (<4) and one large set (>4), suggesting that a single-system, the analog system, was responsible for all number representation in those macaques. Other numerical studies have also supported the analog magnitude hypothesis in multiple primate species (Brannon and Terrace, 1998, 2000; Beran and Rumbaugh, 2001; Smith et al., 2003; Beran and Beran, 2004; Judge et al., 2005; Brannon et al., 2006; Cantlon and Brannon, 2006, 2007) using a variety of testing paradigms. Those data also implicate the analog magnitude system as the core mechanism of number representation in primates.

Growing evidence suggests that the analog magnitude system is the evolutionarily primitive number system shared across animal lineages. Less clear is whether the analog magnitude system is the primary mechanism that non-human animals recruit *spontaneously* to solve quantity problems. There is already some evidence that apes spontaneously show ratio effects in their numerical performance (Beran, 2001, 2004; Beran and Beran, 2004; Hanus and Call, 2007). Although those studies did not compare the animals' performance on small vs. large values during first exposures, the rapid emergence of ratio effects in performance supports the analog magnitude hypothesis. Currently, most studies concluding that primates primarily rely on the analog magnitude system have been conducted with subjects that have long histories of exposure to experimental methods (e.g., Brannon and Terrace, 1998; Smith et al., 2003; Cantlon and Brannon, 2006, 2007; Beran, 2007; Beran et al., 2008). It is sometimes argued that such exposure could influence the strategies that subjects recruit to solve problems. For example, Hauser et al. (2000) argued that experiments that involve extensive training could allow animals to acquire the cognitive abilities necessary for solving numerical tasks. In the Beran (2007) study described above, the subjects had participated in several previous numerical cognition studies where they received thousands of trials of experience with numerical discriminations. Thus, there remains the possibility that the training period associated with the laboratory experiments caused the discrepancy in results between the laboratory experiments (e.g., Beran, 2007) and the naturalistic experiments (Hauser et al., 2000).

In the current study, we tested quantity discrimination in experiment-naive olive baboons using a naturalistic food choice task that is similar to the Hauser et al. (2000) and Beran (2007) designs but without the extensive training regimen of Beran (2007). In the current experiment, baboons were presented with two sets of one to eight peanuts placed simultaneously or sequentially into two of three cups, and were rewarded with the contents of the cup they chose. The baboon subjects were experiment-naive, having never participated in psychological experiments. Together, these design elements allowed us to test for the spontaneous quantitative representations that baboons use naturally, during food choices.

In Experiment 1, we examined the spontaneous quantity representations of eight olive baboons by analyzing their quantity choices on first exposure to each number pair. Subjects compared numerical values in pairs of both small (<5), both large (>4), and span sets (one small and one large value). This range of sets allowed us to test the object-file and analog magnitude hypotheses. If the baboons are successful only with contrasts of small sets, then the object-file hypothesis will be supported. If the baboons are successful with small and large, but not span sets, we can conclude that both the object-file and the analog magnitude systems are engaged by baboons, as in human infants, but that the object-file and analog magnitude representations are incompatible resulting in failure on span sets. Finally, prior research with infants found that infants succeeded at discriminating large and span pairs in simultaneous but not sequential presentations (Feigenson et al., 2002). The argument is that the object-file mechanism is selectively recruited during sequential presentations due to its primary function as an object tracking system. Evidence for object-file-based quantity judgments in monkeys would thus include failures on both large and span pairs only for sequential presentations. However, if we find that our subjects can accurately make choices no matter the set size, and that accuracy on a particular numerical pairing is explained by numerical ratio, then we will have evidence that the analog magnitude system is the dominant mechanism for number representation in baboons, similar to human adults. In addition to testing these hypotheses, we were also interested in the effects of experience on primate number representation. In Experiment 2, we extended the testing of two baboons that participated in Experiment 1 for additional sessions, and analyzed changes in their sensitivity to numerical discriminations over time. The results we report aim to further our understanding of the fundamental nature of numerical representation in non-human animals.

EXPERIMENT 1

MATERIALS AND METHODS

Subjects

Eight adult olive baboons (4–14 years old, three male) at the Seneca Park Zoo in Rochester, NY, USA served as subjects in this experiment. These baboons are housed as a social group and have access to large indoor and outdoor enclosures. In addition, these enclosures have multiple compartments that allow us to temporarily segregate one baboon from the rest of the troop for testing purposes. Primate chow and fresh fruits and vegetables are provided every morning, and water is available *ad libitum.* Prior to these experiments, subjects had no experience with cognitive testing. The first experimental experience of these baboons was during the preparation phase of this experiment which trained subjects to choose the cup containing occluded food vs. two empty cups. In the preparation phase task, baboons were trained to use the apparatus by tracking a 1/2-grape hidden below one of three metal compote cups, and were rewarded for touching the port corresponding to the hidden food. Subjects required less than one session to choose the baited cup. Immediately following the preparation phase, the baboons were tested with the numerical food choice discriminations described below. Work with these subjects was approved by the Institutional Animal Care and Use Committee of the University of Rochester.

Apparatus

The apparatus consisted of a small and short rectangular table (75 cm long × 35 cm deep × 17 cm high) that was a comfortable height for a seated baboon (**Figure 1**). One long side of the table top was open so that an experimenter could work the apparatus, but the other three sides were shielded by plexiglass (30 cm high) to prevent baboons from interacting with the apparatus until the appropriate time. When in use, the long side of plexiglass was pushed flush with the mesh of an enclosure, a subject sat behind the plexiglass (and the mesh of the enclosure), and an experimenter sat opposite the subject. There were three equally spaced ports (2.5 cm diameter) in the plexiglass that subjects could use to indicate their choices.

All experimental manipulations were conducted on a sliding panel (75 cm long × 17 cm deep) that sat atop the table. The purpose of this panel, which was the same length as the table, but only half as deep, was to control a subject's access to the experiment until the appropriate time. When the panel was close to the experimenter, the subject did not have access to the experimental items, however, when the panel was pushed forward, toward the subject, the subject could reach through a port in the plexiglass and indicate her choice. The contents of the panel were three identical, opaque, cardstock cylinders, placed upright on a circular end, each in front of one of the ports in the plexiglass shield. The cylinders were open on both circular ends so that the experimenter could drop items into a cylinder and also lift a cylinder up, leaving the contents of a cylinder on the panel. Once items were dropped into the cylinders the items were hidden from a subject. The items to be enumerated were unshelled half peanuts.

PROCEDURE AND DESIGN

General procedure

Each session was conducted by two experimenters. One experimenter worked the apparatus, while a second experimenter recorded the choices made by the subject, monitored the first experimenter for trial accuracy, and also operated a video camera which was used to record each session. Sessions were conducted when a subject could be temporarily isolated from the troop in an enclosure. Individuals were tested between one and three times a week.

Before testing began, the experimenters set up the apparatus: the plexiglass side of the table was placed flush with the subject's enclosure, the sliding panel was placed on the experimenter's side of the table, the three cylinders were set in place on the panel, and one experimenter sat opposite the subject. A trial could only be initiated if the subject was seated at and attentive to the apparatus. To initiate a trial, an experimenter showed the subject one or more peanuts; this was done by displaying peanuts in the palms of one or both hands, about 30 cm from the subject and above the experimental panel (**Figure 1A**). Half of all trials were *simultaneous condition* trials, in which the two number sets to be compared were presented simultaneously, one in each hand. For example,

FIGURE 1 | The apparatus for Experiments 1 and 2. The apparatus consisted of a short and small table, open on one side to the experimenter, and shielded by plexiglass on the subject's side. The table was pushed flush with the subject's enclosure for use. **(A)** To initiate a trial, the experimenter showed a subject a quantity of reward in her hand(s) (simultaneous condition shown). **(B)** The reward(s) were placed into opaque cylinders. **(C)** The panel was pushed forward and the subject indicated his choice by pointing to a cylinder. **(D)** The subject received the reward he selected.

if the subject was to be tested on the contrast 3 vs. 6 items, the experimenter would have three peanuts in the palm of one hand and six peanuts in the palm of the other hand. The experimenter showed these options to the subject for approximately 2 s, after which the experimenter simultaneously placed the contents of each hand into its own cylinder (**Figure 1B**). In doing so, the experimenter touched both cylinders in the same way and for an equal amount of time. The entire process of peanut selection, presentation, and placing it in a cylinder took approximately 4 s. The remaining trials were the *sequential condition* trials, in which only one peanut was presented at a time. Each peanut was presented to the subject for approximately 2 s and then placed into a cylinder. For example, if the experimenter was testing the numerical pair 3 vs. 6, the first three peanuts presented were baited into one cylinder one-at-a-time, and the following six peanuts were then baited into a second cylinder one-at-a-time. Again, the experimenter was careful to touch the cylinders in the same way and for the same amount of time. To ensure that subjects were not basing their choices on the spatial location of the sets, the larger and smaller numerical values were equally likely to appear in any one of the three cylinders across the session. Note, that although there were always three cylinders on the board, only two of these cylinders were baited with food on each trial. The presence of the third cylinder allowed us to monitor subjects' understanding of the general task requirement that only baited cups should be chosen. Subjects almost never selected the empty cylinder (4% of sequential and 3% of simultaneous trials) indicating that they understood the task.

After the cylinders had been baited with peanuts, the panel was pushed forward and the subject was allowed to make a choice from among the three cylinders (**Figure 1C**). Experimenters did not look at the cups after baiting until after the subject indicated their choice. The subject indicated its choice by poking its finger through the port in front of the desired cylinder. Then, the experimenter removed the cylinder from over the desired food, and the food reward was fed, one peanut at a time, to the subject through the same port (**Figure 1D**). In the case that there was no food reward under the chosen cylinder, the subject received no reward. When the subject had received the entirety of its reward, the experimenter removed the other two cylinders from the panel, revealing their contents. The experimenter removed the reward not chosen. Once all peanuts were removed from the board, the experimenter pulled the panel back to her side of the apparatus, and reset the board. The next trial was initiated. This procedure was used throughout the training and testing phases.

Training

In the training phase, we exposed the subjects only to the numerical comparison 1 vs. 2, presented both simultaneously and sequentially. Subjects were given multiple sessions until they chose the larger reward set at above chance levels within a single session as determined by a cumulative binomial analysis (threshold = 24/36 correct). Each session consisted of 36 trials; these trials were counterbalanced for baiting locations, simultaneous vs. sequential conditions, and in the case of sequential trials, for which number set was baited first. Progress through the session was closely monitored. If a gap of 5 min occurred between two trials due to subject inattention, the session was terminated, and training resumed the next time the subject was available. Terminated sessions were rare and excluded from analyses. Once the subject passed the training criterion they immediately began the testing phase of the experiment. Subjects needed 1.5 sessions on average (54 trials) to reach our criterion.

Testing

Testing was conducted over 54 total test trials, across two 30-min sessions. The 27 different number pairs ranging from 1 to 8 items were tested (all possible pairs excluding 1 vs. 2 which was the training pair), with each number pair tested once in sequential and once in simultaneous presentation. The beginning of each testing session consisted of a warm-up of four 1 vs. 2 trials (two simultaneous, two sequential) to ensure the subject was oriented to the task. Two additional trials of 1 vs. 2 (one sequential, one simultaneous) were tested in each session but those trials were not analyzed as 1 vs. 2 was the training and warm-up pair. If the subject failed more than half of these first trials, testing with that subject was terminated for the day. The order of the test trials was randomized within and between subjects. Also, as in training, baiting locations, simultaneous vs. sequential conditions, and in the case of sequential trials, which baited first, were randomized. In addition, pair size, presentation type, and location of the larger quantity were never repeated on more than three consecutive trials. If a gap of

5 min occurred between two trials due to subject inattention, the session was stopped, and the remaining trials were resumed after a warm-up during the next testing day.

Data analysis

Data were coded and analyzed by an independent observer who coded responses from the recorded video files. Weber fractions were calculated using methods reported in Cantlon and Brannon (2006).

RESULTS

Training

Subjects took an average of 1.5 sessions to reach the training criterion of above-chance performance within a single session on 1 vs. 2 numerical comparisons according to a binomial test (range = 1–2 sessions).

Testing

Seven monkeys completed all 54 trials of testing, the eighth completed 21 of 27 sequential trials and 22 of 27 simultaneous trials. As a group, monkeys preferentially selected the larger quantity on the first exposure for simultaneous pairs [chance = 50%, one sample $t(7) = 2.76$, $p < 0.05$] and for sequential pairs [one sample $t(7) = 4.38$, $p < 0.01$]. **Figure 2** shows the overall performance on simultaneous and sequential trials. Simultaneous performance was marginally higher than sequential performance across the group but the difference was not significant [$t(7) = 1.74$, $p = 0.12$]. **Figure 3** shows performance on the three pair types tested: small, large, and span pairs. Monkeys performed significantly above chance on small number pairs [$t(7) = 3.21$, $p < 0.05$] and span pairs [$t(7) = 2.99$, $p < 0.05$] but large pair performance was non-significant [$t(7) = 1.44$, $p = 0.19$]. Poor performance on large numbers could be explained by the fact that large number pairs have inherently more difficult discrimination ratios. Further analyses revealed that on the sequential trials, particularly for large numbers, monkeys had a bias to select the more recently presented food set [$t(7) = 5.17$, $p < 0.01$]. This bias on large sequential trials cannot explain successful performance on the other pair types because the larger number was equally likely to be presented first or second on sequential trials and on simultaneous trials both sets were presented at the same time. Instead, performance across all number pairs was predicted by numerical ratio.

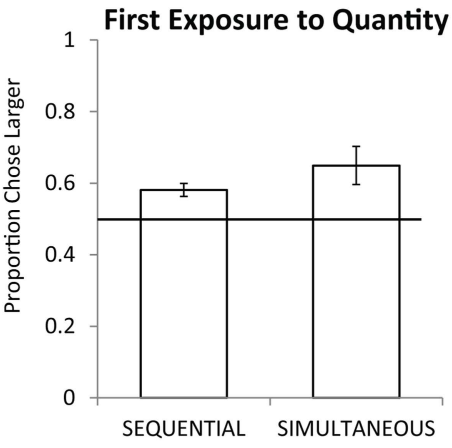

FIGURE 2 | Average accuracy for eight monkeys on sequential and simultaneous trials from their first exposure to numerical discriminations. Chance is a 0.5 probability. Error bars represent the standard error of the mean across monkeys.

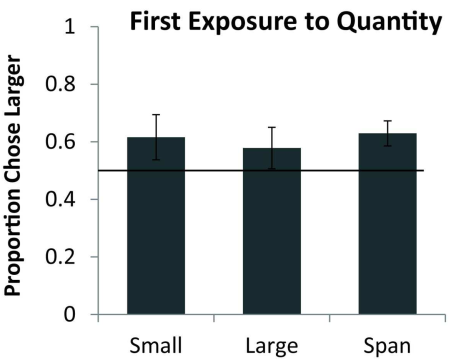

FIGURE 3 | Average accuracy for eight monkeys on the small (both numbers <5), large (both numbers >4), and span pairs (one number <5 and one number >4) on their first exposure to numerical discrimination. Chance is a 0.5 probability. Error bars represent the standard error of the mean across monkeys.

We binned the numerical pairs by their numerical ratio and tested for a linear trend of numerical ratio. Monkeys showed a significant effect of ratio on their simultaneous trial performance indicating that they made choices on the basis of an analog quantity representation [Pearson's $r(19) = -0.38$, $p < 0.05$]. This finding suggests that monkeys struggled to discriminate large values in part due to their more difficult discrimination ratios. **Figure 4** shows the effect of ratio on monkeys' quantity discrimination in this first exposure task. Performance on numerical pairs ranges from approximately 75% on easy ratios to 55% on difficult ratios.

We calculated individual Weber fractions for the five animals that performed above chance overall on the first exposure task. Weber fractions on first exposure ranged from 0.51 to 0.91, which is comparable to the range of Weber fractions exhibited by young children on similar tasks (Halberda and Feigenson, 2008).

EXPERIMENT 2

METHODS AND MATERIALS

Subjects

Subjects for Experiment 2 were two female baboons who participated in Experiment 1 (Pearl, Ursala).

Apparatus, procedure, design, and data analysis

In Experiment 2 we collected more data on numerical comparisons from two subjects in order to detect subtle performance signatures among pair types. We used the same apparatus and procedure as in Experiment 1. Three cups were presented on each trial as choices, two of the cups were baited. In this experiment, monkeys never chose the empty cup. The numerical values presented ranged from 1 to 8. Each session began with a five-trial 1 vs. 2 "warm-up." The test immediately followed the warm-up and contained approximately eight of each small, large, and span test pairs (four each

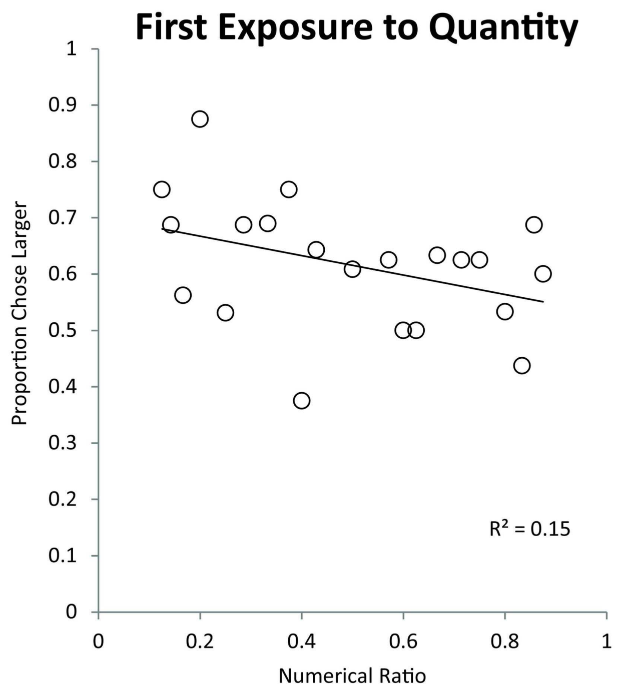

FIGURE 4 | Effect of numerical ratio on monkeys' accuracy during their first exposure to numerical discrimination. The numerical ratio is the smaller number in a given pair divided by the larger number. Each data point represents a different number pair. The trend line represents a linear trend of decreasing accuracy with finer numerical ratios.

of simultaneous and sequential) and four 1 vs. 2 trials randomly interspersed throughout the test trials. Sessions were equated for mean numerical ratio across conditions. The numerical ratio was an average of approximately 0.5 for each pair type in each session. This meant that some pair types were tested more frequently than others. We tested the Experiment 2 subjects until they had multiple exposures to all contrasts in both presentation types. We completed 11 sessions with Pearl and 13 sessions with Ursala, as described in the procedure for Experiment 1. Extra sessions were required due to incomplete trials during some sessions. Ultimately, each animal completed approximately 130 trials per presentation format. There was a total average of approximately 4.5 trials per number pair, per presentation format.

It is important to note that the animals were not trained to select the larger quantity over the course of time. Instead, animals were always rewarded with the cache that they chose. The only way that a longer exposure period could possibly result in learning over time is if the animals are able to discriminate the quantities of the choices they were given. That is, because the animal was rewarded with their chosen food quantity on each trial, in order to learn that the quantity they chose was either greater or lesser than the alternative quantity, they would have to be able to discriminate and compare the quantities of the chosen vs. unchosen rewards.

RESULTS

In this longer exposure task, both monkeys significantly chose the larger food set for both sequential trials [binomial tests, Pearl (83/120 trials), $p < 0.001$, Ursala (91/141 trials), $p < 0.001$] and simultaneous trials [Pearl (96/121 trials), $p < 0.001$, Ursala (114/141 trials), $p < 0.001$]. These data indicate that animals can spontaneously discriminate quantities presented simultaneously and sequentially. Additionally, these monkeys were successful at choosing the larger quantity for small pairs [binomial test, Pearl (62/80 trials), $p < 0.001$, Ursala (63/85 trials), $p < 0.001$], span pairs [Pearl (64/80 trials), $p < 0.001$, Ursala (85/102 trials), $p < 0.001$], and large pairs [Pearl (53/81 trials), $p < 0.01$, Ursala (57/95 trials), $p < 0.05$]. This above-chance performance for small, span, and large quantity pairs supports the conclusion that olive baboons spontaneously use the analog numerical system to solve this task. The only exception is that for large sequentially presented pairs monkeys displayed a bias in selecting the most recently presented set [binomial test on choosing the second cache, Pearl (27/40 trials), $p < 0.05$, Ursala (43/45 trials), $p < 0.001$; all p's for other five pair types >0.05]. However, since monkeys' performance was significantly above chance on sequentially presented span pairs, there is still evidence that spontaneous analog quantity representations were used to solve the sequential task [Sequential span pairs: Pearl (29/40 trials), $p < 0.01$, Ursala (39/52 trials), $p < 0.001$]. In addition, both monkeys showed a ratio effect across both the simultaneous and sequential trials, implicating the analog numerical system [Simultaneous pairs: Pearl: $r(19) = -0.43$, $p < 0.05$; Ursala: $r(19) = -0.59$, $p < 0.01$; Sequential pairs: Pearl: $r(19) = -0.66$, $p < 0.001$; Ursala: $r(19) = -0.36$, $p = 0.05$]. **Figure 5** shows performance for each monkey, for each pair type as a function of numerical ratio. Each data point on **Figure 5** represents a different numerical pair. The individual Weber fractions for both monkeys over longer exposure were 0.44. This fraction is slightly better than Pearl's Weber fraction on the first exposure task (0.57) and comparable to Ursala's (0.39).

Comparison of monkey performance to predictions from the object-file hypothesis

As discussed in the Introduction, failure on numerical pairs with one value greater than three has been taken as evidence for object-file representation in the literature on infant quantity development (Feigenson et al., 2002). In order to test whether monkeys exhibit the same patterns of performance as human infants, we tested monkeys' performance on specific pairs that human infants have been shown to fail at in previous studies. Here, we examined the data from Experiment 1 (first exposure) and Experiment 2 (longer exposure). We tested the numerical pairs 2 vs. 4, 3 vs. 4, and 3 vs. 6, which human infants fail to discriminate. We also tested monkeys' performance on numerical pairs that were previously argued to elicit discrimination failures in monkeys, and were argued to provide evidence of object-file quantity representation in non-human primates (Hauser et al., 2000). **Figure 6** shows monkeys' performance on all numerical pairs which monkeys would be predicted to fail to discriminate under an object-file hypothesis: 2 vs. 4, 3 vs. 4, 3 vs. 6, 3 vs. 8, 4 vs. 5, 4 vs. 6, 4 vs. 8. Again, all of these pairs have been reported as failures in monkeys, infants, or both and those failures have been cited in support of the object-file hypothesis (Hauser et al., 2000; Feigenson et al., 2002). In contrast to prior infant and some non-human primate findings, monkeys performed significantly above chance on these

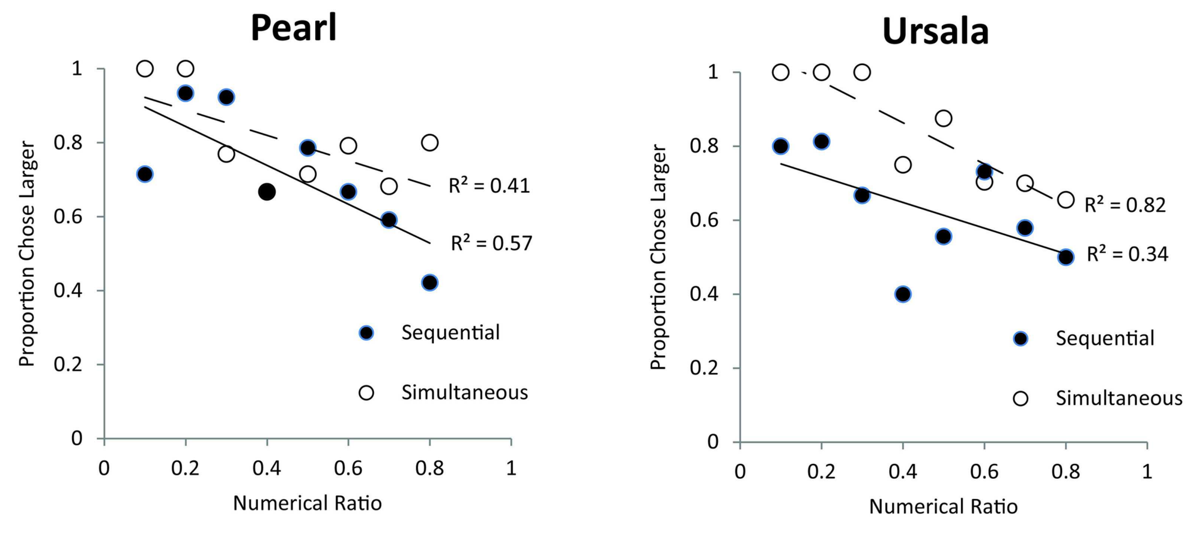

FIGURE 5 | Effect of numerical ratio on accuracy from the two monkeys (Pearl and Ursala) tested in the longer exposure (Experiment 2) for sequential (filled circles) and simultaneous trials (open circles). Trend lines represent linear trends of decreasing accuracy with finer numerical ratios.

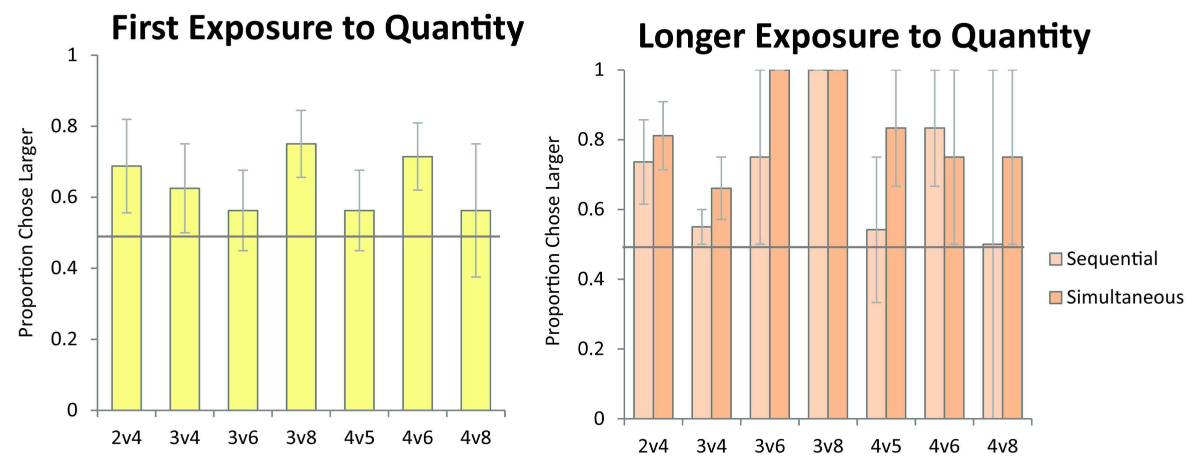

FIGURE 6 | Monkeys' accuracy on numerical pairs which have been previously reported to elicit failures under the object-file system. In contrast to the predictions of the object-file model, monkeys performed significantly above chance across these pairs on their first exposure to numerical discrimination (left panel, data from Experiment 1) and on longer exposure to the numerical task (right panel, data from Experiment 2) for both the sequential and simultaneous conditions. Error bars represent standard error of the mean across monkeys. Chance is a 0.5 probability.

pairs, even on their first exposure in Experiment 1 [First Exposure Group: one sample t-test vs. chance, $t(7) = 2.99$, $p < 0.05$; Longer Exposure Group: Binomial Tests vs. chance, Sequential: Pearl (18/27, $p = 0.06$), Ursala (23/32, $p < 0.01$], Simultaneous: Pearl (22/27, $p < 0.001$), Ursala (25/32, $p < 0.01$). Moreover, seven out of eight monkeys in Experiment 1 performed above 50% on these critical test pairs on the first trial (Binomial test 7/8, $p < 0.05$). Instead of failing to discriminate pairs in which one quantity exceeded the object-file capacity limit of three or four, performance on these pairs was modulated by ratio for both the simultaneous and sequential presentations implicating analog magnitude representations of number (**Figure 7**). The presence of a ratio effect on these critical test pairs indicates that analog magnitude representations were used to compare these quantities.

Finally, in order to confirm that the animals were not learning these "predicted fail pairs" over time, we tested for trends of improving accuracy across the longer exposure period for the predicted fail pairs. Neither monkey showed a significant improvement in accuracy as a function of time for these pairs [Pearl $r(11) = 0.31$, $p = 0.35$; Ursala $r(13) = -0.04$, $p = 0.90$].

Control condition

In Experiments 1 and 2 there is a possibility that animals used subconscious cues from the human experimenters to solve the task. This possibility seems unlikely for several reasons. First, we found

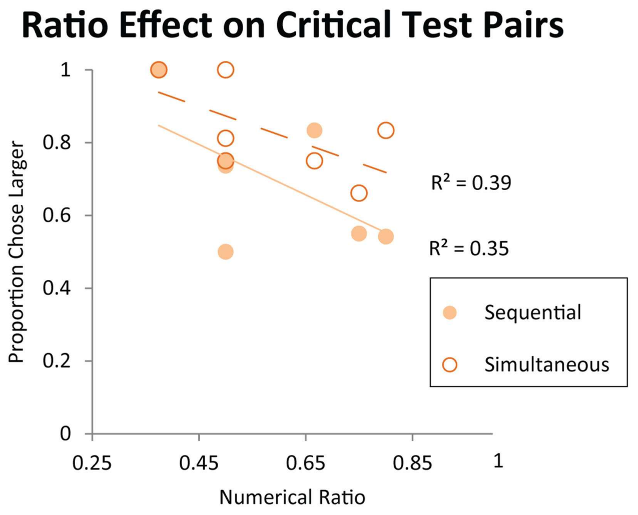

FIGURE 7 | Performance on the critical test pairs for object-file representation: 2 vs. 4, 3 vs.4, 3 vs. 6, 3 vs. 8, 4 vs. 5, 4 vs. 6, 4 vs. 8. All of these pairs have been reported as failures in monkeys, infants, or both and those failures have been cited in support of the object-file hypothesis (Hauser et al., 2000; Feigenson et al., 2002). Each data point on the graph represents a different numerical pair from this set. Trend lines represent linearly decreasing accuracy as numerical ratio gets finer. Contrary to the predictions of the object-file hypothesis, accuracy on these numerical pairs is modulated by numerical ratio in monkeys.

evidence that the animals selected the larger quantity on their first exposure to the task and did not learn the task by trial-and-error, contrary to accounts of human cueing which are hypothesized to require associative learning over the course of training (i.e., Clever Hans; see Beran, 2012). Secondly, as mentioned earlier, in order for these animals to engage in associative learning during our food choice task they would have to be able to discriminate the quantity of the reward they received from the quantity that they did not receive. This is because the animals are rewarded on every trial with some quantity of food: either the larger or the smaller amount. If the animals have the spontaneous quantitative abilities to discriminate the reward they received from the one they didn't, then they would likely use those spontaneous quantitative abilities to choose the larger number of food items rather than using their quantitative abilities to arduously form associations between the relatively larger quantity and human cues. Third, the monkeys' performance was modulated by ratio whereas the human experimenters knew precisely the quantity of food items in each cup and thus would have subconsciously cued precise performance by the baboons. In short, it seems unlikely that human cueing played a role in the animals' quantity decisions. Unfortunately the literature on primates' abilities to use subtle human body language cues is sparse and so, it is unclear what behavioral patterns we should expect to see if the animals in our experiments used subconscious human cues to guide their choices. The main source of data on this issue is the Clever Hans phenomenon, a horse who (it is claimed) used the tension in the body language of his trainer to accurately respond to mathematical tasks. Currently, there are no rigorous experimental data that show whether, when, or how non-human primates are able to use such cues spontaneously or otherwise to guide decisions. And so, in order to rule out the possibility that our animals used subconscious cues from human experimenters to guide their food choices, we conducted a controlled test.

METHODS AND MATERIALS

SUBJECTS

Subjects were the two female baboons who participated in Experiment 2 (Pearl, Ursala).

APPARATUS, PROCEDURE, DESIGN, AND DATA ANALYSIS

In the control condition, the two animals from Experiment 2 were tested by two experimenters, each of whom baited one of the two cups. Each experimenter was blind to the quantity of food items baited into the other's cup and so was unaware of which cup contained the larger quantity. This ensured that the human experimenters could not give subconscious cues to the correct cup because they did not know which cup was correct. Monkeys were tested with approximately 55 trials of the number pairs 1 vs. 2 and 2 vs. 9 in the sequential presentation format. Each session was 24 trials. The procedure was otherwise identical to Experiments 1 and 2.

RESULTS

Both monkeys performed significantly above chance from the first session of testing with the control condition (Binomial tests; Pearl: 19/24, $p < 0.01$; Ursala: 17/24, $p < 0.05$). **Figure 8A** plots the data in five-trial increments from the beginning of testing and illustrates that performance on the control condition was comparable to performance from Experiments 1 and 2. A t-test comparing the first 11 blocks of Experiments 1 and 2 with the 11 blocks of the control condition showed no decrement in performance on the control condition [Experiments 1 and 2: 61%; Control: 78%; $t(10) = 4.03$, $p = 0.002$]. In fact, performance on the control condition was slightly better overall than performance in Experiments 1 and 2. **Figure 8B** illustrates that there was no difference in performance between the first day of performance on Experiment 1 and the first day of performance on the control condition. These results indicate that the baboons' performance was unaffected when the human experimenters were unable to provide subconscious cues to the cup with the larger number. Recall that in this control condition each cup is baited by a different experimenter and neither experimenter knew the quantity of the other's cup. The baboons were able to discriminate quantity despite this modification of the task procedure, which prevented human cueing.

DISCUSSION

Eight olive baboons without any prior experience discriminating quantities in experiments were tested on their ability to spontaneously discriminate quantities of food items. The monkeys were able to discriminate small, large, and most importantly, span number pairs, as evidenced by their ability to choose the larger quantity at a frequency significantly above chance. The data show that olive baboons can successfully discriminate quantities, as many other non-human species are known to do. Our data further demonstrate that non-human primates spontaneously discriminate quantities using analog quantity representations that are constrained by ratio and predicted by Weber's Law.

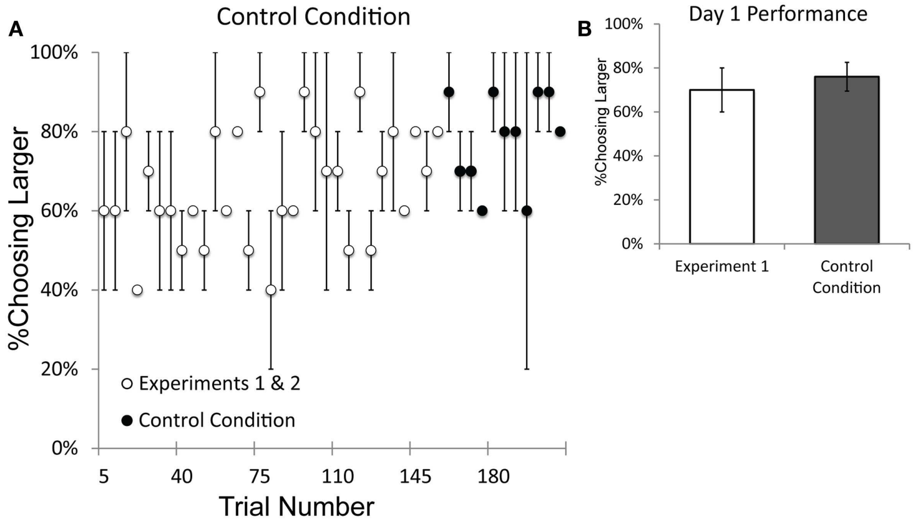

FIGURE 8 | Performance on the Control Condition, which controlled for the possibility of subconscious cueing by experimenters. **(A)** Performance on the sequential trials of Experiments 1 and 2 and the Control Condition, plotted by trial number. Performance on the Control Condition was not impaired relative to performance on Experiments 1 and 2. **(B)** A comparison of performance on the first day of testing for Experiment 1 vs. the first day of testing on the Control Condition. The data presented from Experiment 1 only include numerical pairs that are as easy as those from the Control Condition (numerical ratios ≤ 0.5). Error bars represent standard error of the mean difference between monkeys.

We tested hypotheses that address the underlying nature of the spontaneous quantity representations of non-human primates. The three hypothetical possibilities we outlined in the Introduction were: (1) object-file numerical representation only, with success occurring only for small numbers, (2) dual incompatible object-file and analog magnitude representation, with success occurring for small and large numbers but not span pairs, and (3) analog magnitude representation only with success dependent on numerical ratio independently of set size. Reviewing the data, we find that the performance of these monkeys is best explained by a single-system analog representation model.

First, monkeys were able to discriminate small, span, and large number pairs presented simultaneously and small and span pairs presented sequentially – numerical discriminations which demonstrably exceed the capacity limit of the object-file system. Failures on sequential large sets were likely due to attentional constraints rather than object-file representations because simultaneous and span discriminations with large values were successful. Anecdotally, we observed that baboons were more distractible over the long sequential trials. This could suggest that failures on large sequential pairs were due to failures of sustained attention. Nonetheless, monkeys were capable of accurate discrimination of span pairs presented sequentially, indicating that they are capable of representing numbers larger than 3 or 4 during sequential presentation. Secondly, the finding that baboons successfully discriminated span pairs indicates that monkeys were not simultaneously using both the analog and object-file systems to perform this task as that hypothesis predicts failure on span pairs (but see Cordes and Brannon, 2008). Finally, monkeys' performance was ratio-dependent, the diagnostic signature of analog numerical representations. Together, these strands of evidence support the conclusion that the analog magnitude system is the dominant mechanism engaged for spontaneous numerical representation in baboons.

We also investigated the Weber fractions that characterize the numerical sensitivity of individual baboons. The Weber fractions on the first exposure trials were within the range of Weber fractions previously reported for non-verbal numerical discriminations in human children (Halberda and Feigenson, 2008). In fact, the spontaneous quantity judgments of the olive baboons in this study are much like that of 3- and 4-year-old human children, both in terms of discrimination thresholds and in terms of the absence of a capacity limit in numerical discrimination. Prior studies have demonstrated that non-verbal numerical performance in 3- and 4-year-old children also lacks the signatures of "two system" numerical representation (Halberda and Feigenson, 2008; Cantlon et al., 2010).

On the longer exposure experiment with two monkeys, overall performance was significantly above chance for both simultaneous and sequential set presentations and quantity discriminations were modulated by ratio. Weber fractions on the longer exposure experiment were similar to those from the first exposure experiment and so they are also similar to Weber fractions reported for young children. The baboons did not exhibit substantial improvement in overall performance over these dozen or so sessions indicating that learning did not play a major role in baboons' quantity judgments over across testing. Monkeys' successful quantity choices during the control condition provides evidence that monkeys did not use subconscious cues by human experimenters to solve the food choice task.

A direct comparison of the baboon data with data previously reported for human infants (Feigenson et al., 2002; Feigenson and Carey, 2003, 2005; Le Corre and Carey, 2007) indicates that non-human primate quantity judgments are not subject to the same constraints as those of human infants. The baboons succeeded at discriminating the numerical pairs that infants have been shown to fail, even on their first exposure to those pairs. Similarly, in the longer exposure experiment baboons performed above chance on numerical pairs that infants fail to discriminate during both sequential and simultaneous presentation trials. These numerical pairs are predicted to elicit failure under an object-file hypothesis due to the capacity limits of the object-file system. Rather than eliciting an object-file signature, baboons' performance on these pairs exhibited the signature of analog magnitude representation in that performance was modulated by ratio. Again, learning did not appear to affect judgments on these pairs as there was no evidence of significant improvement over the course of testing on these specific pairs. Thus, although some researchers have suggested parallels in numerical cognition between human infants and adult monkeys (e.g., Feigenson et al., 2002), we did not find support for that hypothesis. In fact, as mentioned above, if any parallels can be drawn between the numerical abilities of humans and non-human primates, our data suggest that monkeys might be more similar to 3- and 4-year-old children, at least in terms of their discrimination thresholds (i.e., their Weber fractions) and analog-format numerical representation.

Our results are consistent with prior studies that have argued for spontaneous analog magnitude numerical judgments in many animal species (e.g., Meck and Church, 1983; Brannon and Terrace, 1998; Cordes et al., 2001; Beran, 2007; Cantlon and Brannon, 2007; see Gallistel, 1990 for review). We obtained similar results to these prior studies while also filling a gap in the experimental designs that were used across the studies. In prior studies it remained unclear whether some design aspect – such as experimental training history – might bias non-humans toward behavior consistent with the analog magnitude system. As described in the Introduction, two prior studies reported divergent results: Hauser et al. (2000) found evidence of the object-file system and Beran (2007) found evidence of the analog magnitude system. In both studies, rhesus macaques were presented with two number sets, presented sequentially and placed into boxes, and subjects were tested for their ability to choose the box with the larger quantity. The only difference between those studies was that the Hauser et al. study tested a real-object food choice task with relatively experiment-naive subjects, while the Beran study used a joystick task with experienced subjects. Using a naturalistic food choice task in which experiment-naive subjects were rewarded with whatever amount they chose, we still obtained evidence consistent with the recruitment of a single analog magnitude numerical system. The evidence presented here in support of the analog magnitude system is consistent with the results of Beran (2007) but our experimental design includes important parallels with the design of the Hauser et al. (2000).

The overall success of these experiment-naive baboons on quantitative discriminations of food items indicates that non-human primates spontaneously represent and compare quantities to make adaptive choices. These discriminations can be made over simultaneously or sequentially presented sets of items. The discriminations can also be made over small numerical pairs, large numerical pairs, and pairs that include one small and one large value. Monkeys' sensitivity in making these discriminations was determined by the ratio between the numerical values of the sets, a signature of analog magnitude representation. The only way to explain the monkeys' successful performance in these experiments is by appealing to spontaneous quantitative abilities. Our data indicate that these spontaneous quantitative abilities in baboons are inherently analog in nature.

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Do social conditions affect capuchin monkeys' (*Cebus apella*) choices in a quantity judgment task?

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Beran et al. (2012) reported that capuchin monkeys closely matched the performance of humans in a quantity judgment test in which information was incomplete but a judgment still had to be made. In each test session, subjects first made quantity judgments between two known options. Then, they made choices where only one option was visible. Both humans and capuchin monkeys were guided by past outcomes, as they shifted from selecting a known option to selecting an unknown option at the point at which the known option went from being more than the average rate of return to less than the average rate of return from earlier choices in the test session. Here, we expanded this assessment of what guides quantity judgment choice behavior in the face of incomplete information to include manipulations to the *unselected* quantity. We manipulated the unchosen set in two ways: first, we showed the monkeys what they did not get (the unchosen set), anticipating that "losses" would weigh heavily on subsequent trials in which the same known quantity was presented. Second, we sometimes gave the unchosen set to another monkey, anticipating that this social manipulation might influence the risk-taking responses of the focal monkey when faced with incomplete information. However, neither manipulation caused difficulty for the monkeys who instead continued to use the rational strategy of choosing known sets when they were as large as or larger than the average rate of return in the session, and choosing the unknown (riskier) set when the known set was not sufficiently large. As in past experiments, this was true across a variety of daily ranges of quantities, indicating that monkeys were not using some absolute quantity as a threshold for selecting (or not) the known set, but instead continued to use the daily average rate of return to determine when to choose the known versus the unknown quantity.

Keywords: quantity judgments, uncertainty, social testing, competition, capuchin monkeys, *Cebus apella*

INTRODUCTION

Individuals from many species are commonly faced with making decisions between two or more mutually exclusive options, particularly when it comes to foraging decisions and the attempt to maximize the amount of food one can get while minimizing the effort required and minimizing the risk that no food will be obtained. In one of the least risky, but more prevalent laboratory situations that is presented, organisms must choose between two quantities, and those individuals who are best at discriminating carefully between the choices and picking the larger one will net the greatest benefit. Perhaps unsurprisingly, many species are quite adept at making such relative quantity judgments (for an overview, see Brannon and Roitman, 2003). These species include insects (Chittka and Geiger, 1995; Dacke and Srinivasan, 2008), fish (Agrillo et al., 2007, 2008; Pfifer et al., 2012), amphibians (Uller et al., 2003; Krusche et al., 2010), birds (Emmerton, 1998; Rugani et al., 2008), and many mammals including voles (Ferkin et al., 2005), dogs (Ward and Smuts, 2007), bears (Vonk and Beran, 2012), elephants (Irie-Sugimoto et al., 2009; Perdue et al., 2012), marine mammals (Kilian et al., 2003; Jaakkola et al., 2005; Abramson et al., 2011), and non-human primates (e.g., Call, 2000; Beran, 2001, 2004, 2012; Anderson et al., 2005, 2007; Hanus and Call, 2007; Tomonaga, 2007; Addessi et al., 2008; Evans et al., 2009).

Recent work in our lab has shown a strong consistency across species in dealing very adaptively with uncertain or incomplete information in a quantity judgment task. Beran et al. (2009) devised a test in which chimpanzees first performed 15 trials in which they always saw each of two sets of food items, and then chose between them when they were covered. As expected, the chimpanzees were consistent in choosing the larger set. The critical test occurred during the second block of 15 trials in each session, when only one set was revealed, whereas the other remained unknown at the point of choosing. The chimpanzees responded in that case by basing their choice (or avoidance) of the unknown quantity on the amount of food in the known quantity. When the known amount was close to, or exceeded, the average quantity of items obtained across the first 15 trials, the chimpanzees selected the known set. But, if the known amount was smaller than the average, they took the risk of choosing the unknown set. This strategy occurred across a range of quantities tested across different days, and so the chimpanzees showed great flexibility in their application of this heuristic for dealing with incomplete information. In a second study Beran et al. (2012) directly compared another primate species, the capuchin monkey, with adult humans, and the same result occurred in both of these groups, providing a strong convergence of evidence that multiple primate species seem to keep a running tally of how well they have been getting rewarded at the task, and can use that information when it might be informative.

Despite this clear evidence of flexible responding in the face of incomplete information, there remain a number of questions about whether participants would sustain this kind of responding under different conditions. One can imagine that certain circumstances may produce a stronger drive to select the known set over the unknown set even when the known set is smaller than the average, for example if the unknown set involved a large degree of risk. One could manipulate risk by using conditions that kept shifting the average rates of return during the training trials, and one could manipulate the potential for extreme gains and losses for either taking or not taking the known set when faced with an unknown option. These manipulations would allow one to determine how robust the heuristic of using the ongoing representation of averages in quantity assessments is, or whether it is sensitive to fluctuations and extremes in quantity judgment.

Another likely candidate for disrupting the patterns of responding found previously would be the introduction of a more competitive circumstance. Often, putting animals in more competitive versus less competitive situations can change the nature of their responding to various tasks. For instance, rhesus monkeys have shown a speed-accuracy trade-off when directly competing against a partner in a computerized paradigm in comparison to working alone, suggesting a shift in individual strategy in response to the altered social nature of the task (Washburn et al., 1990). Moreover, both chimpanzees and rhesus monkeys have shown sensitivity in reasoning about another's potential visual knowledge when placed in a situation where competition over food sources was likely (e.g., Hare et al., 2001; Flombaum and Santos, 2005) but failed to show this same sensitivity to a conspecific's perceptual cues in non-competitive tasks (e.g., Tomasello and Call, 1997; Povinelli, 2000). Primates also appear to be highly sensitive to the mere likelihood for competition and alter their expression of knowledge states in the presence of higher-ranking individuals (Drea and Wallen, 1999). Thus, we tested whether such effects might emerge within our quantity judgment task.

In a standard competitive task, a salient component would be the loss of food to a conspecific, either due to direct competition over the food source or monopolization of the source by a more dominant animal. To incorporate this aspect of competition, we modified the test given to capuchin monkeys (*Cebus apella*) by now giving the unchosen set on every trial to a conspecific who was near the subject and who did not have to do anything to get food. Although the subjects were not directly competing for food, this manipulation should increase the competitive nature of the task for the subject animal because another individual may sometimes receive the greater quantity of food, and perhaps change the subject animal's choice behavior during the trials with incomplete information. If it did, this would demonstrate that some social aspects of the environment can disrupt the perceptual and quantitative processing and decision-making in non-human animals, and would reflect an interaction of a "logical" decision-making process (quantity judgment with ongoing representation of average rewards) and a social factor driven by competitiveness. In that case, capuchin monkeys would respond differently in the face of the exact same quantity comparisons depending on whether a conspecific got what was left after the choice, or did not (the control condition). We were rather agnostic as to the direction of this effect (i.e., whether the monkeys should be more or less likely to choose the unknown set), but perhaps they should be less likely to choose the unknown set and potentially lose a better, and initially visible, outcome to a conspecific.

Giving the unselected food to the conspecific also meant that the focal monkeys now would see the contents of the unknown set even when they had not selected that set, and this differed from the procedure used in Beran et al. (2012). These manipulations should not have any effect during the first 15 trials, because the subject monkey would know the contents of both sets, and so should simply maximize its own reward, but in the second 15 trials, where risk was introduced and uncertainty was involved, performance might differ. At the same time, if it did not, this would demonstrate that the heuristic at work in this species (and, presumably, in humans and chimpanzees) is robust and not sensitive to disruption through this particular social manipulation or the manipulation of showing monkeys what they *did not* receive on each of these trials when they selected the known set.

MATERIALS AND METHODS

PARTICIPANTS

We tested four capuchin monkeys housed at the Language Research Center (LRC). All monkeys had participated in multiple quantity judgment studies (Beran et al., 2007; Evans et al., 2009) including the previous study assessing judgments involving incomplete information (Beran et al., 2012). Each of these four focal monkeys was paired with a partner monkey that served as a passive recipient of food in the Conspecific Present condition. The focal monkeys were Wren (female), Griffin (male), Nala (female), and Liam (male), and they worked with four other monkeys (Drella, Lily, Gabe, and Logan) that only ever served to receive the free pellets from the unselected set. The capuchin monkeys were group housed but voluntarily separated for testing. Monkeys voluntarily entered individual stainless steel mesh test boxes (33 × 46 × 61 cm) that were attached to the group enclosure. There were four test boxes positioned 0.5 m apart in a row. The focal animal was always shifted into the same test box, and the partner was shifted into the same adjacent test box during the partnered condition. While there, both animals had clear visual and auditory access to one another. All other test boxes remained empty during test sessions. Water was available *ad libitum*, and all monkeys were fed manufactured chow and various fruits and vegetables daily between 1600 and 1800 h. This study complied with protocols approved by the Georgia State University IACUC. All procedures were performed in full accordance with the USDA Animal Welfare Act and conformed to the "Guidelines for the use of laboratory animals."

MATERIALS

The apparatus consisted of a rolling cart topped with a moveable tray. The cart was positioned in front of the focal test box and the tray could be pushed toward the focal animal and pulled back to the experimenter. There were two food locations on the tray which could be covered by opaque, removable lids to conceal the contents. Focal monkeys could reach through holes in the mesh of the text box or through a Lexan cover with two arm holes to indicate their choice of one of the two food locations (see **Figure 1**).

PROCEDURES

Participants had previous experience with a similar quantity judgment task (Beran et al., 2012) and were familiar with the basic procedures of the task. In all trials of each session, Experimenter 1 baited both locations on the tray with a predetermined number of food pellets (45 mg, grain-based with banana flavor, *Bio-Serv*, Frenchtown, NJ, USA). The locations were baited out of view of the monkey by tilting the lids upward toward the experimenter, one at a time, and dropping the items all at once behind them. Each session consisted of a learning phase immediately followed by a testing phase.

For the learning phase of each session, focal monkeys were shown both sets of food items, by uncovering and recovering each set one at a time. After the presentation, the tray was pushed forward and the monkey made a choice by touching one of the lids that covered one of the sets of food items. To prevent cuing, Experimenter 1 closed his eyes and looked down while pushing the tray forward using a centrally located handle, and a second experimenter standing to the side of the apparatus (out of direct view of the monkey) announced the monkey's choice. The focal monkey was given the amount of food under the chosen lid. Next, the unselected amount of food was shown to the focal monkey and then removed in one of two ways. In the Conspecific Absent condition, the unselected set of food items was returned to an out of sight food bowl (in the back of the cart). In the Conspecific Present condition, the unselected food was given to the partner animal in the adjacent test box, and this event occurred in full view of the focal monkey (the experimenter paused if the focal animal was not watching). It is noteworthy that, in the previous studies of this kind, the focal participant never viewed the unselected option.

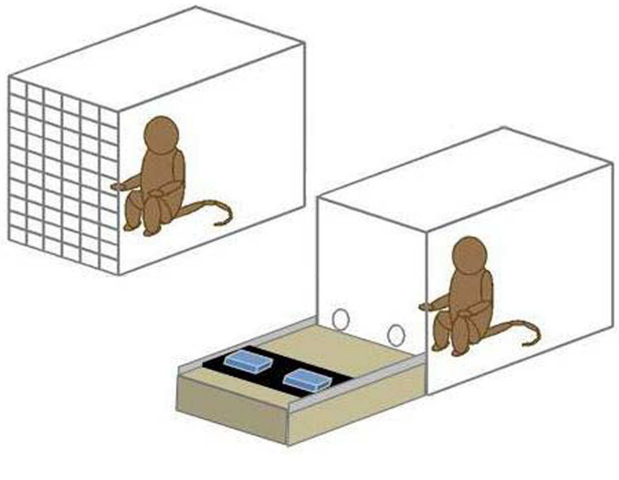

FIGURE 1 | Schematic of the test apparatus. The box at right holds the focal monkey and the tray for presenting the stimulus sets. The conspecific, when present, was in the other box and received the contents of the non-selected set.

Trials of the testing phase were very similar to those of the learning phase, except that the focal monkey was only shown one of the food amounts (always the amount to his or her right), instead of both amounts as in the learning phase, before being given a choice between the two options. Thus, the test phase necessarily instilled uncertainty into the quantity judgments because only one set of food items could be known with regard to its quantity. The second, unrevealed, set could be larger or smaller than the set that had been seen by the monkey. As noted earlier, these monkeys, as well as chimpanzees and humans given similar tests, relied on the approximate mean number of items received across the session's learning phase to guide choice of the known or unknown sets in the test phase (Beran et al., 2009, 2012). When the known set was smaller than the approximate mean number of items that were obtained across the learning trials, participants previously showed a strong bias to select the unknown set (i.e., to risk the known option to try to get more food). However, when the known set was close to or larger than the mean, participants selected that set rather than the unknown option.

We tested monkeys using this procedure in three conditions.

Standard condition

Monkeys were given 15 learning trials and 15 test trials in each session. Four Conspecific Present and four Conspecific Absent sessions were conducted for each monkey in an alternating order. All pairwise comparisons between one and six food pellets were presented (see **Table 1**). For each pair of sessions (Conspecific Absent and Conspecific Present), each pairwise comparison of pellet amounts was included twice, counterbalanced for side, for a total of 30 trials and these were randomly distributed across the

Table 1 | Specific quantity comparisons presented in each of the experimental conditions for each trial type.

Standard condition		Shifting average condition		Extreme wins/ losses condition	
Learning trials	Test trials	Learning trials (small set)	Test trials (small set)	Learning trials	Test trials
1,2	1,2	0,1	1,3	1,2	2,1
1,3	1,5	1,2	2,5	1,2	2,6
1,4	2,3	1,3	3,1	2,1	3,2
1,5	2,4	1,4	3,6	2,1	3,8
1,6	2,6	2,3	4,1	2,4	5,1
2,3	3,1	2,4	4,2	2,6	5,1
2,4	3,5	2,5	4,6	3,2	5,1
2,5	3,6	3,5	4,8	4,1	5,1
2,6	4,1	3,6	5,2	4,8	5,10
3,4	4,3	4,6	5,8	6,3	5,10
3,5	4,6	4,8	6,4	6,10	5,10
3,6	5,2	5,8	8,5	8,5	5,10
4,5	5,4	–	–	–	8,2
4,6	6,1	–	–	–	8,10
5,6	6,5	–	–	–	10,4

two sessions. The test trials in this condition consisted of the comparisons listed in **Table 1**, presented in random order. The number appearing in the leftmost position of each column of **Table 1** indicates the number of food items shown to the monkey on every trial as the first presented set, and the number appearing in the rightmost position of each column indicates the number of food items shown in the second presented set (learning trials) or the number that was placed in the unrevealed set (test trials).

Shifting average condition

In the standard condition, monkeys may have come to expect on every session that the same average number of items would be obtained across trials, because the same comparisons were used in all trials, just in a different order of presentation. Thus, any potential social influences may have been diminished by a learned pattern of behavior (i.e., "always choose five items or more"). To introduce more variability into the task, we varied the average number of items that would be received in the learning phase of each session and alternated between a relatively large and small average across sessions. Twelve learning trials and 12 test trials were completed in each session. Two Conspecific Present and two Conspecific Absent sessions were completed by each monkey in a random order. The smaller average set consisted of the comparisons listed in **Table 1**, repeated twice and counterbalanced for side. The larger set consisted of the same comparisons multiplied by two. These test trials oversampled the middle region of values in order to provide a larger number of critical values for comparison between large-average and small-average sessions. As in the standard condition, trials were randomly ordered across a session.

Extreme wins/losses condition

To assess the impact of increased wins or losses after a decision, we ran a third condition in which the payout differential was more pronounced than in the previous conditions. Specifically, the critical test trials always involved the presentation of five pellets, which were paired with either 1 or 10 pellets in the non-visible set. Thus, choosing the unknown option would result in a large increase in pellets obtained or a large decrease in pellets obtained, compared to the known set. Twelve learning trials and 15 test trials were completed in each session. Three Conspecific Present and three Conspecific Absent sessions were completed by each monkey in a random order. The learning and test trials are listed in **Table 1**, but were randomly ordered across each session.

RESULTS

As would be expected from these monkeys' past quantity judgment performance (Beran et al., 2007, 2012; Evans et al., 2009), the focal monkeys were excellent in choosing the larger of the two sets of food items when they saw both, during the first trials of each session. Performance in the training phases of all conditions is shown in **Table 2**. Performance was very high in all cases, and rarely differed between the Conspecific Present and Conspecific Absent conditions.

Table 2 | Percentage of trials selecting the larger quantity by each monkey during training trials in each condition.

	Griffin	Wren	Liam	Nala
Standard				
Conspecific present	90.0	86.67	93.3	93.3
Conspecific absent	90.0	90.0	91.67	90.0
Shifting average				
Conspecific present	95.83	87.5	100	100
Conspecific absent	87.5	87.5	95.83	91.67
Extreme wins/losses				
Conspecific present	83.3	86.1	94.4	97.2
Conspecific absent	83.3	86.1	91.67	94.4

The results for the Standard Condition are shown in **Figure 2** as the total percentage of trials for all four monkeys in which the known set was selected. During the training trials, perfect performance would have led to an average of 4.4 pellets per trial. The monkeys consistently rejected three or fewer items in the known set and instead selected the unknown option at levels significantly higher than chance, all $p < 0.05$, binomial tests (these and all further binomial tests were two-tailed). For four items, they were indifferent between the two choices in the Conspecific Absent condition ($p > 0.05$, binomial test) but significantly preferred the known set in the Conspecific Present condition ($p < 0.05$, binomial test). For more than four items, they preferred the known set at levels greater than chance, all $p < 0.05$, binomial tests. Chi square tests for independence showed no difference in the frequency of selection of the known set between the Conspecific Present and Conspecific Absent conditions for any of the known quantities [all χ^2 (df = 1) <1.70, $p > 0.05$]. Thus, there was no effect of unselected sets going to the conspecific or not.

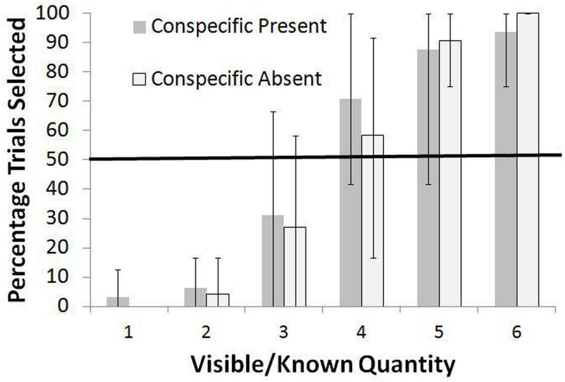

FIGURE 2 | Overall percentage of trials in which the known set was selected when paired with an unknown set in the Standard test. Data are shown for all monkeys combined and are separated at each known quantity into the Conspecific Present and Conspecific Absent conditions. Bars show the range of responses across the monkeys.

The results for the Shifting Average Condition are shown in **Figure 3A** for the smaller range and in **Figure 3B** for the larger range. During the training trials for the smaller range, perfect performance would have led to an average of 4.67 pellets per trial. Because of the lower trial counts, we combined some of the known quantity values to contrast low values, intermediate values, and high values. For test trials in the smaller range, the monkeys consistently rejected three or fewer items in the known set and instead selected the unknown option at levels significantly higher than chance, $p < 0.05$, binomial test. For four items, they were indifferent between the two choices in the Conspecific Present condition and the Conspecific Absent condition ($p > 0.05$, binomial test). For more than four items, they showed a preference for the known set, selecting that set on 16 of 16 trials in the Conspecific Present condition and 14 of 16 trials in the Conspecific Absent conditions, both $p < 0.01$, binomial test. A chi square test for independence showed no difference in the frequency of selection of the known set between the Conspecific Present and Conspecific Absent conditions across all known quantities [all χ^2 $(1, N = 48) < 1.00$, $p > 0.05$].

For the larger range, the pattern was similar. During the training trials for the larger range, perfect performance would have led to an average of 8.16 pellets per trial. In test trials of the larger range, the monkeys preferred the unknown option in both Conspecific Present and Conspecific Absent conditions when the known option now was six items or less (both $p < 0.01$, binomial tests), they were indifferent when the known option had eight items (both $p > 0.05$, binomial tests), and they preferred the known set when it had more than eight items (both $p < 0.05$, binomial tests). And, again, there was no difference in the frequency of selection of the known set between the Conspecific Present and Conspecific Absent conditions across the known quantities [all χ^2 $(1, N = 48) < 1.00$, $p > 0.05$].

The two quantity ranges in this part of the experiment shared three common quantities (four, six, and eight) that were presented as the known set, and the choice of those quantities was significantly different depending on whether they were presented as part of the small or large range. For the small range, known sets with four items were chosen more often than for the large range, χ^2 $(1, N = 64) = 4.06$, $p < 0.05$. This was also true for known sets of six items, χ^2 $(1, N = 24) = 14.18$, $p < 0.05$, and for known sets of eight items, χ^2 $(1, N = 40) = 5.38$, $p < 0.05$.

For the Extreme Wins/Losses Condition, the mean number of items obtained if perfect during the training trials was 5.5 items. The results for this condition are shown in **Figure 4**. The monkeys consistently rejected five or fewer items in the known set and instead selected the unknown option at levels significantly higher than chance, all $p < 0.05$, binomial tests. For more than five items, they preferred the known set at levels greater than chance, all $p < 0.05$, binomial tests. Once again, there was no difference in the frequency of selection of the known set between the Conspecific Present and Conspecific Absent conditions for any of the known quantities [all χ^2 $(\mathrm{df} = 1) < 1.00$, $p > 0.05$].

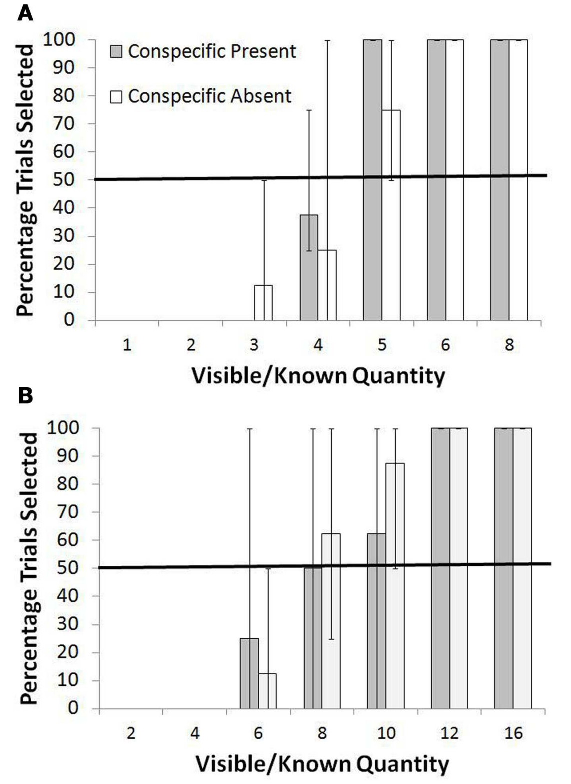

FIGURE 3 | Overall percentage of trials in which the known set was selected when paired with an unknown set in the Shifting Average test. (A) Shows performance with the smaller range of quantities, and **(B)** shows performance with the larger range of quantities. Bars show the range of responses across the monkeys.

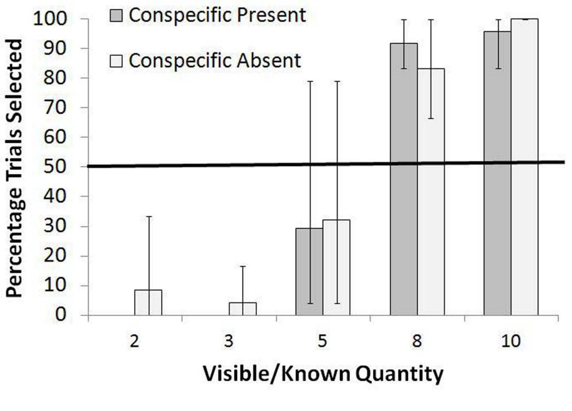

FIGURE 4 | Overall percentage of trials in which the known set was selected when paired with an unknown set in the Extreme Wins/Losses test. Bars show the range of responses across the monkeys.

DISCUSSION

All four focal monkeys performed in a similar manner, and replicated their performance in the earlier experiment on estimating uncertain outcomes in a quantity judgment task (Beran et al., 2012). They approached the trials with incomplete information by responding on the basis of using the approximate average number of items they had received to that point in the test session (during the training trials). If the known quantity was smaller than that amount, they generally gave up that option and instead took the unknown quantity. If the known amount was as large as, or larger than, the average, they selected it. As in the previous studies of this type (Beran et al., 2009, 2012), this performance was not based on some absolute value that was always the threshold for selecting the known set. In the Shifting Average condition, where we could double or halve the average from session to session, the monkeys changed their threshold to accompany those changes. This means that the monkeys did shift their indifference point across the two ranges, in a manner consistent with continued use of the average number of items obtained in training (4.67 for the smaller range and 8.16 items for the larger range if one assumes every training trial was completed correctly). This demonstrated their flexibility in using the heuristic to deal with unknown and incomplete information.

As with the data reported by Beran et al. (2009), it is important to note that the arithmetic mean is not the only measure of central tendency that might be used by non-human animals in this kind of situation. It is sometimes reported that in tests of quantity estimation or comparison that animals' responses are best accounted for by use of the geometric mean (the square root of the product of the anchor values; Roberts, 2005; Jordan and Brannon, 2006; Beran et al., 2008). For the specific quantities in each range we used in this experiment, the geometric means and the arithmetic means were quite similar (range 1–6: geometric mean = 2.99, arithmetic mean = 3.5; range 1–8: geometric mean = 3.44, arithmetic mean = 4.14; range 2–16: geometric mean = 6.89, arithmetic mean = 8.28). Thus, it is difficult to determine which measure of central tendency might have been used by the animals. Future research will be needed to better establish this.

What was novel in the present experiment was the introduction of a social component to the test, and a highly salient one in terms of the task setup. Now, on half of the sessions, the focal monkey watched as its unchosen set was given to a conspecific, who was allowed to eat those pellets in full view of the focal monkey. Although during training trials the focal animal nearly always got the larger amount, the monkeys still observed and attended to the smaller amount being given to the conspecific. Also, during trials with incomplete information, it was possible for the partner animal to get the larger amount, as when a known set was selected by the focal animal but the unknown set was larger, or when the focal monkey selected an unknown set that turned out to be smaller than the known set.

It was also a new manipulation that the focal monkey now got to see the unchosen set on test trials where it took the known quantity. In the past, the monkeys never knew what they forewent in making their selection in the uncertain trials (Beran et al., 2012), whereas here they could see whether choosing the known quantity ended up being a good choice, or a bad one, in terms of the amount of food in the unknown set. However, these new aspects to the methodology appeared to have no effect on the decisions made by focal monkeys, at least as they pertained to the choice behavior. However, what is not clear is whether seeing food items given to other animals might change the "running average" held by a subject in other circumstances. For example, the monkeys may have reacted differently if the set given away was unexpectedly larger than would have been predicted by what had occurred to that point in the session. Perhaps more extreme outcomes, coupled with the social manipulation, would change the performance of monkeys in making these judgments.

Putting animals in tests in which there is actual competition, the appearance of competition, or even just situations in which conspecifics are given food for the efforts of the subject, can change the behavior and performance of the focal subject (e.g., Washburn et al., 1990). This can be true even at the level of judging the perspective of others. For example, chimpanzees and rhesus monkeys seemed to respond differently in judging other animals' visual knowledge when placed in a competitive task versus a non-competitive task (Tomasello and Call, 1997; Povinelli, 2000; Hare et al., 2001; Flombaum and Santos, 2005). This effect, however, does not seem to occur for perception of quantity, even in contexts in which judgments about the likelihood of getting more food for taking a risk occurs. Rather, the capuchin monkeys in this experiment, when faced with incomplete information, seemed to disregard the presence or absence of a conspecific that received whatever the subject did not choose. Instead, the monkeys sustained what appeared to be an optimal heuristic response in using the average number of pellets they had been receiving up to that point in the session as a threshold for making choices when they could not know both sets. Prior experience from earlier studies along with information feedback may have impacted the monkeys' reliance on the heuristic, potentially overshadowing any deleterious effects of a competitive-like situation. Thus, perception and decision-making in a quantity judgment task appear to be insulated from any negative effects of a more competitive test environment, although other more overt manipulations to an animal's social environment might yet evoke less optimal responding.

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Prosimian primates show ratio dependence in spontaneous quantity discriminations

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We directly tested the predictions of the approximate number system (ANS) and the object file system in the spontaneous numerical judgments of prosimian primates. Prior work indicates that when human infants and a few species of non-human animals are given a single-trial choice between two sequentially baited buckets they choose the bucket with the greater amount of food but only when the quantities are small. This pattern of results has been interpreted as evidence that a limited capacity object file system is used to track small numbers of objects and that the ANS is not invoked under these circumstances. Here we tested prosimian primates in food choice comparisons that were chosen to contrast predictions of the ANS and object file systems. We found that prosimian primates consistently chose the larger of two sets when they differed by a 1:3 ratio regardless of whether both values were small (≤ 3), both values were large (>3), or there was one small and one large value. Prosimians were not able to robustly discriminate quantities that differed by a 1:2 ratio for the same three conditions, nor did they show a preference for small quantities that differed by a 2:3 ratio. These results implicate the ANS in the spontaneous numerical discriminations of non-human primates.

Keywords: non-human primates, numerical cognition, quantity discrimination, prosimians, numerosity, ratio dependence, object file

Preverbal human infants and a few non-human animal species have exhibited two contrasting patterns of behavior when faced with quantity judgments. In some tasks, performance is independent of set size and is modulated by the ratio between the two values being compared. In other tasks, successful discrimination is limited to very small values and shows no signs of ratio dependence. This has led to the proposal that there are two cognitive systems that underlie non-verbal numerical discrimination: a limited capacity object file system, which allows the accurate representation of a small number of objects through attentional tracking, and an approximate number system (ANS), which is ratio-dependent and has no upper limit in its capacity (e.g., Uller et al., 1999; Feigenson et al., 2004). The ANS is ubiquitous throughout the animal kingdom and has been shown to operate for large values throughout human development and adulthood (for reviews, see Brannon, 2006; Beran, 2008c). The object file system has been well-documented in human infants under a limited set of circumstances (e.g., Feigenson et al., 2002; Feigenson and Carey, 2003, 2005), and to a much lesser extent, in non-human animals (e.g., Hauser et al., 2000; Agrillo et al., 2007, 2008; Rugani et al., 2008; Uller and Lewis, 2009).

Object files are not explicitly numerical representations, but instead represent individual objects in attention. Each object file "sticks" to a unique object as it moves about the visual scene, and may contain identity or featural information (Kahneman et al., 1992). The object file system represents individuated objects, with the number of open object files providing an implicit way to represent the numerosity of a set. However, as only three or four object files can be maintained simultaneously, the ability of this system to provide a means of representing numerosity is limited to small numbers (e.g., Feigenson et al., 2002; Feigenson and Carey, 2003, 2005; vanMarle, 2013; but see Alvarez and Cavanagh, 2004; Alvarez and Franconeri, 2007).

In contrast, the ANS represents the cardinality of a set of objects as a single mental magnitude. The ability to discriminate between two numerosities in the ANS is ratio-dependent, in accordance with Weber's Law and is not limited by set size. Small values that are within the capacity of the object file system could be represented with greater precision than the ANS can afford. Thus babies and animals, both of which lack a verbal counting system, could potentially maximize reward in food choice paradigms were they to use the object file system to discriminate small pairs accurately and the ANS to discriminate large pairs approximately.

Studies in animals and human infants typically show ratio dependence across the entire range (e.g., Cantlon and Brannon, 2006b; Beran, 2007; vanMarle and Wynn, 2009) or alternatively show a set size limit such that if either numerosity exceeds the limit, discrimination drops to chance levels of accuracy (e.g., Hauser et al., 2000; Feigenson et al., 2002). However, recent work by Agrillo et al. (2008, 2012) indicate ratio dependence for large values, but not for the values 1–4 in both humans and fish. There is convergent evidence from multiple behavioral paradigms that human infants discriminate between small numerosities (≤ 3) accurately (e.g., Starkey and Cooper, 1980; Strauss and Curtis, 1981; Wynn, 1992; Koechlin et al., 1997; Feigenson et al., 2002; Feigenson and Carey, 2003, 2005; Xu, 2003; Wood and Spelke, 2005). A subset of these studies have provided strong evidence for the object file system as opposed to the ANS, specifically success with small values (≤ 3) at a given ratio and simultaneous failure with large sets (>3) at the same ratio (e.g., 2 vs. 3 and 6 vs. 9). The food choice task used by Feigenson and colleagues has repeatedly shown a set size limitation in quantity discriminations in infants (Feigenson et al., 2002; Feigenson and Carey, 2005). In this paradigm, infants are shown food items being dropped into two opaque containers and then allowed to approach one of the containers and consume its contents. Feigenson et al. (2002) demonstrated that 10–12 month old infants reliably crawled to the container with a greater number of food items when both contained three or fewer food items. Thus, 10 and 12 month old infants succeeded at choosing the larger in a 1 vs. 2 and a 2 vs. 3 condition, but performed at chance in a 2 vs. 4 or a 3 vs. 6 condition. Controls for overall duration, complexity, and motivation caused no change to this pattern of performance. In a separate experiment, they demonstrated that infants performed at chance in a 1 vs. 4 condition, but successfully chose the larger in a 0 vs. 4 condition, indicating that infants were capable of representing the existence (vs. non-existence) of crackers, but were unable to compare two numerical values if one exceeded the object file limit (Feigenson and Carey, 2005).

Set size limitations consistent with the object file system have also been reported in numerical discriminations by non-human animals, although there is far more evidence for the ratio-dependent hallmark of the ANS. Hauser et al. (2000) used a single-trial food choice task similar to the food choice task used by Feigenson et al. (2002) with semi free-ranging, untrained rhesus macaques. Monkeys watched as apple slices were placed into each of two opaque boxes. Monkeys were then allowed to approach and consume the apple slices in one box. The monkeys chose the greater number of apple slices as long as the contents of each box did not exceed the set size limit of 4. On comparisons where one box exceeded that limit the monkeys performed at chance, showing no preference for the greater number of food items. This was true even with favorable ratios: 4 vs. 8 and 3 vs. 8. Oddly however, monkeys successfully discriminated 3 vs. 5 in the same study. Wood et al. (2008) demonstrated a set size limitation with non-solid food portions in the same population of rhesus macaques.

Beyond primates, set size limitations have been demonstrated in the spontaneous choices of animals as diverse as horses (Uller and Lewis, 2009), amphibians (Uller et al., 2003), and fish (Agrillo et al., 2007). Agrillo et al. (2007, 2008) found the set size limit (≤ 3) characteristic of the object file system in the numerical comparisons of mosquito fish, such that fish were more likely to move toward the larger of two shoals in comparisons of 1 vs. 2, 2 vs. 3, and 3 vs. 4, but were not more likely to select the larger shoal for comparisons of 4 vs. 5, 5 vs. 6, 6 vs. 7, or 7 vs. 8. Importantly, Agrillo and colleagues also showed evidence of ratio-dependent performance with large numbers such that they were able to discriminate large numbers at a 1:2 ratio (e.g., 8 vs. 16), but failed at a 2:3 ratio (8 vs. 12).

Two studies have documented a set size limit in the ability to train animals to discriminate between visual arrays. Rugani et al. (2008) trained young chicks to peck at arrays of dots depending on their numerosity. Chicks successfully learned to discriminate 2 vs. 3, but failed to learn to discriminate 4 vs. 6, which suggests that the animals were using the object file system rather than the ANS. Gross et al. (2009) showed a similar result with honeybees: bees successfully learned to distinguish between 2 and 3, but not 4 and 6 items.

One possibility is that untrained animals spontaneously invoke the object file system whenever they are faced with quantity comparisons. However, this hypothesis is not supported by the fact that untrained animals have in some circumstances exhibited ratio-dependent performance indicative of the ANS (e.g., Hauser et al., 2003; Flombaum et al., 2005). Thus, lack of training is insufficient to selectively invoke the object file system over the ANS for numerical comparisons. Nor is the food choice task itself sufficient to reliably tap the object file system. Non-human primates trained and tested on a food choice task have shown ratio-dependent discrimination of simultaneously visible sets (e.g., Anderson et al., 2007; Hanus and Call, 2007; Addessi et al., 2008) and of sequentially presented sets (e.g., vanMarle et al., 2006; Hanus and Call, 2007).

The majority of research on numerical abilities in non-human primates has focused on a few representative species: rhesus macaques, capuchin monkeys, and chimpanzees (e.g., Boysen and Berntson, 1989; Brannon and Terrace, 1998, 2000; Hauser et al., 2000; Cantlon and Brannon, 2006a,b, 2007a,b; Beran, 2007, 2008a,b; Addessi et al., 2008; Beran et al., 2008; Tomonaga, 2008). Very few studies have examined numerical abilities in prosimian primates (e.g., Lewis et al., 2005; Santos et al., 2005; Merritt et al., 2011; Jones et al., submitted). Including prosimian primates in comparisons of primate cognition is likely to be important in attempting to identify cognitive profiles of the primate ancestral state. Prosimian primates have been hypothesized to be morphologically and behaviorally similar to the last common primate ancestor (Tattersall, 1982; Yoder, 2007). Thus, if prosimians primates share cognitive traits that are common among other primates, it is likely that these traits were present in the last common ancestor.

Lewis et al. (2005) showed untrained mongoose lemurs grapes sequentially placed into a bucket with a false bottom. The experimenter surreptitiously hid some subset of the grapes in the false bottom. When the lemurs were allowed to retrieve the grapes from the bucket, they were predicted to search longer if they expected there to be more grapes than they had already retrieved from the bucket. Lewis et al. (2005) reported a pattern of results consistent with ratio-dependent numerical discrimination.

In contrast to the Santos et al. (2005) and Lewis et al. (2005) studies which examined spontaneous numerical discrimination, Merritt et al. (2011) and Jones et al. (submitted) used a touch-screen task to measure numerical comparison abilities in lemurs and macaques. Both studies showed the ratio-dependent hallmark of the ANS in these numerical comparisons. Jones et al. (submitted) tested three different lemur species and macaques and found overlapping numerical acuity for the four species. Thus, to date, both spontaneous numerical comparisons and training have led to evidence for the ANS in lemurs. However, it is important to note that while Lewis et al. (2005) used a spontaneous measure of numerical discrimination, each subject participated in multiple trials. As repeated trials may increase the likelihood of cuing the ANS (vanMarle et al., 2006), it is unclear whether prosimian primates will show a set size limit consistent with object file representations, or the ratio dependence of the ANS, in a single-trial measure of spontaneous numerical comparisons.

Here we use a modified spontaneous food choice task based on Hauser et al. (2000) and Feigenson et al. (2002) to test the spontaneous quantity discriminations of prosimian primates housed at the Duke Lemur Center. We chose a set of numerical values that directly contrasted the predictions of the object file and ANS proposals (see **Table 1**). We used a 2 × 3 design. There were two numerical ratios (1:2 and 1:3) and three magnitude conditions (small–small, small–large, and large–large).

An object file system would be implicated if: (1) Accuracy was significantly above chance levels of performance only when both numerosities were smaller than the set size limit. (2) Accuracy drops to chance for pairs of numerosities that exceed the set size limit even when the ratio between them is successfully discriminated with smaller numbers (e.g., success at 2 vs. 3 and failure at 4 vs. 6). In contrast, the ANS would be implicated if: (1) Lemurs successfully discriminate pairs with large values, (2) Lemurs show ratio-dependent response functions, with accuracy dropping to chance as the ratio (larger/smaller) approaches 1. A third possibility is that lemurs use object files to represent small values and ANS representations to handle large values but that they are unable to compare incommensurate representations from two different systems and consequently perform at chance on small–large comparisons (e.g., Xu, 2003).

EXPERIMENT 1

METHODS

Subjects

Subjects were 113 diurnal and cathemeral prosimian primates (61 females and 52 males; mean age 13.01 years, SD 9.57), housed at the Duke Lemur Center. Each subject participated in one condition with the exception of seven subjects that participated in two conditions, resulting in 120 total trials. Twenty-seven additional trials were excluded due to subject's failure to participate ($N = 22$) or experimenter error ($N = 5$).

The 120 trials consisted of 20 trials for each of six conditions: two numerical ratios (1:2 and 1:3) and three magnitude pairings (small–small, small–large, and large–large). Participants included individuals from five different genuses and 15 different species (**Table 2**). Members of each genus were equally distributed among the six conditions, such that each condition contained five *Lemurs*, eight *Eulemurs*, three *Varecia*, three *Propithecus*, and one *Hapalemur*. All animal procedures were conducted in accordance with a Duke University IACUC protocol.

Table 1 | Predictions of the object file system, the ANS, and the two system theory of numerical discrimination for success (✓) or failure (x) in each of the conditions of Experiment 1.

	Quantities	Object file system	ANS	Both systems – incommensurate representations
1:3 ratio	1 vs. 3	✓	✓	✓ (Object file)
	2 vs. 6	X	✓	X
	4 vs. 12	X	✓	✓ (ANS)
1:2 ratio (if 1:2 is beyond the sensitivity limit of the ANS for this task)	1 vs. 2	✓	X	✓
	3 vs. 6	X	X	X
	6 vs. 12	X	X	X

PROCEDURE

Set up

Each subject remained in its home enclosure for testing, but was temporarily restricted from access to cage mates. Each subject was assigned quasi-randomly to one condition. Each trial involved three experimenters. One experimenter operated the camera (E1) and the other two experimenters dropped food items into the buckets (E2 and E3). The numerical conditions were assigned before testing and were known only to E1. E1 gave E2 and E3 each an index card that indicated the number of food items they were to drop into their bucket, which side they were to stand on (left or right), and whether they were to bait the bucket first or second. Experimenters were blind to the number of food items the other experimenter was baiting.

On each trial E2 and E3 stood 2–3 feet apart, immediately outside of the subject's enclosure, and each held a black bucket that was approximately 30 cm in diameter and 25 cm in height. E1 stood behind the other two experimenters. At the onset of each trial E1 said "start" at which point the two experimenters faced the cage and tipped their buckets on their sides to show the subjects that the buckets were empty.

Presentation

E2 and E3 held the buckets with both hands at chest level. E3 closed his/her eyes and remained motionless as E2 baited the bucket with raisins or nuts (depending on dietary restrictions of each species). Each food item was removed from the experimenter's left breast pocket and held up for the subject to see. Once the experimenter was certain the subject had seen the food item he/she placed it in the bucket. This was repeated until E2 had presented all food items, at which point he/she said "done" and closed his/her eyes. E3 then opened his/her eyes and baited the bucket following the same procedure including stating "done" and closing his or her eyes.

After all food items were presented, E1 determined when the subject had moved to a location approximately equidistant from both buckets and/or averted their gaze from either bucket. E1 then said "buckets down," at which point E2 and E3 opened their eyes, crouched down and simultaneously set their buckets on the ground against the exterior cage wall. E1 and E2 then stood up, turned 180°, and walked to the other side of the hallway. E1 also turned 180° and watched the subject's choice via the small finder on the camera.

Selection

A trial ended when E1 determined that the subject had made a choice by moving in front of one of the two buckets and orienting toward it, or when 3 min passed and no choice was made (**Figure 1**). All data was re-coded by an independent observer who was blind to the hypotheses of the study.

Table 2 | A comprehensive list of the species used in each experiment.

Exp.	Genus	Species	*N*	Sex	Mean age (years)
1	*Eulemur*	*albifrons*	4	2 Females, 2 males	25.64 (SD 3.63)
		collaris	5	3 Females, 2 males	23.69 (SD 5.17)
		coronatus	6	4 Females, 2 males	15.65 (SD 8.62)
		fulvus	1	1 Female	26.64
		macaco flavifrons	8	3 Females, 5 males	10.84 (SD 9.91)
		macaco macaco	3	1 Females, 2 males	25.17 (SD 3.02)
		mongoz	8	4 Females, 4 males	15.31 (SD 8.31)
		rubriventer	7	3 Females, 4 males	22.35 (SD 4.04)
		rufifrons	1	1 Male	29.03
	Hapalemur	*griseus*	5	4 Females, 1 male	14.24 (SD 1.93)
	Lemur	*catta*	31	22 Females, 9 males	7.60 (SD 7.89)
	Propithecus	*coquereli*	16	8 Females, 8 males	8.65 (SD 7.17)
		diadema	1	1 Male	18.26
	Varecia	*rubra*	11	4 Females, 7 males	11.18 (SD 9.77)
		variegate	6	2 Females, 4 males	11.98 (SD 12.09)
2	*Eulemur*	*collaris*	1	1 Male	18.63
		coronatus	1	1 Female	16.87
		macaco flavifrons	3	2 Females, 1 male	7.95 (SD 11.21)
		macaco macaco	1	1 Male	23.09
		mongoz	2	2 Females	13.37 (SD 17.60)
	Hapalemur	*griseus*	1	1 Female	13.50
	Lemur	*catta*	5	4 Females, 1 male	5.57 (SD 3.80)
	Propithecus	*coquereli*	3	1 Female, 2 males	11.54 (SD 5.79)
	Varecia	*rubra*	2	1 Female, 1 male	15.51 (SD 16.69)
		variegate	1	1 Female	7.00
3	*Eulemur*	*albifrons*	1	1 Female	31.09
		collaris	2	2 Females	19.19 (SD 4.16)
		coronatus	1	1 Female	24.10
		macaco flavifrons	1	1 Male	1.22
		macaco macaco	2	1 Female, 1 male	24.71 (SD 3.52)
		mongoz	3	2 Females, 1 male	21.30 (SD 5.31)
	Hapalemur	*griseus*	1	1 Female	17.24
	Lemur	*catta*	2	1 Female, 1 male	5.10 (SD 2.82)
	Propithecus	*coquereli*	2	2 Males	9.82 (SD 10.41)

FIGURE 1 | A photograph of a ring-tailed lemur reaching into one of two buckets.

RESULTS

E1 and the independent observer agreed on which bucket had been chosen on 116 trials (96.67% agreement). For the four trials on which they disagreed, an additional experimenter blind to the condition coded the video and the majority decision was included. Furthermore, the coding of these four trials does not change the reported pattern of results.

Overall subjects selected the larger quantity more often than predicted by chance (82 out of 120 trials, $p < 0.001$). Binomial sign tests indicated that subjects chose the larger number of food items significantly more often than predicted by chance for 1 vs. 3 (16 out of 20 trials, $p < 0.01$, one-tailed), 2 vs. 6 (16 out of 20 trials, $p < 0.01$, one-tailed), and 4 vs. 12 (15 out of 20 trials, $p < 0.05$, one-tailed). In contrast, binomial sign tests indicated that subjects chose the larger number of food items no more often than predicted by chance for 1 vs. 2 (14 out of 20 trials, $p = 0.06$, one-tailed), 3 vs. 6 (10 out of 20 trials, $p = 0.59$, one-tailed), or 6 vs. 12 trials (11 out of 20 trials, $p = 0.41$, one-tailed). It should be noted that subjects showed a trend toward selecting the larger number for the 1 vs. 2 condition ($p = 0.06$; **Figure 2**).

EXPERIMENT 2

Given the trend toward selecting the larger in the 1 vs. 2 condition, the goal of Experiment 2 was to test lemurs with a 2 vs. 3 comparison which comprises a more difficult ratio but should be within the capacity of the object file system.

METHODS

Subjects

Subjects were 20 diurnal and cathemeral prosimian primates (13 females and 7 males; mean age 11.16 years, SD 8.74), housed at the

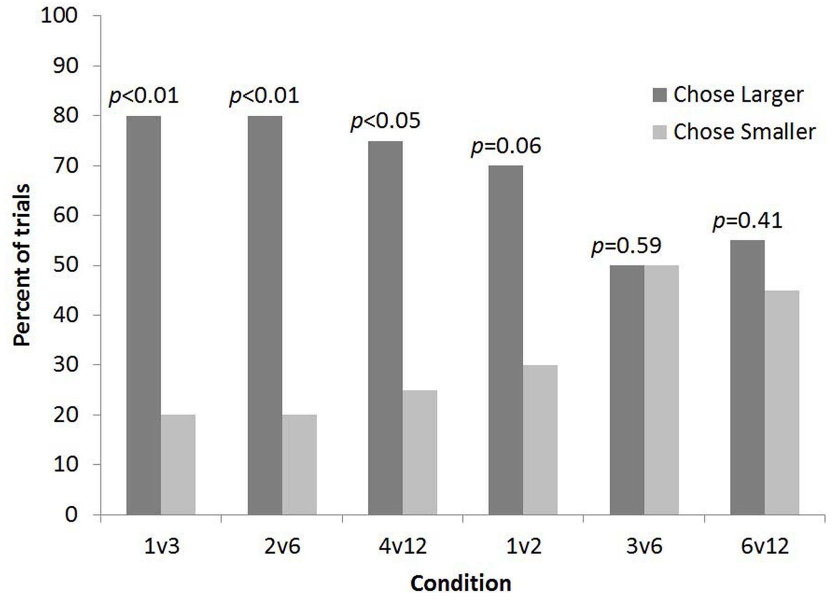

FIGURE 2 | The percent of trials lemurs chose the bucket with the smaller and larger number of food items for each condition in Experiment 1.

Duke Lemur Center. An additional five trials were excluded due to subject's failure to participate. Subjects represented a similar distribution of species as reported for the conditions in Experiment 1 (**Table 2**). Due to a limited number of naïve animals available for testing, 4 out of the 20 subjects had already participated in Experiment 1.

PROCEDURE

The procedure was identical to Experiment 1.

RESULTS

Subjects selected the larger quantity no more often than predicted by chance for 2 vs. 3 (8 out of 20 trials, $p = 0.25$, one-tailed; **Figure 3**). The four subjects who had been tested in Experiment 1 showed no consistent pattern of responding and the exclusion of these trials would not change the pattern of results: one chose the larger in both experiments, one chose the smaller in both experiments, one chose the larger in Experiment 1 but the smaller of 2 vs. 3, and one chose the smaller in Experiment 1 but the larger of 2 vs. 3.

EXPERIMENT 3

The goal of Experiment 3 was to provide a scent control. To this end we tested lemurs with a 2 vs. 6 comparison and pre-baited the bucket that was designated for the smaller quantity such that the two buckets provided the same olfactory cues.

METHODS

Subjects

Subjects were 15 diurnal and cathemeral prosimians (eight females and seven males; mean age 17.01 years, SD 9.53), housed at the Duke Lemur Center. Subjects represented a similar distribution of species as in Experiment 1 (**Table 2**). Thirteen out of 15 subjects had been previously tested in Experiment 1.

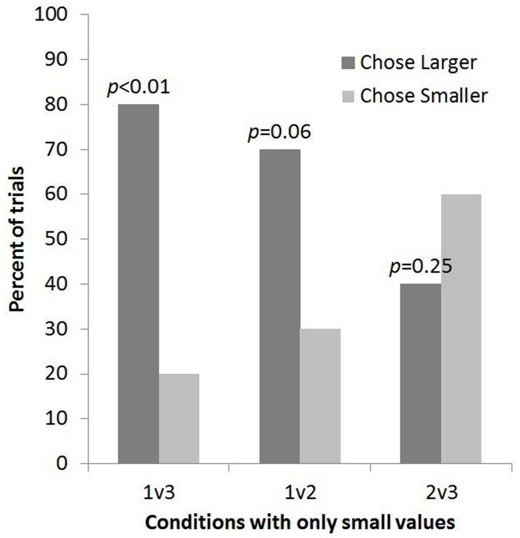

FIGURE 3 | The percent of trials lemurs chose the bucket with the smaller and larger number of food items for each condition in Experiment 2 (2 vs. 3 condition) alongside data from the other small number comparisons tested in Experiment 1.

PROCEDURE

The procedure was identical to Experiment 1 except that all trials consisted of a 2 vs. 6 comparison in which the bucket that was baited with two already contained four food items hidden in the bottom. This meant that when the baiting was complete, both buckets contained six food items providing the same olfactory cues[1].

RESULTS

Subjects chose the bucket into which they had observed six food items placed significantly more often than predicted by chance (12 out of 15 trials, $p < 0.05$, one-tailed).

GENERAL DISCUSSION

Our findings provide little support for the idea that prosimian primates use object file representations to track food items. Instead the data are consistent with the idea that lemurs spontaneously represent and compare quantities using the ANS. Subjects were able to successfully select the larger quantity with a 1:3 ratio but not a 1:2 ratio or a 2:3 ratio. The fact that lemurs were able to successfully discriminate two from six is also counter to the predictions of incommensurate representations. Failure to differentiate two from three food items further suggests that ratio dependence rather than set size limited their performance. It is important to note that this does not indicate that lemurs are incapable of discriminating small values. Indeed, our results indicate that they are just as capable of discriminating small values as large values. Instead, this points to a ratio-dependent system that is equally sensitive across magnitudes.

Is the reason our results differ from others due to genus or species differences? Other work from our research group suggests that lemurs and monkeys have quantitatively similar numerical discrimination capacities (Jones et al., submitted). In that study, rhesus macaques, ring-tailed lemurs, mongoose lemurs, and blue-eyed black lemurs were trained to select the numerically larger of two visual arrays on a touch-screen. Despite the large variation in social structure, home range size, and diet in the species tested, all four species showed similar weber fractions. Thus, we find it unlikely that the lack of evidence for a set size limit in the spontaneous numerical comparisons of lemurs reflects a difference between prosimian primates and old world primates. Alternatively, the lack of evidence for a set size limit reported here may reflect subtle differences in the testing conditions in our study and the prior studies with rhesus macaques (Hauser et al., 2000; Wood et al., 2008). Candidates for these factors include, but are not limited to, satiation, inhibition, arousal, competition, dominance, and inadvertent social cues from the experimenter. For example, testing conditions differed from Hauser et al. (2000) in that while the macaques were semi-free-ranging, the subjects in the present study were caged and were separated briefly from conspecifics during testing to reduce interruptions and competition. Future research will need to address the contexts that cue the object file system in spontaneous discrimination tasks.

While we did include Experiment 3 to provide a scent control condition, we did not include a control for auditory cues or total duration. Previous research using this task have included such controls with infants and monkeys and resulted in no change to the pattern of responding (Hauser et al., 2000; Feigenson et al., 2002). Given these previous findings, we believe it is unlikely that controls for auditory cues or duration would impact performance in this task however we cannot rule out these alternative possibilities.

We made an additional modification of the protocol used by Hauser et al. (2000) that may account for different patterns of results by attempting to eliminate the possibility of a *Clever Hans effect*. In the majority of quantity discrimination research, the experimenters presenting food items have been aware of which container held the larger quantity. It is thus possible that subjects made selections based on unintentional social cues from the experimenters. We established a simple modification to the design, which allowed the experimenters presenting food items to be blind to the condition on any given trial. At the time of testing, each experimenter was given an index card that indicated the number of food items they were to drop into their bucket and they were unaware of the number being baited in the other bucket.

A number of authors have proposed that small quantities may be represented by both ANS and object file systems, and that contextual factors may determine which system is cued (e.g., Wynn et al., 2002; Feigenson, 2005; Barner et al., 2008; Cordes and Brannon, 2008, 2009; Hyde, 2011). The simplest possibility is that different systems are used when animals make spontaneous judgments compared to when they perform tasks for which they have extensive training. Hauser and others suggested that the object file system might be primary when animals engage in spontaneous numerical judgments without training and that extensive training might be required for animals to represent large values outside the purview of the object file system (Hauser et al., 2000; vanMarle et al., 2006). However, we tested untrained animals in the same spontaneous cognition circumstances and found no evidence for the object file system. These results emphasize the importance of selecting values that can directly contrast the predictions of two systems and test the limits of each system.

Others have proposed more nuanced explanations for the contextual factors that elicit object file vs. ANS representations. For example, a recent study showed that exact enumeration of small numbers (<4) is inhibited during a task with high attentional load, but approximate numerical representation is not (Burr et al., 2010; but see Vetter et al., 2008, for contrasting evidence that the enumeration of both small and large numbers is equally affected by attentional resources). Another study showed that individual differences in small number representation correlated with working memory, but ANS acuity did not (Piazza et al., 2011). Hyde and Wood (2011) suggested that spatial attention impacts which system will represent the numerical value of a small set (1–3 items). Specifically, they report that when the spatial distribution of visual objects allowed for individuation, ERP responses showed a pattern consistent with parallel individuation. In contrast, when attention could not select individual objects, ERP responses showed a pattern consist with ratio dependence. Hyde (2011) hypothesized that conditions that allow attentional selection of individuals cue the object file system, while conditions in which items are presented outside attentional limits result in approximate numerical representations. Our findings do not support this hypothesis: small quantities were presented sequentially without additional attentional requirements, and yet still resulted in approximate representations.

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[1] In contrast to Experiments 1 and 2, experimenters were not blind to the number of food items the other experimenter was baiting.

Other explanations for the contextual factors that elicit object file vs. ANS representations involve features of the sets, such as heterogeneity and movement. Feigenson and colleagues (Feigenson et al., 2002; Feigenson, 2005) reported a double dissociation in infants' representations of small object arrays such that infants responded to changes in the numerosity of heterogeneous, but not homogeneous arrays when area is controlled for. Additionally, several authors have proposed that the movement of items within a set may impact which system of representation is elicited. Wynn et al. (2002) and Barner et al. (2008) suggested that objects which undergo common motion are more likely to be represented as a collective entity than objects that move independently. For example, when all objects within a set move together, two sets of five elements may be more likely to be perceived as two entities than as 10 independent objects. Thus, common motion may result in an array being represented as a single set with an approximate numerical magnitude.

As our paradigm involved individually presented food items, we cannot address these hypotheses regarding heterogeneity or common motion. It is clear, however, that multiple contextual factors appear to be involved in eliciting object file or approximate representations, rather than a simple explanation in which different systems are used for spontaneous judgments and trained numerical tasks. It is important to note that we do not claim that our results mean that lemurs, or non-human primates more generally, never use the object file system. Rather, we argue that a spontaneous food choice task is not a sufficient context to elicit a set size limit on quantity discrimination and that the ANS is robust even over these spontaneous decisions.

In sum, by employing conditions designed to specifically address the predictions of the ANS and the object file system, we found that spontaneous numerical comparisons in prosimian primates are likely to be driven by the ANS. Given these results, the factors that may lead non-human primates to compare quantities using the object file system rather than the ANS remain unclear. What is clear, however, is that the ANS is spontaneously accessed by non-human primates to compare quantities regardless of the magnitude of those values being tested.

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Ten-month-old infants' reaching choices for "more": the relationship between inter-stimulus distance and number

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Animals and human infants discriminate numerosities in visual sets. Experiments on visual numerical judgments generally contrast sets in which number varies (e.g., the discrimination between 2 and 3). What is less investigated, however, is set density, or rather, the inter-stimulus distance between the entities being enumerated in a set. In this study, we investigated the role of set density in visual sets by 10-month-old infants. In Experiment 1, infants were offered a choice between two sets each containing four items of the exact same size varying in the distance in between the items (ratio 1:4). Infants selected the set in which the items are close together (higher density). Experiment 2 addressed the possibility that this choice was driven by a strategy to "select all in one go" by reducing the size and distance of items. Ten-month-olds selected the sets with higher density (less inter-stimulus distance) in both experiments. These results, although bearing replication because of their originality, seem consistent with principles in Optimal Foraging in animals. They provide evidence that a comparable rudimentary capacity for density assessment (of food items) exists in infants, and may work in concert with their numerical representations.

Keywords: density assessment, number, infancy, representation

INTRODUCTION

From neonates and pre-crawling babies, to toddlers and preschoolers, research indicates that numerical representations may be found early in development. While some researchers reach consensus that numerical understanding exists early in infancy, perhaps even innately (Uller et al., 1999; Feigenson et al., 2004; Cordes et al., 2007; Spelke and Kinzler, 2007; Cordes and Brannon, 2008; Uller, 2008), others prefer to claim that most numerical representations in children develop as a function of learning (e.g., Piaget, 1952). Another point of contention regards the nature of these abilities. Some argue that such representations may be conceptual (e.g., Carey, 2009), while others would prefer to link these abilities to perceptual cues (Clearfield and Mix, 2001; Cohen and Marks, 2002; Clearfield and Westfahl, 2006). Although several studies have used stimuli in a more "abstract" format to show that infant numerical abilities cannot be explained solely on the basis of a perceptual mechanism (auditory sets: Lipton and Spelke, 2003; events: Wynn, 1996; Wood and Spelke, 2005; cross-modal: Starkey et al., 1983; Feigenson et al., 2002; Kobayashi et al., 2004; Kobayashi et al., 2005; Uller, in preparation), researchers do not unanimously agree that these results may be indicative of a rudimentary form of numerical representations.

Another area of investigation to challenge the perceptual-only hypothesis comes from evidence that infants can approximate the number of items in large sets (e.g., visual objects: Xu and Spelke, 2000; Brannon, 2002; Brannon et al., 2004; puppet jumps: Wood and Spelke, 2005; auditory sets: Lipton and Spelke, 2003). For example, given a choice between two quantities, 8 versus 16, infants will discriminate between the two sets, either whether habituated to 8 or 16. These findings show that infants are not only able to represent small sets, but are also able to discriminate large sets, an ability which requires, at a very minimum, a representation of amount.

Control experiments contrasting number with variables such as cumulative surface area, perimeter contour, etc., also represent a challenge to perceptual explanations. Most of the number studies with infants control for various continuous variables, and the results suggest that the discriminations infants make are based on number (e.g., Xu and Spelke, 2000; Lipton and Spelke, 2003; Brannon et al., 2004; Xu and Arriaga, 2007; Cordes and Brannon, 2008). Cordes and Brannon (2008), for example, showed six-month-old infants conditions where cumulative surface area remained constant but number varied in a visual discrimination task. The babies detected the changes based on number rather than tracking total continuous extent of stimulus surface area.

While there is an emerging bulk of evidence for the number argument, contention with regards to variables which confound with number still persists. An aspect of visual sets controlled for is inter-stimulus distance, or set density. The adult visual perception literature on the relation between number and density seems to indicate that, in adults, estimated numerosity and density are negatively correlated (Krueger, 1972, 1984; Allik and Tuulmets, 1991, 1993; Durgin, 1995). For example, in the perception of dot patterns, dots are understood as less numerous when bunched together than when spread out (Krueger, 1972). Similarly, when judging relative numerosity, adults will judge as more numerous the dot pattern that occupies the larger space (Allik and Tuulmets, 1991).

In children, the first observation by Piaget (1952; Piaget and Inhelder, 1969) of the relationship between density and number was found in conservation tasks. Children 6–7 years of age were shown two lines of objects – eggs and egg cups – placed in one-to-one correspondence with equal inter-stimulus distances. After stipulation that the sets contained the same number, the children saw one set spatially transformed: the distance between the egg cups was increased. The children then saw the lengthened set as containing more. Piaget drew a few conclusions: children understand spatial displacement as a dimension relevant to number, and children do not understand that number is invariant, that physical attributes of sets are irrelevant to the (abstract) computation of number (Piaget and Inhelder, 1969; Gelman and Baillargeon, 1983). These observations by Piaget, together with the evidence from the adult literature on the perception of number and density, lead to the conclusion that, the more spread items are, the more likely we are to perceive number as "more."

Speculations on the basis of experiments with animals, however, are driven by another set of findings. Quantity assessment of food items in patches of potential foraging by animals have been observed and analyzed by theories of optimal foraging (MacArthur and Pianka, 1966; Pyke et al., 1977; Stephens and Krebs, 1986) which predict that animals go for more. Animals evolved foraging strategies that maximize their net energy gain when foraging, namely, the energetic profit when foraging exceeds the energetic loss during foraging.

Suppose you are a baboon. You're hungry. In the Namibian desert, food is scarce. You need to be selective where you forage in order not to waste energy and die. You strike lucky, and find two bushes of edible fruit to be harvested from. It is a simple matter: you'll go for the bush containing more items. Evidence for non-human animal (monkeys: Hauser et al., 2000; horses: Uller and Lewis, 2009; salamanders: Uller et al., 2003) and human baby (Feigenson et al., 2002) selection of the larger of two sets is widespread. Now suppose, theoretically, that the shrubs you are assessing as possible feeding sources contain the same number of food items of same size. Which bush will you choose: the one in which the fruit are spread apart, or the one in which the fruit are close together? One of the chief constructs of Optimal Foraging models concerns energy expenditure. Marginal Value Theorem (Charnov, 1976) predicts when an animal should move to a new patch based on rate of return. There is a point when an animal would spend more energy searching for the next item within its current patch than it would to physically move to a new patch containing more items. Rate of return is correlated with the density of items within a patch. The closer packed items are within a patch, the less energy the individual will spend moving between the items. It is theoretically possible that the net gain of energy for a patch containing more items could be less than for a patch containing fewer items, if those items were spaced so widely apart that the animal wasted energy traveling between them. It would be highly adaptive for an individual to be sensitive not only to the number of items within a patch but also their relative density.

These two theoretical constructs – theories of numerosity perception in adults and Piagetian assessments in conservation tasks, versus optimal foraging theory – generate conflicting predictions. Optimal Foraging Theory would predict a choice for *more* – the closer together items are (more dense), the less energy an individual has to expend in gathering them up. Piagetian Theory and Theories of Adult Perceived Numerosity would also predict a choice for *more* – but here, the individual would be equating more distant with more (less dense).

It is clear, however, that there may be a difference between the numerical representation of objects (dots on a page/slide) and the numerical representation of edible items, as is the case of optimal foraging. And indeed, research with infants seems to indicate that the domain of food might be uniquely understood (Shutts et al., 2009). Recently, Van Marle and Wynn (2011) showed that infants will compare quantities of a food substance differing by a 1:4 ratio only when they can use density as a cue. This is preliminary evidence that infants use inter-stimulus distance to assess quantity.

In addition, animals seem to prefer higher density in sets of objects. Stevens et al. (2007) tested monkeys in conditions where only the density of the food items varied, not number. The results showed that they had a preference for a more dense set. These preliminary results suggest that both babies and monkeys may be sensitive to the distance between food items in a set. We set out to investigate this hypothesis with infants in the present study.

EXPERIMENT 1

METHODS

Participants

Twenty (12 ♀) full-term infants participated in the study (Mean age = 10 months, 10 days; range 10;01–10;29). Five additional infants were excluded from the sample because of fussiness, namely, the infants did not make a choice during the familiarization phase. Participants were recruited as volunteers in the Essex/Suffolk/Cambridgeshire area through advertisements and were taken to the baby lab by their parent or caregiver.

Materials

The stimuli used for testing were *Sainsbury's Economy*™chocolate chip cookies measuring 50 mm in diameter. The trays used to display the cookies measured 300 mm × 290 mm and were made of dark gray sheet of metal. The four cookies were fixed to the trays using a combination of glue and *Blu tack* adhesive. They were laid out on each tray in a square configuration, so that each cookie formed one of the four edges of the square. The density of each set was determined by the distance between the cookies that formed the square. The inter-stimulus distance between the inner edges of the cookies was 40 mm (1 = more dense) and 160 mm (4 = less dense, ratio = 1:4). The "squares" were positioned so that they radiated out from the bottom inner corner of each tray. This was done to make the distance from the infant to the closest cookie on each tray the same for both sets. Neutral colored tea-towels covered the trays during the familiarization phase, so that the infant would not see the stimuli before the test phase. The display table measured 800 mm × 1200 mm. It was covered with a plain beige plastic tablecloth and was located in the center of the room. The testing room measured 1800 mm × 1800 mm, had white walls and was lit by an overhead halogen tube. It was empty apart from materials of the testing.

Design

The more dense array was presented on the left for half the babies, and on the right for the other half. Choice was coded as the set that the infant pointed to or touched. A testing session was considered over when (a) the infant made a choice by either touching one of the four stimuli or the tray on a clear reach to other (rather than the other) side, (b) the infant did not reach for or point to either tray after 60 s, or (c) if the infants choice was unclear, for example, if the infant simultaneously reached for or pointed to both trays. Infants were excluded when (b) and (c) were the case.

Procedure

The infants sat in the caregiver's lap facing the experimenter and the stimuli. They were positioned so that their hands rested on the edge of the table. Throughout the experiment, babies were shown toys and edible items. They were allowed to chew on chewable toys shown to them, but they were not allowed to eat the cookies.

Familiarization phase. The experiment began with a pre-testing familiarization phase. The purpose of this was to (1) get the infant used to reaching for items on a tray and (2) familiarize the infant with the experimental stimuli. The familiarization phase began with the experimenter placing a toy onto an empty tray (identical to the trays the stimuli were presented on) and saying "Look [baby's name]! Look at this! Would you like to pick it up?" This process was repeated until the infant readily picked up toys (ball, plastic keys, cup) from the tray. Following this, the experimenter hid the toys behind her back and picked and placed one of the cookies onto the tray saying "What's this? You haven't seen one of these before! Would you like to have a look?" As soon as the infant picked up the cookie and examined it, the caregiver was instructed to take the cookie from the infant and pass it back to the experimenter. Both cookie and tray were hidden underneath the table immediately thereafter.

If the infant did not respond after 30 s, having made no attempt to reach for the toys, the experimenter provided verbal encouragement: "Here, baby, would you like to grab it for me?" and would simultaneously draw the infant's attention to the tray whilst speaking. If the infant did not respond after a further 30 s the trial was terminated.

Test phase. The test phase began directly after the removal of the cookie. The experimenter would say to the infant "Here, baby, we have some more cookies to play with!" The experimenter then uncovered both trays simultaneously. Following this, the experimenter simultaneously displayed both trays in a vertical position before pushing them within reaching distance of the infant. The experimenter and the caregiver would immediately avert their gaze downwards with a neutral facial expression until the infant reached for one of the trays. This method is generally used in infancy research (e.g., Feigenson et al., 2002), and has proven to be adequate for this kind of experiment. In a control experiment (not reported here) we contrasted this method with one in which parents/caregivers were blind-folded. No differences in result were observed.

The trial was terminated as soon as the infant hand made contact with one of the cookies on either tray. All trials were recorded with a *Sony DCR-TRV 900E* digital video camera for blind independent coding. The online data were recorded on a pre-printed record sheet by the experimenter following the trial.

RESULTS

Data from 17 infants who reached for either the more dense (1) or less dense (4) set were coded as choice. Thirteen infants selected the more dense set and four infants selected the less dense set. A binomial test revealed a significant difference between the two choices, $p = 0.049$, two-tailed.

DISCUSSION

The results of this experiment indicate that 10-month-old infants preferred to select the more dense set of four items. There are two interpretations for this finding. One is that human babies have an intrinsic natural propensity to go for more (density) in sets, namely, babies, like other non-human animals, prefer sets that are more compact, in which items are closer together.

Another interpretation is that 10-month-old infants prefer the more dense set because they equated the greater inter-stimulus distance in the less dense display with the impossibility of getting all the cookies at once with one hand ("all in one go" hypothesis), which could easily be done in the more dense set. Although we see this alternative too as part of the intrinsic preference to "go for more dense," it could also be considered a strategy. To test the latter hypothesis, we decided to run another group of 10-month-old infants in Experiment 2.

EXPERIMENT 2

The aim of Experiment 2 was to investigate whether the result of Experiment 1 was due to (1) an intrinsic preference to "go for more dense," or (2) a strategy to select the set with items closer together (select all in one go hypothesis).

In order to address this possibility, we reduced the size of the stimuli while keeping inter-stimulus distance the same. By reducing the size of the stimuli we enable both sets to be kept within grabbing distance for a 10-month-old. That is, a 10-month-old hand would be able to grab all four stimuli at once whether the intra-stimulus distance was small or large. The inter-stimulus distance ratio (1:4) was kept the same.

METHOD

The method was the same as in Experiment 1, except as follows.

PARTICIPANTS

Eighteen (8 ♀) full-term infants participated in the study (Mean age = 10 months, 16 days; range 10;03–10;28). Four additional infants were excluded from the sample due to fussiness/no reach. Participants were recruited in the Essex/Suffolk/Cambridgeshire area through advertisements and were taken to the Lab by their parent or caregiver.

Materials

The food stimuli used were *Galaxy Minstrels*™. They measured 15 mm in diameter. The four candies were laid out in the same configuration as in Experiment 1 with a distance ratio of 1:4. The inter-stimulus distance between the inner edges of the candies was 10 mm (more dense) and 40 mm (less dense).

Design

Side of density ratio (1-L, 1-R) was counterbalanced across participants. The infant's choice recorded as one level of density or the other (1 or 4). A testing session was considered over when the infants had made a choice. If the infant did not reach for or point to either tray, or if the infants choice was unclear (e.g., if the infant simultaneously reached for or pointed to both trays), this was coded as "no choice" and the participant was excluded.

RESULTS

Data from 16 infants who reached for either the more dense (1) or less dense (4) set were coded as choice. Thirteen infants selected the more dense set and three infant selected the less dense set. A binomial test revealed a significant difference, $p = 0.020$, two-tailed.

DISCUSSION

The findings in Experiment 2 supports the proposal that infants selected the more dense set because there is some mechanism at play that makes them prefer higher density than lower density. There is no evidence for the strategy explanation, whereby infants in Experiment 1 selected the more dense set because it was the set that enabled them to grab all four items at once as opposed to the less dense set, in which the four cookies were too far apart to grab all at once. Together, the results from Experiments 1 and 2 suggest that density assessment of sets of equal numerosity may be determined by a preference for things that are closer together.

GENERAL DISCUSSION

The present experiments were developed to start to address questions involving a variable that is generally conflated with numerical assessment and controlled for – set density. We contrasted two hypotheses in the fields of human perception and development (theories of numerosity perception in adults and Piaget's number conservation ideas) and animal behavioral ecology (optimal foraging ideas). Evidence with children (Piaget's conservation tasks) and adults (literature on numerosity perception) suggests that we tend to equate more as "more length" or "more space" in between items, while Optimal Foraging Theory predicts that patches of food containing items more packed together yield a better rate of return: animals seem to engage in evaluative computations which enable them to maximize profit and minimize cost. Although tentative and speculative at this stage, we pitted these two frameworks against each other because they predict opposite behaviors – children may prefer more as in *bigger* inter-stimulus distance, while animals may prefer more as in *smaller* inter-stimulus distance.

We set out to test these alternatives with two experiments addressing the question of inter-stimulus assessment in visual displays. Our results in Experiment 1 showed that, at 10 months, infants selected the more dense set by touching the chosen set. That is, infants reached and made a choice for the set in which elements were displayed closer together at the ratio of 1:4. Infants at 10 months make use of the variable "density" to make a numerical choice. This evidence supports preliminary evidence to show that infants have the ability to assess and compare quantities of a food substance (Van Marle and Wynn, 2011).

The alternative interpretation for the results of Experiment 1, that 10-month-old infants preferred the more dense set because they equated the smaller inter-stimulus distance in the more dense display with the possibility of getting all the cookies at once with the hand was addressed in Experiment 2. Two sets holding a 1:4 ratio between them, both with close enough items to be grabbed with one hand at once, were used in Experiment 2. Ten-month-old infants showed a preference for the more dense set, even though both sets could be grabbed with one hand at once. The preference observed in Experiment 1, therefore, cannot be attributed to a preference based on a "grab all in one go" strategy. Altogether, our results provide novel evidence that infants make decisions on numerical choices taking into account inter-stimulus distance (set density). The fact that the infants were not random in their choices means that this variable plays a role in numerical assessment.

A second conclusion stemming from these experiments is that there is a predisposition in young infants to select sets that contain items closer together. The data suggest that, at 10 months, infants are equipped with a capacity to discriminate two sets of equal number. What is even more extraordinary is that not only do infants detect the differences in density, but also make a particular choice, and reach for it. It is possible that these choices may apply uniquely to "foraging" situations, and indeed, the domain of food (Shutts et al., 2009) may be a special one. Further studies will be required to shed light onto this possibility.

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Numerical cognition in bees and other insects

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The ability to perceive the number of objects has been known to exist in vertebrates for a few decades, but recent behavioral investigations have demonstrated that several invertebrate species can also be placed on the continuum of numerical abilities shared with birds, mammals, and reptiles. In this review article, we present the main experimental studies that have examined the ability of insects to use numerical information. These studies have made use of a wide range of methodologies, and for this reason it is striking that a common finding is the inability of the tested animals to discriminate numerical quantities greater than four. Furthermore, the finding that bees can not only transfer learnt numerical discrimination to novel objects, but also to novel numerosities, is strongly suggestive of a true, albeit limited, ability to count. Later in the review, we evaluate the available evidence to narrow down the possible mechanisms that the animals might be using to solve the number-based experimental tasks presented to them. We conclude by suggesting avenues of further research that take into account variables such as the animals' age and experience, as well as complementary cognitive systems such as attention and the time sense.

Keywords: bees, insects, counting, learning, memory, numerical cognition, quantity discrimination

INTRODUCTION

Insects are not the hardwired reflex automats they were once believed to be. Especially central place foragers like ants and bees, who venture out to provide the nest with a constant flow of resources, show impressive navigation and communication skills. The animals cover large distances in search of food and nesting material, and usually take the shortest route back home, even when the nest entrance is out of sight. Insects have evolved sophisticated ways to acquire, memorize, and act upon information collected from the environment. When navigating to a food source, honeybees employ a celestial compass (Von Frisch, 1949) and a visual odometer (Esch and Burns, 1995; Tautz et al., 2004) to measure the distance and the direction of their movement. This information is integrated to continuously update a homeward vector, so that the forager can return to the nest from any point on the foraging route in a straight line (Wehner et al., 1990). Bees memorize the most profitable flowers depending on the location (Zhang et al., 2006), and the time of day (Pahl et al., 2007). Ants navigate by a similar mechanism, albeit the distance information is acquired by integrating steps, rather than using optic flow (Wittlinger et al., 2006). "Number" is another property of visual scenes which animals can learn and use, in order to maximize foraging efficiency. Most studies on numerical competence have focused on vertebrates, but there is a growing body of evidence showing that the ability to use numerical information is not restricted to this group. For example, the use of quantity in predatory behavior has recently been demonstrated in an araneophagic spider. These communal predators base their decision about settling near a prey spider nest on the number of conspecifics already present, preferring one spider over zero, two, and three (Jackson and Nelson, 2012; Nelson and Jackson, 2012). There is evidence that 17-year periodical cicadas (*Magicicada* sp.) could be counting the seasonal cycles of trees in order to hatch after precisely 17 years, instead of using the passage of real time or degree days (Karban et al., 2000). Mealworm beetles (*Tenebrio molitor*) have been shown to discriminate between odor bouquets containing the scents of different amounts of females (Carazo et al., 2009), and to keep a running tally of the number of encountered males to inform mate-guarding decisions (Carazo et al., 2012). Most of the work on invertebrate numerical competence has focused on social insects, because they may particularly benefit from a sense of number. As central place foragers, they face more demanding navigational problems than animals without a nest to return to between foraging bouts. In this paper, we review the advances in our understanding of how and why insects use numerical information in mating strategies (Carazo et al., 2009, 2012), navigation (Chittka and Geiger, 1995; Reznikova and Ryabko, 1996; Wittlinger et al., 2006; Dacke and Srinivasan, 2008), foraging (Bar-Shai et al., 2011a,b), and visual decision-making (Leppik, 1953; Gross et al., 2009).

Gelman and Gallistel (1978) have defined a set of five criteria for true counting: one-to-one correspondence, stable order, cardinality, abstraction, and order irrelevance. Since symbolic labels are required for the items to be labeled, these criteria are difficult to apply to non-verbal animals. True counting according to Gelman and Gallistel has thus so far only been shown in Chimpanzees (Matsuzawa, 2009) and grey parrots (Pepperberg, 2006) using arabic numerals. The data on numerical competence in insects presented in this review shows different levels of sophistication, but none of the animals displayed true counting in the sense of Gelman and Gallistel. Number-related behavior in animals in which not all of the strict "true counting" criteria are fulfilled can be described as "proto-counting" (Davis and Pérusse, 1988).

WHAT IS THE ADVANTAGE OF A "SENSE OF NUMBER"?

Numerical competence can be useful in many ways, i.e., when selecting the best foraging and mating grounds, tracking predators, in social interactions, in parenting and preventing brood parasitism. Social insects, as central place foragers, can profit from a sense of number in navigation. A running count of landmarks can inform the navigator about its progress, or indicate when it is approaching the destination. A sequence of landmarks along a route could also be helpful in calibrating a bee's odometer – since landmarks interact with odometric information to enhance the accuracy of navigation (Chittka et al., 1995; Srinivasan et al., 1997; Vladusich et al., 2005). There is evidence that landmarks are memorized together with a vector encoding distance and direction to the hive or the food source (Cartwright and Collett, 1983), and used to update the internal homeward vector (Collett, 1992). The number of a landmark might also be helpful when one landmark in a row has to be identified, e.g., a particular tree from a row of trees may be combined with a vector memory, or the correct entrance to the nest in an array of hives in a large apiary could be identified by its numerical order. Desert ants (*Cataglyphis fortis*) use a "step counter" to measure traveled distances, enabling them to constantly update information about the distance and direction of the nest entrance (Wittlinger et al., 2006). Bees are often flower-constant, and numerical information could be used to identify nectar-bearing flowers, along with color, shape, and scent (Leppik, 1953; Gross et al., 2009). Visual information about number may also inform foraging decisions based on the number of bees already present on a flower. Numerical regularities in flowers can be used to forage more efficiently, by avoiding revisits at already depleted nectaries (Bar-Shai et al., 2011b).

NUMBER IN MATING STRATEGIES

The polygynandrous mating system of the yellow mealworm beetle (*Tenebrio molitor*) leads to intense sperm competition. Male beetles have evolved several strategies to turn the odds in their favor, some of which require quantity estimation and – discrimination. In order to optimally adjust their mating behavior, male beetles need to acquire information about the number of male and female animals in the group. Carazo et al. (2009) have tested if male beetles discriminate between odor bouquets containing the odors of 1, 2, 3, and 4 female beetles in a 2 choice situation. They found that the animals discriminated between 1 vs. 4, and 1 vs. 3 females, but not between 1 vs. 2, or 2 vs. 4 females. The results suggest that males are capable of chemically discriminating between two odor sources based on the number of females contributing to the odor – if the ratio exceeds 1:2. In order to maximize his mating opportunities, the male beetle will always go for more.

In a further study, Carazo et al. (2012) investigated if male mealworm beetles adjust the amount of time spent mate-guarding in response to the amount of rival males encountered before the mating event. During mating, sperm is transferred to the female's bursa in a spermatophore. The release of the sperm, however, occurs 7–10 min after the copulation. If the female re-mates with a second male in this time window, the second male can prevent the sperm release from the first spermatophore. Thus, a male beetle should guard its mate for a while after copulation – if the risk of spermatophore inhibition is high. To test whether male beetles can estimate the number of present males, Carazo et al. staged matings in which they varied the number of rivals the experimental male encountered before the mating event. They found that the beetles increased the time spent guarding the female in response to the amount of rival males encountered before mating. The authors conclude that the animals keep a running tally of serially encountered individuals, and use numerosity estimation to inform their mate-guarding decisions.

Numerical competence is likely to play an important role in many different species for which the assessment of sperm competition risk and intensity is vital. Shifferman (2012) argues that its role in determining males' responses to sperm competition can expose quantity estimation to selection, and thus facilitate its evolution.

NUMBER IN NAVIGATION

In times of scarce resources, honeybees often fly four or more kilometers from the hive to collect pollen or nectar. On those long foraging trips, the bee's on-board dead reckoning system constantly integrates the distance flown and the angle of movement, by measuring the optic flow over the retina (Esch and Burns, 1995; Esch et al., 2001) and the body angle relative to the solar meridian (Labhart, 1980; Rossel and Wehner, 1986). In theory, this enables the animal to know the distance and direction back to the hive from any point on her outward route (Wehner et al., 1990). On long trips, however, errors in the measurements accumulate, and the bee needs additional strategies in order to reset or calibrate its path integrator (Srinivasan et al., 1997; Cheung et al., 2007; Merkle and Wehner, 2010). One way bees achieve this is by memorizing landmarks on the route together with a vector encoding distance and direction to the hive or the food source (Cartwright and Collett, 1983), and using those landmarks to update the internal homeward vector (Collett, 1992). Landmark memory can guide bees to the hive even after artificial displacement of up to 11 km (Pahl et al., 2011). Another possible way to supplement the distance measurement is counting the landmarks passed on the way to a goal. Two studies have investigated this hypothesis so far.

Chittka and Geiger (1995) set out to test if bees can use a sequence of identical landmarks to estimate the distance to a goal. They set up a series of four yellow tents, and trained bees to forage at a feeder between the third and the fourth tent. A control experiment with empty feeders showed that the bees had learned to collect sugar water from this location, as only few bees landed on a distraction feeder on the way. By changing the number of tents in the setup, the experimenters created a contradiction between the perceived distance and the number of landmarks at which the bees expected the feeder. Would the bees search for the feeder at the learned distance, or after the learned number of landmarks? When the number of tents was increased to five (while keeping constant the distance of the last tent from the feeder), 74% of the bees landed at the feeder close to the trained distance, after passing four tents, and 26% of the bees landed at a shorter distance, at the position after the third tent. Increasing the number of landmarks to six caused most bees (58%) to land after tent four, a compromise between the trained distance and the number of landmarks passed during training. Thirty-three percent of the bees chose the feeder at the trained distance, after flying past five landmarks, and 8% of the bees landed after passing three tents. When the landmark arrangement was extended, so that the trained distance was reached after two landmarks, 78% of the bees chose the feeder at the training distance, and 22% flew 100 m further to a feeder after the third landmark. Thus, an increased density of landmarks led some bees to estimate the distance flown as being shorter, while a decreased landmark density led them to search at a greater distance. Chittka and Geiger (1995) concluded that the bees which did not land at the training distance must have had a representation of the number of landmarks to be passed between hive and food source, and referred to this behavior as "proto-counting."

One criterion of true counting is the abstraction principle: the animal has to demonstrate the ability to use the number learned in one context in a transfer test on different objects (Gelman and Gallistel, 1978). As the landmarks were always yellow tents of identical size, this abstraction principle was not shown in this experiment. The bees' numerical competence demonstrated here may be related to a serial memory for landmarks, since bees store stimuli along a route together with information about the next expected target (Collett and Kelber, 1988; Collett et al., 1993). Another possible explanation for the results is the change in optic flow caused by the tents on the way to the feeder. Since bees measure distance by the amount of movement over the retina, more tents on the way would cause them to underestimate the distance, while fewer tents would lead to an overestimation.

Dacke and Srinivasan (2008) revisited the question of sequential counting in bees in a carefully controlled tunnel setup, in which the bees could not rely on odometric information to find the feeder. They trained bees to forage in a 4 m long and 20 cm wide tunnel containing five landmarks consisting of yellow stripes (**Figure 1A**). The position of the landmarks and the feeder was varied at 5 min intervals in order to prevent the bees from learning the feeder position based on its distance from the entrance. Different groups of bees were trained to find the feeder at landmark 1, 2, 3, 4, or 5, and their search distributions were measured. When the bees' search behavior was at its best, the experimenters tested the bees in a new tunnel without reward, and recorded the bees' search distribution. The animals trained to the first landmark searched mostly close to landmark 1 (**Figure 2A**), bees rewarded at the second landmark searched mostly around landmark 2 (**Figure 2B**), and so on (**Figures 2C–E**). Clear search peaks were only visible when the bees were trained to forage at landmarks 1–4. With an increasing number of landmarks to fly past, however, the search distribution became wider (**Figure 2E**). In the next experiment, Dacke and Srinivasan tested whether the bees could still identify the correct landmark in a different spatial layout. The animals were trained to collect sugar water from the third landmark as in **Figure 1A**, and then tested in one condition where the landmarks were closer together, and in a second condition where the landmarks were spaced irregularly. In both cases, the bees' searches were centered on the third landmark. A third experiment was conducted to investigate whether the bees were using the number of landmarks, or the amount of yellow they passed on the way through the tunnel, to find the feeder. After training was conducted just as in Experiment 1, the animals were tested in a new tunnel without reward, and with yellow disks instead of stripes as landmarks (**Figure 1B**). With only 55% of area of the stripes, summing up the amount of yellow passed on the way would lead the bees to overshoot the feeder. The bees, however, showed a search pattern similar to the first experiment, with clear search peaks at the trained landmarks 1–4, and a wide distribution in case of landmark 5 (Dacke and Srinivasan, 2008). The bees were not summing up the amount of yellow, but were using the landmark number passed en route to locate the feeder. In a last experiment, the experimenters trained a group of bees in a tunnel with overlapping baffles as landmarks (**Figure 1C**). Unable to see from one baffle to the next, the bees were forced to count the landmarks in a truly sequential way in order to identify the correct one. After training the bees to forage at the third landmark, the test in an unrewarded tunnel showed that the animals still centered their search on the third landmark.

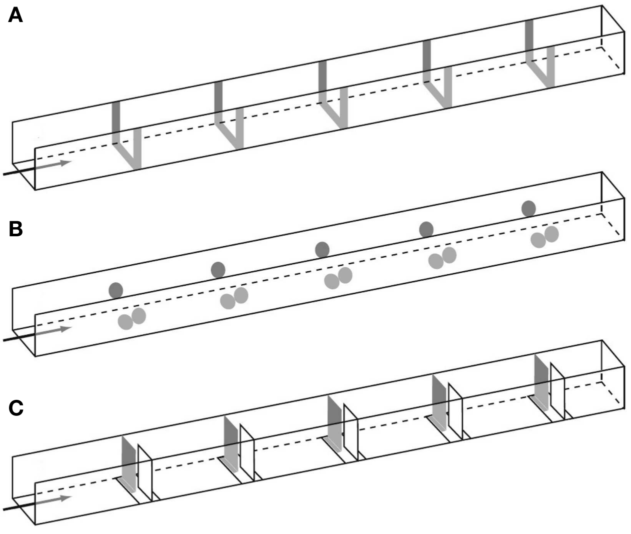

FIGURE 1 | Illustration of the experimental tunnels with landmarks consisting of (A) stripes, (B) circles, and (C) baffles spaced at regular intervals. Adapted with permission from Dacke and Srinivasan (2008).

Dacke and Srinivasan showed that bees can keep track of a maximum of four landmarks passed en route. They also demonstrated that this behavior is not restricted to the type of landmark encountered in training, but can be applied to different landmarks in an abstract, object-independent way. Because the bees had a tendency to learn distance rather than number, the authors took pains in training the bees to disregard other information, leaving number as the only reliable cue to find the feeder.

In the featureless habitat of desert ants (*Cataglyphis fortis*), landmarks cannot help the animals to locate the nest entrance after a successful foraging trip. The ants constantly integrate distance and direction of their movement, enabling them to return home in a straight line from any position on their outbound path (path integration). The directional reference for the homeward vector is the polarization pattern in the sky, which the ants perceive in the specialized dorsal rim area of their compound eyes (Wehner, 2003). The mechanism by which distance is gaged was elucidated by Wittlinger et al. (2006). In a series of elegant experiments, they tested the hypothesis that *Cataglyphis* is using a "step counter" to measure travel distances. By elongating or shortening the ant's legs (stilts and stumps), they caused the animals to overestimate (stilts) or underestimate (stumps) the travel distance, showing that the ants were really using the amount of steps taken to gage the traveled distance. The animals most likely do not literally "count" the number of steps, but integrate some parameter of leg movement during walking (Wittlinger et al., 2007). Further experiments are required to address the exact mechanism of the stride integrator. In contrast to desert ants, who use a discrete (countable) quantity to measure distance, honeybees use optic flow; a continuous (uncountable) quantity for distance measurement. Future studies should investigate the costs and benefits of discrete and continuous variables for distance measurement in different ecological contexts.

In 1996, Reznikova and Ryabko reported that red wood ants (*Formica* sp.) can assess the number of turns in a maze, and communicate this information to nest mates. They placed a scout ant near a sugar reward in a maze, where the ant could feed. The scout would then head home to the nest, and get in antennal contact with its group of foragers. After a timespan of antennal contact proportional to the number of turns in the maze, the foragers then headed out without the scout – and found the location of the feeder in the majority of trials. Olfactory cues were excluded by replacing the maze with a fresh, identical maze when the scout had returned to the nest. The authors conclude that the experimental animals estimate the number of objects passed along the way back to the nest to memorize the food location, and communicated this number to their nest mates. The foragers then used the communicated number to locate the correct branch on the maze (Reznikova and Ryabko, 1996, 2011). There is, however, no direct evidence that the number of branches was memorized by the scout, or received by the forager ant. Since ants can measure distance quite accurately, as shown in the study by Wittlinger et al. (2007), further experiments are required to exclude this possibility. The concept of symbolic communication in ants, however, is in itself extremely interesting, and should be investigated further.

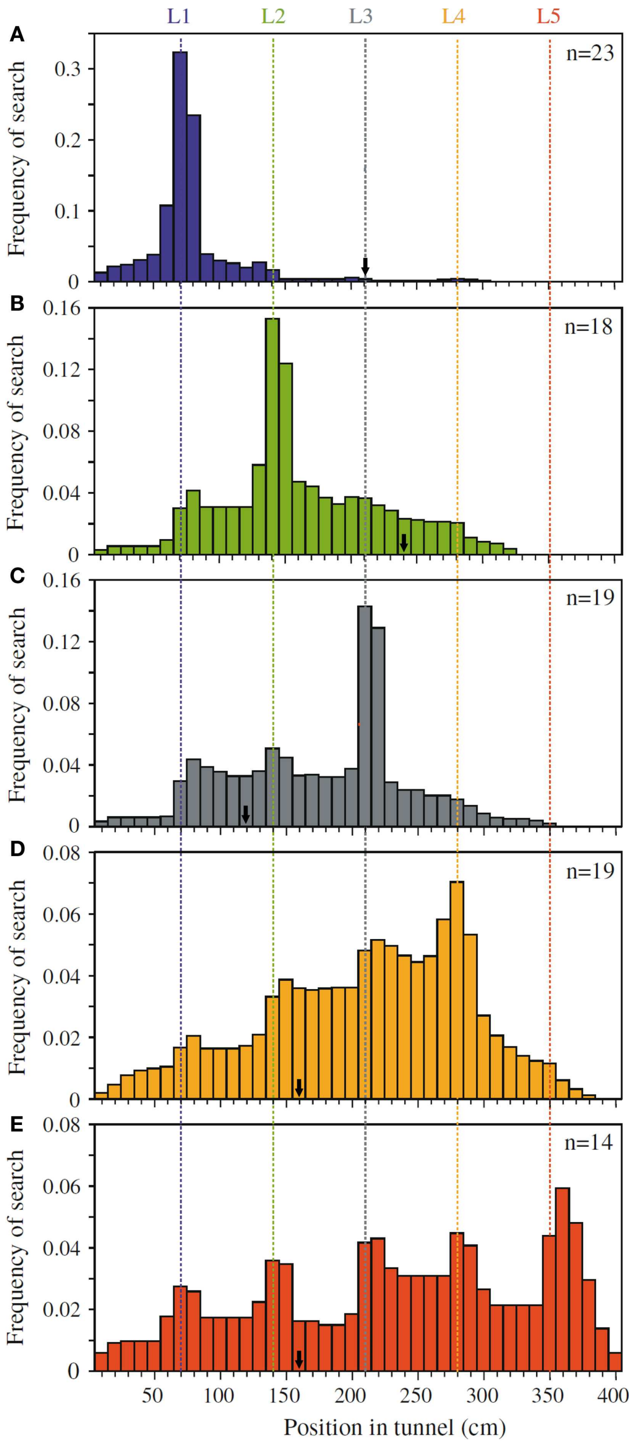

FIGURE 2 | Pinpointing the rewarded landmark in a series of landmarks. Shown are the search distributions of bees that are tested after being trained to receive a reward at **(A)** landmark 1, **(B)** landmark 2, **(C)** landmark 3, **(D)** landmark 4, and **(E)** landmark 5. Bees trained to landmark 1 show a strong preference to search around landmark 1 **(A)**. Bees trained to landmark two similarly prefer to search near landmark 2 **(B)**, and so on **(C–E)**. The arrows mark the position of the rewarded landmark in the training, just prior to each test. Adapted with permission from Dacke and Srinivasan (2008).

NUMBER IN VISUAL DISCRIMINATION

Since Karl Von Frisch's initial visual discrimination experiments showed that honeybees can see colors (Von Frisch, 1914), the bee's visual system has been investigated thoroughly in a large number of studies. Behavioral experiments on free-flying bees have played an important role in finding out about what a bee can see. Those studies revealed that bees can extract general identifying information from a stimulus, such as orientation (Van Hateren et al., 1990), radial symmetry (Horridge and Zhang, 1995), and bilateral symmetry (Horridge, 1996) including the orientation axis (Giurfa et al., 1996). Other characteristics of images such as color and size can be extracted and memorized as well (Horridge et al., 1992b; Ronacher, 1992).

One of the first studies on the visual use of number in insects was published in 1953 by Elmer E. Leppik. Inspired by the latest discoveries on the honeybees' dance language (Von Frisch, 1951), he became interested in the question of whether, and how, insects

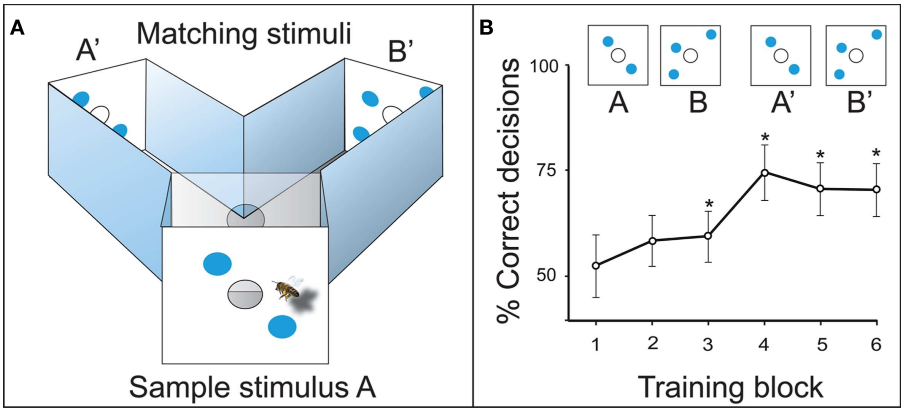

FIGURE 3 | (A) Delayed match-to-sample (DMTS) setup in a Y-maze. The bee has to memorize sample stimulus A, and compare it to the matching stimuli A' and B' inside the maze. A' leads to the reward in this example. **(B)** Learning curve of the DMTS experiment. *Denotes a preference for the matching stimulus significantly different from random choice.

could use numbers. Since many flowering plants which depend on insect pollination have a constant number of petals, he wanted to test whether pollinators had evolved a certain ability to discriminate blossoms based on the number of petals (Leppik, 1953). Despite the lack of controls and statistical tests, Leppik made some interesting observations. He found that the trained bees did well distinguishing between 1, 2, and 3, but had trouble discriminating between 3 and 4 petals. They remembered higher numbers only if these were expressed in symmetrical flower shapes. Since honeybees have an innate preference for symmetrical visual stimuli (Lehrer et al., 1995), the bees were probably using the overall shape of the flowers for the discrimination tasks involving numbers above 4. The limit to the bees' numerical competence between 3 and 4, however, is similar to the findings in several recent studies reviewed here (Chittka and Geiger, 1995; Dacke and Srinivasan, 2008; Gross et al., 2009).

The studies by Chittka and Geiger (1995) and Dacke and Srinivasan (2008)have demonstrated that bees can keep track of the number of objects passed sequentially, i.e., one object at a time. The question remains, however, if bees can extract information about the number of simultaneously presented objects from a visual scene. Honeybees have been shown to generalize visual stimuli (Mazochin-Porshnyakov, 1969), and can learn concepts of "sameness" and "difference" in a delayed match-to-sample (DMTS) task (Giurfa et al., 2001). In order to investigate this question, Gross et al. (2009) trained bees in the DMTS paradigm to make decisions about the sameness or difference of visual stimuli based on the number of objects present in a stimulus.

In the initial training, the experimental bees learned to fly into a Y-maze (**Figure 3A**). The animals had to memorize the sample stimulus at the maze entrance, recall it inside the decision chamber, and choose the matching stimulus to get a sugar reward. When the two-dot stimulus A was the sample at the maze entrance, the bees were rewarded for choosing the two-dot matching stimulus A' inside the maze. When the three-dot sample B was presented, they had to choose the three-dot matching stimulus B' to collect their sugar reward (**Figure 3A**). The animals learned to solve this task with a precision of 70–75% after three to four training blocks, which is 20–30 visits per individual bee (**Figure 3B**). This relatively simple task could be solved in a number of ways which do not require counting, i.e., by image matching, adding combined area or edges, or by matching the illusory contours formed by the objects (Horridge et al., 1992a). Therefore, a number of experiments were designed to exclude other information – so that the number of elements was the only reliable cue for the bees.

As a first step, the bees were presented stimuli where the positions of the blue dots had been randomized. The animals solved this without any additional training, showing that they did not use image matching to find the reward (**Figure 4A**). In the next experiment, the blue dots were exchanged for yellow stars; new objects which the bees had never encountered during training. They transferred the matching rule to the new objects without decreasing choice performance (**Figure 4B**). In the next step, the sample stimulus consisted of blue dots – while the matching stimuli contained yellow lemons. The bees solved this task as well, with a high accuracy of around 80% (**Figure 4C**). These results show clearly that the bees were applying the learned rule in an abstract, object-independent way, which is one criterion for true counting (Gelman and Gallistel, 1978). In two further experiments, the blue dot stimuli were controlled for edge length and combined area, which did not decrease the frequency of correct choices (Gross et al., 2009). Thus, the bees were not using spatial frequency or area summation to choose the rewarded stimulus. When a new number of objects was introduced (3 vs. 4 blue dots), the animals had no trouble solving the 3 to 3 match. In the 4 to 4 match, however, the choice frequency dropped to chance level (**Figure 4D**). In another experiment with similar objects as sample and choice stimuli (yellow lemons and yellow stars), the bees could solve the four to four match as well (Gross et al., 2009). Thus, the limit of the bees' number discrimination ability seems to be between 3 and 4. When they were tested on configurations with 4 vs. 5 (**Figure 4E**) or 5 vs. 6 objects (**Figure 4F**), the choice distribution dropped to chance level. Interestingly, when the bees were tested on 4 vs. 6 objects, they could do the 4 to 4 match, but failed to do the 6 to 6

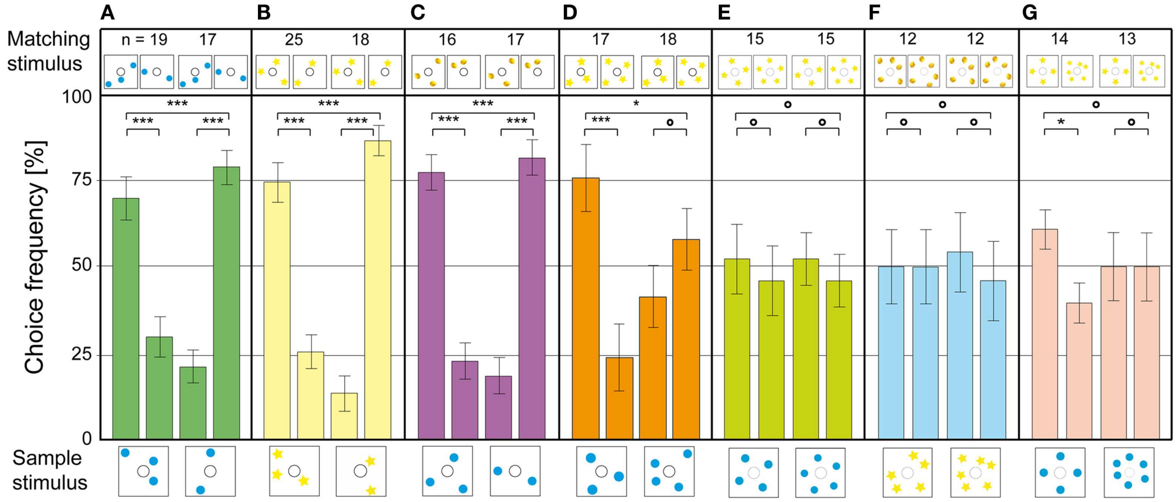

FIGURE 4 | Number-based decision-making in a delayed match-to-sample task. The stimulus below each pair of bars is the sample, and that above each bar is the respective matching stimulus. The data represent the pooled first choices of individual bees. **(A)** The configuration of dots on the sample and matching stimuli is randomized. **(B)** The blue dots are replaced by yellow stars, to test for abstraction to unknown stimuli. **(C)** Sample and matching stimuli are composed of different elements. **(D–G)** Bees trained to discriminate between 2 and 3 are tested on stimuli with **(D)** 3 and 4 elements, **(E)** 4 and 5 elements, **(F)** 5 and 6 elements, **(G)** 4 and 6 elements. *n* Denotes number of bees per condition. Error bars show standard error. ***Denotes statistically significant difference at $p < 0.001$, **denotes $p < 0.01$, *denotes $p < 0.05$, and O denotes $p > 0.05$. Modified from Gross et al. (2009).

match. The honeybee's sense of number does not follow Weber's law, which states that the just-noticeable difference between two stimuli is proportional to the magnitude of the stimuli. If the bees were making relative numerousness judgments, a 2 vs. 3 discrimination would mean that they should be able to discriminate 4 vs. 6 as well. The fact that this is not the case indicates that the bees were using absolute number, instead of relative quantity, to identify the matching stimulus. These results are similar to those obtained for 22 weeks old human infants in a habituation – dishabituation procedure. The infants noticed a difference between arrays of 2 and 3 objects, but not between arrays of 4 and 6 objects (Starkey and Cooper, 1980).

Honeybees can perceive illusory contours formed by elements on a visual stimulus (Horridge et al., 1992a). Since two objects always form a line, and three objects tend to form a triangle, additional experiments were carried out to control for those lower order cues. The objects were arranged in straight lines of equal length, to prevent the bees from using the overall shape of the elements for the matching task (**Figures 5A,B**). Additionally, the stimuli were made as dissimilar as possible, by using different objects in sample and choice stimuli. An attempt was made to guide the bees deliberately to the wrong stimulus: in the 2 to 2 matches in **Figures 5A,B**, the green leaf is the only object present in the sample and in a choice stimulus; the other objects are all unique. If the bees were to match the stimuli based on individual objects, the green leaf would guide them to the wrong side of the maze. In the 3 to 3 match in **Figures 5A,B**, the purple flower serves the same purpose. As the data in **Figures 5A,B** show, the choice performance in this experiment was still high. Even this deliberate effort did not fool the bees: they clearly based their decisions on the number of objects present in the stimuli.

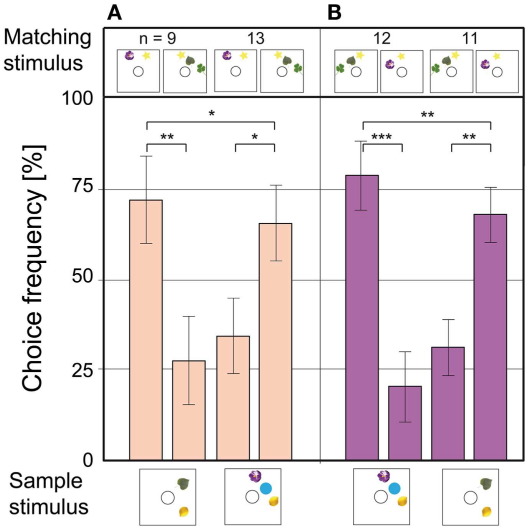

FIGURE 5 | Control test for illusory contours and misdirecting cues. The objects are arranged in lines of equal length to prevent the formation of illusory contours. In each configuration, only one object appears both in the sample and in the matching stimuli as "misdirecting" cue. **(A,B)** Misdirecting cues are the green leaf in the 2 to 2 match and the purple flower in the 3 to 3 match. Notations used here are the same as in **Figure 4**. Modified from Gross et al. (2009).

NUMBER IN FORAGING STRATEGIES

Bees can visit hundreds of flowers on one of their excessive foraging flights. Since the nectar content cannot be judged from a distance, the animals have evolved a number of strategies in order to prevent revisiting previously depleted flowers. When foraging across several patches of flowers, bumblebees use fixed foraging routes between the patches. This increases foraging success when competing with other pollinators [reviewed in Ohashi and Thomson (2009)]. The sequence of flower visits is at first learned in the order of flower discovery – and subsequently optimized for shortest flight distance (Lihoreau et al., 2010, 2011). When foraging on inflorescences, bumblebees tend to visit the flowers sequentially, from the bottom to the top (Pyke, 1979; Waddington and Heinrich, 1979). Honeybees mark visited flowers with a repellent scent – and reject recently visited flowers (Giurfa and Nunez, 1992; Giurfa, 1993).

In 2011, Bar-Shai et al. proposed that the number of nectaries visited per flower could be used as an information source to prevent revisits of depleted nectaries, as long as the number of nectaries is constant. If the animals were using number as a departure cue, they should flexibly adapt their departure strategy to the number of available food sources. The authors tested this hypothesis in field observations and lab experiments. Bumblebees naturally collect nectar from *Alcea setosa* flowers, which offer a constant number of five nectaries (Bar-Shai et al., 2011b). Observing foraging bees in the field, the authors found that the bees most commonly departed after having probed the five nectaries (92% of visits). Revisits of depleted nectaries happened rarely, in only 1.1% of the cases. In order to test whether the bees could adapt their foraging strategy to a different number of available food sources per patch, the authors trained bumblebees to forage at artificial feeders, set up in two patches with three feeders each. Only two rewards could be accessed per patch. After probing two feeders, the remaining one was closed so that the bee had to visit the other patch to gather more sugar water, or return to the hive. The bees adjusted their frequency of patch probings before departure, and the probability of leaving a patch after receiving the second reward significantly increased during the experiment. Non-numerical flower departure cues, such as ingested nectar volume, time spent on flower, spatial attributes of the flowers, and scent marks on the flowers could be excluded. It took the bees exceptionally long to learn to leave a patch after two rewards, indicating that number is more difficult cue to learn than color, size, or scent. The study shows that bumblebees can learn to leave a feeding location after receiving a fixed number of rewards. This involves sequential tagging of items in a fixed order (ordination), and using the last tag to determine number of items (cardination); two of the underlying basic principles of numerical ability (Gallistel and Gelman, 2005).

The authors conclude that bumblebees can use numerical regularities in food distribution to enhance their foraging efficiency, and that this may provide the selective drive in the evolution of numerical competence (Bar-Shai et al., 2011b). In order to investigate this hypothesis, the authors observed more primitive, solitary *Eucera* sp. bees that forage on the same *A. setosa* flowers for comparison (Bar-Shai et al., 2011a). In the solitary bees, flower departure after probing five nectaries was less common (26%) than in bumblebees (48%), and the likelihood of revisiting a nectary already depleted by the same individual was higher in *Eucera* sp. (7.8%) than in bumblebees (1.1%). The solitary bees also displayed "inspection turns," where they approached a nectary, but encountered a scent mark and turned back. When these cases are taken out of the analysis, departures after six probings become more likely than departure after five probings. Measuring the duration of each inspection, the authors found that the last inspection before departure was usually the shortest. Time spent on a flower, departure after ingesting a certain volume of nectar and spatial characteristics of the flower could be excluded as departure clues. Most likely, the bees were using a reward-based patch departure rule, assisted by scent marks: whenever a nectary is empty, or carries a scent mark, depart, and visit the next flower. Non-numerical cues are the most parsimonious explanation for the results, but the use of number by solitary *Eucera* sp. bees cannot be ruled out. If they do possess a form of numerical competence, it is less exact than in bumblebees (Bar-Shai et al., 2011a,b).

CONCLUSIONS

The papers reviewed above have shown that numerical competence in insects is a worthwhile topic of investigation, with a variety of experimental approaches being available to test the limits of these animal's abilities. The fact that a range of very different behavioral assays has indicated the number 4 to be the upper limit of insect numerical competence, strongly suggests that this is a key cognitive constraint that requires detailed and rigorous study. The same limit was found when stimuli were encountered sequentially (Chittka and Geiger, 1995; Dacke and Srinivasan, 2008; Bar-Shai et al., 2011a,b) as well as simultaneously (Leppik, 1953; Gross et al., 2009; Gross, 2011). Other questions raised by the above studies that need to be properly investigated include an elucidation of the exact mechanism(s) by which insects discriminate between these small numbers, as well as the interactions, if any, of numerical discrimination with other cognitive capacities, such as a time sense. Vertebrate studies have revealed striking parallels between these two faculties, especially for smaller values [i.e., small numbers and short time intervals; Buhusi and Cordes (2011)]. Since bumblebees can be trained to learn specific time intervals (Boisvert and Sherry, 2006), these insects, along with honeybees, appear to be an ideal model organism in which to study the neural correlates of both the numerical and interval timing abilities, as well as the commonalities between the two systems.

In summary, the studies presented in this review reveal the great potential of insects to inform current theories of numerical perception and competence. Given the complex nature of this cognitive domain, however, future studies should address often-neglected variables such as age and experience, and individual differences (Dyer, 2012) to arrive at a more accurate and comprehensive picture of numerical ability. Fortunately, these are variables that, in social insects, can be manipulated with some effort, so as to produce better-controlled experimental protocols. The effects of attention-like processes, as have been seen in honeybees (Giurfa, 2004) and in *Drosophila* (Van Swinderen and Flores, 2007), also have the potential to indicate more precisely the mechanism by which the former group of insects is able to discriminate between small numbers. Is attention more important in maze studies, such as that of Gross et al. (2009), where the bees are allowed to examine the visual stimuli for an extended period of time, before making a decision? Or might attention play a greater role in studies such as that of Chittka and Geiger, where the bees need to extract the information relevant to a landmark from a noisy background – as she flies past it en route to a feeder? Finally, the recent proposal that bees may possess different visual systems for pattern discrimination at close range vs. at a distance (Dyer and Griffiths, 2012) may also have a bearing on the counting procedure being used by individual foragers. The experiments described in this review required bees to either estimate number by, e.g., flying very close to a visual pattern, or from a distance, by, e.g., flying past a prominent landmark, and it is possible that different mechanisms are employed by the bees in these two scenarios.

"Number" is a primary visual feature of a scene, along with color, contrast, size and speed (Burr and Ross, 2008), and many animals have evolved the ability to make use of this information. The visual recognition of small numbers of items could be achieved during early sensory processing, and the same may be the case for olfactory and auditory "scenes." In order to understand the complexity of numerical cognition, a bottom-up approach investigating the neural circuitry required for number recognition is necessary (Chittka et al., 2012).

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$1 < 2$ and $2 < 3$: non-linguistic appreciations of numerical order

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Ordinal understanding is involved in understanding social hierarchies, series of actions, and everyday events. Moreover, an appreciation of numerical order is critical to understanding number at a highly abstract, conceptual level. In this paper, we review findings concerning the development and expression of ordinal numerical knowledge in preverbal human infants in light of literature about the same cognitive abilities in non-human animals. We attempt to reconcile seemingly contradictory evidence, provide new directions for prospective research, and evaluate the shared basis of ordinal knowledge among non-verbal organisms. Our review of the research leads us to conclude that both infants and non-human animals are adapted to respond to monotonic progressions in numerical order, consonant with mathematical definitions of numerical order. Further, we suggest that patterns in the way that infants and non-human animals process numerical order can be accounted for by changes across development, the conditions under which representations are generated, or both.

Keywords: ordinality, numerical cognition, quantity, non-verbal, infants, non-human animals

INTRODUCTION

Mathematicians Frege (1879/1967) and Russell (1903/1996) defined number as the class of all classes that shows a one-to-one correspondence with a given class in an attempt to cast number in terms of logic. Piaget (1941/1965) described number as the property of a set that remains invariant when other perceptual characteristics (e.g., color, size, and density) of the set change. What both definitions mean is that "oneness" is the class of all singletons, "twoness" the class of all doubles, and so forth. For example, "threeness" characterizes the number of sides of a triangle, leaves of a shamrock, and notes in a musical triplet. Describing number in this way indicates that number is an abstraction – a characteristic based on a *single* property of stimuli independent of other properties – that conceptualizes a collection of discrete things.

The aforementioned definitions of number rest on the observation that the natural world is filled with things that exist in aggregates, collections, or sets (Mill, 1859; Conant, 1896). Cardinality answers questions about "how many" things are in a collection, illustrating a set's size. We know that infants as young as 6 months of age appreciate differences in the size of large sets when there is at least 1:2 magnitude of difference between sets (e.g., 4 vs. 8, 8 vs. 16, 7 vs. 21, and 16 vs. 32; Xu and Spelke, 2000; Lipton and Spelke, 2003, 2004; Xu, 2003; Wood and Spelke, 2005; Xu et al., 2005; Cordes and Brannon, 2008a). Additionally, infants appreciate differences in the size of small sets (e.g., 1 vs. 2 and 2 vs. 3), but in contrast to large set discriminations, their ability to discriminate changes in the cardinality of small sets does not appear to be ratio-dependent (Feigenson, 2005; Kobayashi et al., 2005; Cordes and Brannon, 2009b). Furthermore, knowledge about numerical cardinality is not restricted to humans. Non-human animals like primates, birds, and fish discriminate between sets based on the number of things that each collection contains (Emmerton, 1998; Jordan and Brannon, 2006b; Jordan et al., 2008b; Tomonaga, 2008; Merritt et al., 2009; Agrillo et al., 2010).

Collections possess only one size, but they can be arranged in a variety of ways. The idea of arranging collections such that relations of order stand between the cardinality of sets concerns ordinality[1]. Ordinality answers questions about "which one" the set is relative to other sets. To recognize numerical ordinal relations, an organism first must detect differences between the cardinality of sets. Thus, cardinal and ordinal understandings about number are intertwined. The ability to discriminate numerical cardinality, however, does not imply an ordinal understanding of number. In other words, being able to determine that various sets contain a different number of things does not mean that one knows that one set contains more or less items than another set.

Ordinality is an important aspect of numerical cognition. For one, it concerns mathematical ideas. In mathematics, the inequalities "greater than" and "less than" are example relations possessing the four properties that must hold for order to exist[2]. The formal counting system (counting 1, 2, 3, 4, etc.) is based on ordering

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[1] There is another aspect of ordinality in which the quantitative attribute defining order is time, not cardinality. Serial order involves the position or place of a single thing within a sequence. For example, one would say that the black horse crossed the finish line first, the brown horse second, and the white horse third. Indeed, first, second, third, and so forth are called ordinal numbers in mathematics.

[2] For an order relation to exist, four properties must stand (Russell, 1903/1996; Stevens, 1951): (1) irreflexivity ($a \neq b$, $a \neq c$, etc.), which means that no term is related to itself; (2) asymmetry, which means that a series is unidirectional (if $a \to b$ then it does not hold that $b \to a$); (3) connectedness, which indicates that the relation holds between all pairs in the series (if $a \to b \to c \to d$ then $a \to b$, $a \to c$, $a \to d$, $b \to c$, $b \to d$, and $c \to d$); and (4) transitivity, which relates to the relationship that exists between trios in the series (if $b \to c$ and $c \to d$ then $b \to d$).

successive sets of things so that any set paired with its nearest neighbor leaves one member left over (Stevens, 1951). Furthermore, the ability to numerically order sets of things is a basic skill linked to the mathematical skills of preschoolers, adolescents, and adults (Halberda et al., 2008; Libertus et al., 2011; Lyons and Beilock, 2011). Ordinality is also important because a fully developed concept of number involves integrated cardinal and ordinal knowledge that holds across sensory modalities and research methods and allows organisms to perform math-like operations. The aforementioned idea comes from the various ways that researchers attempt to define a non-verbal concept of number. Piaget (1941/1965) characterized the development of a number concept as the synthesis of a child's understanding about the cardinal and ordinal aspects of number. Using the language of mathematics, Gallistel, 1989, 1993 and Gallistel and Gelman (1992) wrote that a concept of number is demonstrated when one can perform operations that are isomorphic to arithmetic and mathematical relations (e.g., $>$, $<$, $=$, and $\neq$). Other authors focus on transfer of learning across modalities and methods (Davis and Pérusse, 1988; Dehaene, 1997). For these reasons, investigating the extent to which non-verbal organisms, both human infants and non-human animals, appreciate numerical order is important for assessing the richness of their conceptual knowledge about number.

The goal of this paper is to integrate what we know about how preverbal human infants process and represent numerical order with literature about the same abilities in non-human animals[3].

Our review revealed that both infants and non-human animals are adapted to respond to monotonic progressions in numerical order and positive mappings between number and other quantities. There are, however, notable differences in the way that human and non-human species process numerical order. These differences could be accounted for by development, the conditions under which representations were generated, or both of the aforementioned. Our comparative examination among non-verbal organisms provides information about when an appreciation of numerical order emerged in the phylogenetic scale, how it increases in complexity with development, and the extent to which it is independent of language.

NON-VERBAL SYSTEMS OF QUANTIFICATION

Before reviewing the literature, it is important to characterize the cognitive mechanisms putatively responsible for processing and representing the cardinality. Evidence from both non-human animals and humans throughout the life span supports the existence of two distinct systems for representing quantity: an analog-magnitude system and an object-based individuation system. Given it would be impossible to identify order among quantities without the ability to track cardinality, one or both systems are necessarily involved in the processing of numerical order. In reviewing the literature, we aim to take a comparative approach to determining the level of involvement of these two systems in developmentally and evolutionarily early appreciations of numerical ordering.

The most prominent system for representing discrete quantity is the analog-magnitude one. The analog-magnitude mechanism supports continuity in the mode of processing because the system handles both large and small values (Gallistel and Gelman, 2000; Cordes et al., 2001). In analog-magnitude systems, discrete quantities are encoded as continuous noisy magnitudes such that an accumulator fills up in nearly equal increments for each entity counted (Gibbon, 1977; Meck and Church, 1983; Church and Meck, 1984; Gibbon and Meck, 1984). There is a scalar property to the noise in the accumulator such that variability in how much the accumulator fills up increases proportionally to the mean value in the accumulator. This results in discriminations becoming less precise as the quantity increases. When detecting differences between quantities, the measure of closeness between a current value and a value stored in memory is the ratio between the values.

An accumulator with scalar noise coupled with ratio-based comparisons is consonant with the observation that quantity discriminations obey Weber's law. Specifically, that the discriminability of two objective values is dependent up on their ratio, not their absolute difference. In particular, if values are encoded and processed as noisy magnitudes then (a) the closer two values are, the harder it is (and longer it takes) to determine which is the larger or smaller one and (b) the larger two values are, the harder it is (and longer it takes) to determine which is the larger or smaller one. These response patterns have been named the numerical distance and size effects. Together the aforementioned effects create the numerical ratio effect, the finding that discrimination ability declines (and response latency increases) when the numerical ratio between compared values approach a value of one (Dehaene et al., 1998). In summary, the analog-magnitude system generates fuzzy, approximate representations of both small and large quantities.

The second system proposed to account for how non-verbal organisms processes and represent quantitative information is based on precise or exact individuation of objects (Simon, 1997; Leslie et al., 1998; Carey and Xu, 2001; Hyde and Wood, 2011). Object-based individuation mechanisms draw upon theories of visual object attention (FINST mechanism, Pylyshyn, 1989; object-file model, Kahneman et al., 1992) and parallel individuation and working memory storage for objects (Vogel et al., 2001; Feigenson, 2008). The idea is that temporary placeholders (object-files, indexes, or unique mental symbols) are assigned in parallel to each relevant object perceived by the visual system when organisms scan an array. Object-based individuation systems attempt to place currently perceived placeholders in one-to-one correspondence with the placeholders from preceding scenes that are in working memory.

In general, infants can hold an exact representation of no more than three items in working memory. This limit is based on evidence that infants can discriminate between small sets (Jordan and Brannon, 2006a), but not discriminate small from large sets (Xu, 2003; see also Cordes and Brannon, 2008b; Cordes and Brannon, 2009a). For example, infants can resolve manual search problems with no more than three items. When 14-month-olds watch an experimenter place three balls in an opaque box and then remove two balls, they search for the third ball in the box. When four balls

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[3] Note that we reviewed only evidence gathered from non-language-trained animals. We did so because researchers theorize that language promotes a kind of flexible thinking that leads to the development of higher levels of conceptualization (Kotovsky and Gentner, 1996; Hauser and Carey, 1998; Fabre-Thorpe, 2001).

are placed in the box and two balls are removed, infants do not search for balls remaining in the box (Feigenson and Carey, 2003; Feigenson and Halberda, 2004). In contrast, the limit for non-human animals and human adults is slightly higher. Based on empirical evidence about the limits of parallel individualization and working memory capacity, human adults and non-human animals can hold an exact representation of four or five items in working memory (Feigenson, 2008; Wood et al., 2008). Object-based individuation systems, thus, support discontinuity in the mode of quantitative processing. The number of objects that can be simultaneously tracked or held in working memory is limited so the processing of large values must be left to a secondary system (i.e., the analog-magnitude system).

ORDINAL BASIS OF RELATIVE QUANTITY JUDGMENT

Humans and non-human animals have access to two distinct systems for representing cardinality, but how do they make ordinal judgments about these representations? Humans and non-human animals encounter situations in their daily lives to which the use of relative quantitative information would be advantageous (Gallistel, 1989; Hauser, 1997; Tomasello and Call, 1997; Wynn, 1998). For example, infants may reach for the hand that contains the greater number of cereal bits and animals may engage in aggressive interactions only with conspecifics that possess a fewer number of allies than they do. Number, though, tends to vary with other continuous quantities (e.g., surface area, density, volume, brightness, inter-item distance, perimeter/contour length, etc.) in systematic ways. For example, the amount of exposed Cheerio surface increases as the number of Cheerios in your father's hand increases. Because a variety of quantitative information is available in situations like these, an organism's decisions may not be based solely on number.

Number is naturally so tightly interwoven with other quantitative properties that it is difficult for researchers to design experimental tasks that isolate number. Early contributions to the literature, thus, focused on describing how preverbal human infants and non-human animals processed ordinal relations about quantitative information without specifically isolating number's contribution using relative quantity judgments (RQJ). RQJ tasks rest on an organism's natural tendency to choose the greatest amount of desirable things (or choose the least of undesirable things) if they are capable of distinguishing between unequal quantities. RQJ is described as the simplest quantitative skill because it does not require the comprehension of precise or absolute number (Davis and Pérusse, 1988). This means that reliably choosing the most of something does not imply knowledge about how divergent the collections are. RQJs are still an important ordinal skill because they give animals the means to maximize food intake (Davis, 1993). For these reasons, we look to the literature about RQJ with discrete quantities to provide insight about the shared basis of processing and representing ordinal relations that involve number.

RELATIVE QUANTITY JUDGMENT IN INFANTS

Unlike non-human animals, human infants are not forced to forage for food for survival. Thus, very few studies have used RQJs to investigate ordinal understandings in human infants. Evidence from these studies, however, reveals that infants are capable of making active responses to determine which of two locations contains the greater amount of desirable items, whether they be toys or food. These ordinal abilities, however, appear to be dictated by the cardinal values of the sets under question.

An early experiment involving RQJ in infants showed that 14-month-olds were able to identify the larger of two small sets of non-visible discrete quantities (Sophian and Adams, 1987). Two sets of toys (1 vs. 2) were shown to infants and then covered with transparent boxes. Infants were then allowed to reach for the box they desired. If the smaller set was chosen, contact with that set was prevented and the infant was verbally encouraged to select the larger set. The procedure was nearly identical during testing except that opaque boxes were used to cover the two sets of toys and insertion-deletion transformation problems (e.g., 1 vs. $1 + 1$; and 3 vs. $2 - 1$) were also presented. Infants selected the set with the most toys more often than chance, which demonstrated infants were capable of making a judgment about the ordinal relation between two small quantities, at least after training.

Two more recent studies demonstrated that infants spontaneously make RQJs between sequentially presented, non-visible amounts as early as 10-months of age (Feigenson et al., 2002; Feigenson and Carey, 2005). Ten- and 12-month-olds were shown two sets of crackers that were sequentially placed into two opaque buckets. The infants were then allowed to crawl toward the bucket that they desired on a single-trial. By only presenting a single-trial, researchers were able to evaluate spontaneous ordinal judgments in which training played no part. Both 10- and 12-month-old infants chose the set with the most crackers for comparisons that were defined by small quantities (1 vs. 2 and 2 vs. 3), but not for comparisons in which one set was small and the other large (1 vs. 4, 2 vs. 4, 3 vs. 4, and 3 vs. 6). This was the case even though the ratio between quantities was the same for certain small and large quantity comparisons (e.g., for a 1:2 ratio: success with 1 vs. 2, but failure with 2 vs. 4 and 3 vs. 6). Successful ordinal comparison of small sets (<4 items) and failure when sets span the small/large size divide suggests that the infants relied on an object-based representation system that was capable of storing up to three items. When ordinal comparisons crossed the small/large boundary, incompatibility between representations of small (via object-based individuation) and large sets (via analog-magnitude) resulted in a failure to choose the larger set.

It is important to note that there is also evidence that suggests that infants use analog-magnitude representation when making judgments about ordinal relations. Using procedures similar to Feigenson et al. (2002), a study found that 10- to 12-month-olds were equally successful at choosing the larger amount of discrete food items with a set that was below (1 vs. 2) and above (5 vs. 10) the capacity limit predicted by object-based individuation models (Van Marle and Wynn, 2011). This result suggests that an approximate representation system is at work when responding to quantitative order. Because only one large comparison was presented, we do not know if RQJs involving large sets display a ratio signature during infancy. Additional experiments are needed to provide information about the conditions under which preverbal infants use analog-magnitudes when making decisions about the ordinal relations that stand between large quantities.

In sum, both object-based and analog-magnitude representations appear to play a role in RQJs during infancy. When choosing between two small sets, like 1 vs. 2 pieces of cereal, or choosing between two large sets, like 5 vs. 10 pieces of cereal, infants as young as 10-months of age successfully reach for, and crawl toward, the largest discrete amount. When ordinal comparisons cross the small/large set size boundary, like choosing between 1 vs. 4 pieces of cereal, incompatibility between representations generated via object-based individuation and analog-magnitude systems results in infants failing to choose the larger discrete amount.

RELATIVE QUANTITY JUDGMENT IN NON-HUMAN ANIMALS

A similar small/large set size distinction holds with the spontaneous judgments that non-human animals make about the ordinal relations between quantities. Set size limits in keeping with a limited capacity, exact object-based individuation system were reported in rhesus monkeys (Hauser et al., 2000), salamanders (Uller et al., 2003), and horses (Uller and Lewis, 2009) who chose between two unequal sets of food items. Specifically, even when the ratio between quantity pairs was equivalent across the small/large quantity divide: (a) rhesus monkeys selected the larger of two sets when at least one set contained four or fewer items (e.g., 2 vs. 3, 3 vs. 4), but failed otherwise (e.g., 4 vs. 6, 4 vs. 8); (b) salamanders selected the larger of two sets when both sets contained three or fewer items (1 vs. 2 and 2 vs. 3), but failed otherwise (3 vs. 4 and 4 vs. 6); and (c) horses selected the larger of two sets when both sets contained three or fewer items (1 vs. 2 and 2 vs. 3), but failed otherwise (4 vs. 6)[4]. Together, these findings point to the conclusion that non-human animals can store and represent from three to four objects when making ordinal decisions about quantities.

Furthermore, the existence of a phylogenetically shared analog-magnitude system for processing and representing ordinal relations is supported by many studies. When apes and monkeys are allowed to choose between sets of unequal discrete food and non-food items, their responses are dependent on the ratio between quantities (Call, 2000; Beran and Beran, 2004; Anderson et al., 2005, 2007; Suda and Call, 2005; VanMarle et al., 2006; Beran, 2007; Hanus and Call, 2007; Stevens et al., 2007; Addessi et al., 2008; Beran et al., 2008a,b; Tomonaga, 2008; Evans et al., 2009; Schmitt and Fischer, 2011).

Evidence of ratio-dependent RQJs is not limited to non-human primates. African elephants (Perdue et al., 2012), crows and African gray parrots (Zorina and Smirnova, 1996; Al Ain et al., 2009; Bogale et al., 2011), coyotes and dogs (Ward and Smuts, 2007; Baker et al., 2011), bears (Vonk and Beran, 2012), sea lions (Abramson et al., 2011), salamanders (Krusche et al., 2010), and swordtail fish (Buckingham et al., 2007) show ratio-dependent ordinal judgments consistent with the predictions of analog-magnitude representation[5]. It is important to note that a set size signature was not found in these studies. This was the case even though some subjects did not receive an extensive number of training or test trials (Ward and Smuts, 2007; Krusche et al., 2010; Baker et al., 2011) and some subjects were experimentally naïve (Anderson et al., 2005, 2007; Buckingham et al., 2007; Ward and Smuts, 2007; Krusche et al., 2010; Abramson et al., 2011; Bogale et al., 2011).

Additional evidence supporting the involvement of analog-magnitudes in ordinal quantity judgments is found when non-human animals make RQJs with non-visual sets. Male beetles choose to spend more time inspecting substrates on which the most female beetles had been located, but only when there was at least a three-fold ratio of difference between compared sets (i.e., succeeded with 1 vs. 3 and 1 vs. 4; failed with 2 vs. 4 and 1 vs. 2; Carazo et al., 2009). In addition, a non-human primate selected the largest quantity after hearing discrete food items dropped into two opaque containers (all pairs from 1 to 5) even when item presentation time was unconfounded with quantity. The subject's responses were affected by the ratio between quantities when making auditory RQJs (Beran, 2012)[6]. Overall, these tasks reveal ratio-dependence, even for small sets, which is indicative of the modality-independence of ordinal understanding[7].

Similar to the findings from RQJs with human infants, a non-human animal study (Hunt et al., 2008) indirectly suggests that two core representation systems are at play during RQJs. Consonant with the predictions of object-based individuation, robins chose the larger of two sets of food items when both sets contained four or fewer items (1 vs. 2, 2 vs. 3, and 3 vs. 4), but not when both sets contained four or more items (4 vs. 5, 4 vs. 6, 6 vs. 8, and 8 vs. 10) even though the ratio between some quantity pairs was equivalent across the small/large quantity divide. On the other hand, the robins successfully chose the larger set for one quantity pair that had a large ratio of difference (i.e., 1:2 ratio between 4 vs. 8), which is suggestive of an analog-magnitude system at work. Thus, songbirds respond to ordinal relations when both sets contain small quantities or when there is a 1:2 ratio of difference between large quantities. Because only one large comparison was presented, we cannot say that the ordinal responses of robins showed a ratio signature, though.

More compelling evidence in support of the two-system view is provided in recent empirical work investigating the social judgments of gregarious fish that prefer to join large rather than small groups (Bisazza et al., 2010; Agrillo et al., 2012). When guppies and mosquitofish made RQJs between two large shoals (>3 members), choices were dependent upon the ratio between shoal sizes. In contrast, when both shoals contained four or fewer members (1 vs. 2, 1 vs. 3, 1 vs. 4, 2 vs. 3, and 3 vs. 4), their choices were more accurate and consistent with object-based representation (Bisazza et al., 2010; Agrillo et al., 2012). Notably, the ability to appreciate ordinal relations with analog-magnitude representation showed

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[4] The data from one report (Irie-Sugimoto et al., 2009) suggest that Asian elephants possess either an exact representation system capable of holding up to six items or a relatively precise analog-magnitude system that is similar to adult humans (e.g., 7:8 ratio; Halberda and Feigenson, 2008).

[5] Ibid footnote 4, p. 8.

[6] Beran (2012) also reported that the chimpanzee continued to make the ordinal response when one set in the pair was made visible, which resulted in the ratio-dependency disappearing. This finding is consistent with the claim that the object individuation system is used only for representing visual sets (vanMarle and Wynn, 2009).

[7] Lion prides were more likely to approach the location of playback roars from a single rather than three intruders regardless of the number of defending adults in their own pride (McComb et al., 1994). Because no other numerical comparisons were tested, though, it is impossible to ascertain whether the data are consistent with an analog-magnitude or object-based individuation mode of representation.

developmental progression in guppies (Bisazza et al., 2010). Newborn guppies chose to spend more time near the larger of two small shoals, which illustrates that the exact, object-based representation system is at work at birth. Their ability to make RQJs between larger shoals (>4 members) emerged with increasing age and social experience, suggesting that analog-magnitudes are less salient early in development.

In sum, these findings illustrate that the ordination of quantities is modality-independent and extends across animal taxa. Both core representation systems are involved when non-human animals make ordinal judgments. When non-human animals are given a single opportunity to select the larger of two desirable discrete quantities, they do so by creating: (a) exact object-based representations if both sets are small, (b) approximate analog-magnitudes if both sets are large, and (c) both kinds of representations if one set is small and the other is large, which results in incompatibility. When making repeated ordinal judgments about quantities, non-human animals are largely dependent on analog-magnitude representation of both small and large discrete quantities. In other words, non-human animals show ratio-dependent responses without a set size signature when making repeated ordinal judgments about quantities.

CONCLUSIONS ABOUT RELATIVE QUANTITY JUDGMENT

When it is advantageous to choose the larger set of discrete things, infants and non-human animals do so, within the limits of their representation systems. Infants and non-human animals travel to, and reach for, the largest collection of desirable items, whether they be food, toys, or social partners. Some animals are even able to do so solely from the sound of items dropping into containers. Ordinal choices occur via an approximate analog-magnitude representation when the ratio between compared sets is large enough and via an exact object-based representation system when the sets being compared are both small. Furthermore, the ordinal quantity judgments of both infants and non-human animals indicate an interaction between these two core systems of representation.

Evidence of both systems at work is most prominent in single-trial investigations of spontaneous ordinal judgments in both human infants and non-human animals. Under this constraint, infants and non-human animals reveal ordinal competence when both to-be-compared sets are small or both are large (provided a favorable ratio). In contrast, when ordinal comparisons cross the small/large size boundary, incompatibility between representations of small (via object-based individuation) and large sets (via analog-magnitude) results in a failure to choose the larger quantity. This pattern mirrors how infants discriminate cardinal number. In particular, young infants can tell that two numerical sets are different in size when both sets are small or when both sets are large (Jordan and Brannon, 2006a; Cordes and Brannon, 2009a), but fail to do so when one set is small and the other is large (e.g., 2 vs. 4; Xu, 2003; Wood and Spelke, 2005; Cordes and Brannon, 2009a).

The ordinal quantity judgments of infants show a three-item limit for object-based representation, which is consistent with the literature about the detection of differences in the numerical size of sets during infancy. Non-human animals, even those that are newly born (Bisazza et al., 2010), show a more flexible three- to four-item limit when making RQJs. Note that the limit for adult humans is closer to no more than four or five objects for exact, object-based individuation (Feigenson, 2008; Wood et al., 2008). Together, this information reveals a dichotomy in the development of the exact object-based representation system across human and non-human animals. Humans experience expansions in working memory from infancy to adulthood, which co-occur with an increase in the capacity limit of the object-based representation system. In contrast, one study (Bisazza et al., 2010) suggests that non-human animals are endowed with a larger, but fixed-capacity object-based individuation system at the time of birth. Future research should investigate if non-human animals experience similar developmental expansions in their working memory or if their object-based representations are fixed throughout development.

Even so, at least one non-human species shows developmental advancement in the analog-magnitude system (Bisazza et al., 2010). The findings showed that newly born guppies are less likely (or not able) to use analog-magnitudes when deciding to affiliate with the larger of two shoals. This phenomenon mirrors the increase in precision seen in analog-magnitude representations across human development. The ratio that must exist for humans to discriminate that the size of two large sets differs decreases from a threefold magnitude of difference (e.g., 4 vs. 12) at birth to a twofold magnitude of difference (e.g., 4 vs. 8) at 6 months of age to a 1.5 ratio (e.g., 4 vs. 6) around 10 months of age to a 1.14 ratio (7 vs. 8) in adulthood (Xu and Spelke, 2000; Lipton and Spelke, 2003, 2004; Xu, 2003; Wood and Spelke, 2005; Xu et al., 2005; Xu and Arriaga, 2007; Cordes and Brannon, 2008a; Halberda and Feigenson, 2008; Izard et al., 2009).

When given repeated trials, though, the RQJs of non-human animals are almost entirely ratio-dependent. This pattern points to an analog-magnitude base for representing discrete quantity when given more than a single opportunity make choices. In this case, analog-magnitude representation holds across the small/large set size divide even for experimentally naïve subjects given a low number of reinforced trials. For example, experimentally naïve dogs were presented with eight pairs of discrete quantities (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) only once, but still their responses showed a ratio signature (Ward and Smuts, 2007). Further, analog-magnitude representation when making RQJs mirrors the pattern found when non-human animals discriminate that two numerical sets are the same (or different) in size (Boysen and Berntson, 1989; Emmerton, 1998; Jordan and Brannon, 2006b; Jordan et al., 2008a; Tomonaga, 2008; Merritt et al., 2009; Agrillo et al., 2010). The parallel that exists between cardination and ordination means that repeated assessments about whether two quantities are different or the same in size are governed by the same representation systems as repeated assessments about whether one numerical set is larger or smaller than another set. Unfortunately, only one infant study has broached the topic of large set RQJs (Van Marle and Wynn, 2011) so it remains to be seen whether the same pattern holds for our youngest counterparts.

In sum, we can conclude that ordinal quantity judgments are an evolutionarily ancient, developmentally early, non-linguistic capacity in the phylum Chordata that spans a species' social system and ecological niche. Although providing evidence of primitive ordinal understanding in non-verbal organisms, it should be noted that the RQJ paradigm fails to disentangle number from other quantitative information like surface area, presentation time, volume, and hedonic value[8]. For this reason, it is unclear whether infants and non-human animals in these studies relied upon number, continuous quantity, or both number and continuous quantity when making their judgments. In fact, follow-up experiments to these studies and control trials within some studies suggest that non-numerical quantities dictated responding in some infant (Feigenson et al., 2002) and non-human animal studies (Zorina and Smirnova, 1996; Stevens et al., 2007; Tomonaga, 2008; Krusche et al., 2010; Vonk and Beran, 2012; but, see, Hauser et al., 2000; Beran, 2007; Bogale et al., 2011). As such, these studies provide indirect evidence suggestive of evolutionarily and developmentally early appreciations of number-related ordinal relations. They do not, however, distinguish number as the driving force behind successful ordinal judgments. If and under what conditions preverbal human infants and non-human animals store and compare exact object-files, approximate analog-magnitudes, or both kinds of representations about numerical information in the absence of covarying cues from continuous quantity is the matter that we consider in the next sections.

UNDERSTANDING NUMERICAL ORDER IN THE ABSENCE OF NON-NUMERICAL CUES

Why do scientists attempt to understand the unique influence of number on the behavior of non-verbal organisms, particularly if number varies systematically and reliably with other quantitative properties (e.g., as the number of my allies increases so does the overall loudness of their vocalizations)? Some researchers argue that the origins of quantitative competence are rooted in discrete number, whereas, others argue for non-numerical origins in which initial representations are amount-based (for reviews, see, Mix et al., 2002; Henik et al., 2012). For this reason, attempts must be made to capture the potential differences that exist when non-verbal organisms order sets of things based on number and when they order using a host of non-numerical quantitative cues. Surprisingly, developmental investigations of this sort have provided a range of conflicting results making it unclear whether or when infants are truly capable of understanding numerical order unconfounded with continuous quantities. In contrast, non-human animal studies reveal a robust pattern of successful ordination. In this review, we attempt to shed light on the apparent inconsistencies within and between the two bodies of literature.

Ordinal numerical knowledge in preverbal infants is typically assessed via looking-time measures in which infants are exposed to numerical sequences. Infants are habituated to sequentially presented sets of items that illustrate an ordinal direction (e.g., $1 \rightarrow 2 \rightarrow 3$, if the arrow denotes "comes before") and then tested with novel sequences that illustrated a reversal in ordinal direction (e.g., $6 \rightarrow 5 \rightarrow 4$). Infants can be said to recognize order among numerical sets if they look longer at sequences that do not obey the ordinal rule that they viewed during habituation or familiarization. To study how non-human organisms process and represent numerical order, researchers turned to mathematical definitions of an order relation (Green and Stromer, 1993). In this paradigm, sequential responses that illustrate a direction of order are established (e.g., $1 \rightarrow 2 \rightarrow 3$, if the arrow denotes "responded to before"). If organisms apply the learned sequential response to numerically novel sequences (e.g., $4 \rightarrow 5 \rightarrow 6$) in the absence of reinforcement then the inference is that they appreciate ordinality.

Regardless of experimental paradigm, this line of research necessarily prevents continuous quantity from influencing an organism's responses so that number's unique contribution can be evaluated. In the experiments we review, the effects of cumulative area, item perimeter or contour length, and array density or inter-item distance are controlled (except where otherwise noted). Thus, the sets that infants and non-human animals view are numerical sets for which cardinality is the only property relevant to be discriminated, and the order that exists among these sets is a function of progressions in cardinality[9].

ORDINAL NUMERICAL KNOWLEDGE IN INFANCY

There are only a handful of studies looking at ordinal numerical knowledge in infancy. This is likely because the earliest investigations did not show ordinal competence in infants. Cooper (1984) reported that 10- to 12-month-old infants did not detect ordinal relations between quantity sequences in which number was confounded with other quantitative properties (e.g., surface area). Infants habituated with ascending ($1 \rightarrow 2$; $2 \rightarrow 3$; and $3 \rightarrow 4$) or descending ($4 \rightarrow 3$; $3 \rightarrow 2$; and $2 \rightarrow 1$) two-set sequences failed to dishabituate to reversed order novel test sequences even though continuous extent was confounded with number. Similarly, Strauss and Curtis (1984) reported that 16- to 18-month-olds did not recognize ordinal relations between two simultaneously presented numerical sets. Using a simple discrimination procedure, infants were reinforced for selecting the larger or smaller number of dots with a single training pair (1 vs. 2, 2 vs. 4, or 3 vs. 4). Then, transfer of the learned ordinal response was assessed by presenting the infants with two numerically novel pairings (pairs from 1 to 5). Although most infants learned to select the larger or smaller numerical set with the original training pair, only a minority of infants continued to make the correct ordinal response with novel numerical pairings. These failures suggested that infants as old as 1.5 years of age did not appreciate ordinal relations.

Given the lack of promise, very little work was done in this area of inquiry for nearly 20 years until the work of Brannon (2002) and Suanda et al. (2008), which capitalized on new knowledge about the ratio-dependency of cardinality discrimination during infancy. In their studies, 9- and 11-month-old infants were habituated to three-set numerical sequences presented sequentially in monotonically ascending ($1 \rightarrow 2 \rightarrow 4$; $2 \rightarrow 4 \rightarrow 8$; and $4 \rightarrow 8 \rightarrow 16$) or descending order ($16 \rightarrow 8 \rightarrow 4$; $8 \rightarrow 4 \rightarrow 2$; and $4 \rightarrow 2 \rightarrow 1$).

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[8] Hedonic value refers to the idea that differences in affective and appetitive responses account for subjects responding in an ordinal manner. For example, choosing and receiving the largest quantity when presented with two vs. three food items induces more salivation and satiation and elicits a stronger affective response than choosing and receiving the smaller quantity.

[9] Compare this to assessments of serial order. Subjects respond or are habituated to arbitrary stimuli in an experimenter-specified sequential order (if the letters denote different colored boxes, $Y \rightarrow B \rightarrow G \rightarrow R \rightarrow O$). Alternatively, in the transitive inference paradigm, subjects are trained to select the positive stimulus in a pair across an overlapping series of stimuli ($Y+/B-$, $B+/G-$, $G+/R-$, and $R+/O-$).

Once habituated, a numerically novel ascending and descending sequence was presented (3 → 6 → 12 and 12 → 6 → 3) to test whether a monotonic reversal of ordinal direction would be detected. The 11-month-olds looked longer at, and dishabituated to, the reversed order test sequence. That is, if they were habituated with ascending sequences, they looked longer at the descending sequence during the test phase and vice versa (Brannon, 2002; Suanda et al., 2008). This was the case even when sequences were modified to ensure that absolute set sizes did not serve as a reliable cue for discrimination (Suanda et al., 2008). In contrast, the 9-month-olds looked equally long at ascending and descending test sequences, revealing no evidence of an ordinal appreciation. Based on these findings, the authors concluded that an understanding of numerical order develops between 9 and 11 months of age[10].

Recent experiments, however, indicate that ordinal number understanding may be present earlier than the 9- to 11-month age range that was initially reported. Using methods similar to Brannon (2002), infants as young as 7-months of age detected changes in ordinal relations when sequences contained only large values (Picozzi et al., 2010). When habituated to numerical sequences that ascended (6 → 12 → 24; 9 → 18 → 36; and 12 → 24 → 48) or descended (48 → 24 → 12; 36 → 18 → 9; and 24 → 12 → 6), 7-month-old infants looked longer at novel numerical sequences that illustrated a reversed monotonic ordinal direction compared to a non-reversed one (4 → 8 → 16 and 16 → 8 → 4). In contrast to Brannon (2002), all sequences contained only large numerical values instead of a mixture of large and small values. Similarly, a study of cross-dimensional transfer of ordinal understanding also provides evidence to suggest that infants appreciate numerical ordinality between large sets earlier than 11-months of age (de Hevia and Spelke, 2010; Lourenco and Longo, 2010). Eight-month-old infants were habituated to a five-set numerical sequence that monotonically ascended (4 → 8 → 16 → 32 → 64) or descended (64 → 32 → 16 → 8 → 4) and then tested with novel five-item *line length* sequences that had a reversed and non-reversed direction of order. Infants looked longer at line length test sequences that illustrated a reversed ordinal direction (de Hevia and Spelke, 2010). Importantly, to distinguish between the ordinal direction of line length sequences during testing, infants needed to encode the ordinal direction of the numerical sequences during habituation.

Why did the 9-month-olds fail to detect ordinal reversals in one study (Brannon, 2002) yet 9- and 7-month-olds succeeded in another study (de Hevia and Spelke, 2010; Picozzi et al., 2010)? Set cardinality is the additional factor responsible for this divergent pattern of results. That is, numerical order is processed and represented at a younger age when numerical sequences contain only large values exclusively represented via the analog-magnitude system. In the most recent studies revealing early ordinal competence (de Hevia and Spelke, 2010; Picozzi et al., 2010), infants were presented exclusively with large sets (>3 items). In contrast, small sets were either exclusively presented or mixed in with large sets in those studies in which all age groups (Cooper, 1984; Strauss and Curtis, 1984) or the youngest age groups (Brannon, 2002; Suanda et al., 2008) failed to detect a reversal in numerical order. These findings indicate that representations from the two core systems are incompatible such that infants fail to recognize changes in ordinal direction when sets within sequences span the small/large set size divide because both core systems are engaged.

Not only are infants tuned to detect cross-dimensional ordinal mappings between number and other quantities, they are also adapted to detect ones that mirror the way number covaries with other quantitative attributes in the natural world. In additional experiments, de Hevia and Spelke (2010) found that 8-month-olds who were familiarized with number-line pairs that illustrated positive ordinal interrelations (smaller set sizes paired with shorter line lengths and larger set sizes paired with longer lines) readily learned these relationships and discriminated between novel stimuli revealing positive (i.e., consistent) and inverse (reverse) pairings of this relationship. In contrast, infants familiarized to inverse ordinal interrelations (small lines paired with large set sizes and vice versa) failed to learn the relationship, showing no difference in the time they looked at positive and inverse ordinal interrelations during the test phase. These experiments provide additional evidence that infants appreciate the ordinal relationships that exist between numerical stimuli, even as young as 8 months provided set sizes are large. But further, these data show that early recognition of ordinality must be consistent with how quantities covary in the real world, suggesting that there is something privileged about the inherent ordering of these quanties, at least in the preverbal mind.

Additionally, there is one more study using a unique design that reveals early detection of numerical ordinality discrimination across small and large sets alike prior to 11 months. In Lourenco and Longo's (2010) associative learning task, 9-month-olds were habituated to two numerical pairs (2 vs. 4, 3 vs. 6, or 5 vs. 10) for which the relative magnitude of numerical pairs was tied to the color/pattern information of sets. For example, items in the smaller numerical set were always white with black dots, whereas, items in the larger numerical set were always black with white stripes. In the test phase, the numerical pair not presented during habituation was shown with a reversed relative magnitude color/pattern mapping (i.e., items in the smaller set were black with white stripes and items in the larger set were white with black dots). The results revealed that infants looked longer at the reversed number-color/pattern mapping during the test phase. In other words, they expected numerically novel pairs to follow the ordinal rule that they experienced during habituation.

Similarly, a second experiment examining cross-dimensional transfer of ordinal interrelations indicated that young infants process and abstract numerical order across small and large sets (Lourenco and Longo, 2010). Nine-month-olds were habituated to numerical pairs for which there was a systematic mapping between the relative magnitude and color/pattern information. For example, if infants were habituated to a display in which the numerically smaller set was white with black dots (and the larger set was black with white stripes), then during test, holding set size constant, the set with a smaller cumulative area was depicted

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[10] Evidence from Suanda et al. (2008) indicates that 9-month-olds detect ordinal direction changes in sequences that have multiple redundant cues (i.e., when cumulative item area, individual item size, *and* the number of items were positively correlated within sequences), but not when number is the sole cue to ordinal direction.

as white/black dots (consistent ordinal direction) or alternatively, depicted as black/white stripes (reversed ordinal direction). The findings showed that 9-month old infants detected reversals in ordinal direction across the dimensions of space and time. Again, cross-dimensional detection of monotonic reversals in ordinal direction could only occur if infants detected ordinal direction in the numerical sequence. These findings demonstrate ordinal numerical competence in 9-month-olds despite set sizes crossing the small/large set size boundary, which contrasts with the findings of Brannon (2002) and Suanda et al. (2008). We explore one explanation for this discrepancy in the conclusion section.

ORDINAL NUMERICAL KNOWLEDGE IN NON-HUMAN ANIMALS[11]

Like human infants, the behavior of non-human primates reveals that they understand ordinal relations among numerical sequences. Rhesus monkeys were trained to touch two-set numerical sequences in ascending (1 → 2; 1 → 3; 1 → 4; 2 → 3; 2 → 4; and 3 → 4) or descending monotonic order (Brannon and Terrace, 1998, 2000; Brannon et al., 2006)[12]. Intermixed with trials of the training sequences were non-differentially reinforced trials of numerically novel test sequences (all possible pairing of 5–9 elements). Monkeys responded in the appropriate order to the numerically novel sequences more often than predicted by chance, which showed that they abstracted ordinal relations. A subsequent experiment showed that learning how to sequentially respond in ascending order to two-set numerical sequences (all possible pairs from 1 to 9 elements) resulted in two of the rhesus monkeys understanding ordinal relations between novel two-set sequences that had values well outside the originally learned range (i.e., all possible pairs of 10, 15, 20, and 30 elements; Cantlon and Brannon, 2006). In contrast, researchers were unable to train a rhesus monkey to sequentially respond in an arbitrary non-monotonic order (3 → 1 → 4 → 2; Brannon and Terrace, 2000), suggesting that responding relied upon the ordinal relationships inherent in the numerical stimuli. Together, findings reveal that rhesus monkeys understand ordinal relations between numerical sets and they can apply their learned ordinal understanding across a wide range of numerical values.

Ordinal understanding of this type is not restricted to the genus *Macaca* or even to non-human primates. Replications with other species reveal that a hamadryas baboon and squirrel monkey (Smith et al., 2003), one of three capuchin monkeys (Judge et al., 2005), and pigeons (Scarf et al., 2011) gain an understanding of ordinal numerical relations from learning to sequentially respond in an ascending manner to numerical sequences. In addition, two bottlenose dolphins gained an understanding about ordinal relations between simultaneously presented numerical pairs (Jaakkola et al., 2005). In particular, they generalized the ordinal rule "choose the least" from training sets (2 vs. 6, 1 vs. 3, 3 vs. 7, 1 vs. 8, 3 vs. 7, 2 vs. 4, and 4 vs. 7) to new pairings (all possible pairs from 1 to 8 items). Together, these findings reveal that ordinal understanding about number spans Old and New world monkeys and the class Mammalia and Aves.

Importantly, the findings indicate that analog-magnitude representations of number governed the ordinal responses of non-human animals. Accuracy and/or response time conformed to Weber's law for most monkeys, pigeons, and dolphins (Brannon and Terrace, 1998; Smith et al., 2003; Jaakkola et al., 2005; Brannon et al., 2006; Cantlon and Brannon, 2006; Scarf et al., 2011) in support of analog-magnitude numerical representation. In particular, response accuracy declined and response time increased as the ratio between the numerical values being compared approached a value of one. In contrast to the human infant literature, there was no evidence that ordinal knowledge was limited to sets with no more than three or four items, which suggests that object-based representation systems were not involved. There also was no evidence that ordinal knowledge was disrupted by the employment of two distinct systems of representation for number as ratio-dependent responding held across all cardinal values, which implicates the analog-magnitude system. Although some animal subjects were experimentally sophisticated in discriminating between large and small numerical values (Brannon and Terrace, 1998; Brannon et al., 2006; Cantlon and Brannon, 2006), others were not (Smith et al., 2003; Jaakkola et al., 2005; Judge et al., 2005; Scarf et al., 2011). Experimental history, therefore, does not offer a satisfactory explanation for not finding evidence of set size limits. Instead, the findings suggest that non-human animals are less likely to engage an object-based individuation system when tracking numerical order.

CONCLUSIONS ABOUT ORDINAL NUMERICAL KNOWLEDGE

The empirical evidence indicates that both non-human animals and preverbal infants are capable of detecting changes in numerical order. Comparative analysis, however, indicates that the representation systems that infants and non-human animals rely on to detect numerical order differ. Monkeys, birds, and dolphins respond according to numerical order, and the primary representations that they form when doing so are fuzzy, analog-magnitudes. Further, their ordinal responses are dependent on the ratio between numerical sets, not the size of sets. Analog-magnitude representation when responding sequentially to numerical order is in keeping with the representations that non-human animals generate when determining that numerical sets differ in size (Boysen and Berntson, 1989; Emmerton, 1998; Jordan and Brannon, 2006b; Jordan et al., 2008a; Tomonaga, 2008; Merritt et al., 2009; Agrillo et al., 2010). This indicates that the same analog-magnitude system is used to represent numerical information for cardination and ordination; indeed, cardination must occur for ordination to occur.

On the other hand, two core representation systems – an object-based individuation system that processes small sets exactly (<4 items) and an analog-magnitude system that processes large sets approximately (>3 items) – are involved when human infants recognize numerical order. This is illustrated in the finding that infants younger than 11-months of age appear unable to process and represent numerical order with numerical sequences that cross

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[11] There is a large body of evidence showing that non-human animals can be trained to order symbolic representatives of quantity (Boysen et al., 1993; Boysen and Berntson, 1995; Harris et al., 2007, 2010; Beran et al., 2008c). For the purposes of this review, however, we focus on appreciations of number-related ordinal relationships that are independent of linguistic or symbolic systems.

[12] These tasks followed training to touch the full sequence in ascending (e.g., 1 → 2 → 3 → 4) or descending order (e.g., 4 → 3 → 2 → 1).

the small/large set size boundary. The same processing incompatibility exists when infants discriminate differences in the number of things that sets contain (Xu, 2003; Wood and Spelke, 2005; Cordes and Brannon, 2009a). This again speaks to the idea that cardination via object-based or analog-magnitude representation must occur for infants to detect order among numerical sets.

We provide two non-mutually exclusive explanations to account for the divergent pattern between human infants and non-human animals. First, the divergent pattern may arise because associative learning paradigms activate a continuous, broadly applicable system for understanding small and large numerical values (i.e., analog-magnitudes). When non-human animals are repeatedly reinforced for touching numerical sets in a progressing order, they rely on analog-magnitude representations to abstract ordinal relationships. On the other hand, when infants are familiarized or habituated to numerical sets (passive viewing conditions), they rely on both core systems. Consistent with the animal literature, infant looking-time patterns did not point to a small/large set size boundary in one study employing associative learning to investigate ordinal knowledge (Lourenco and Longo, 2010). Infants could predict a set's ordinal class ("larger than" and "smaller than") from the color and patterning of the elements in sets (e.g., the larger set black rectangles with white dots vs. smaller set white rectangles with black stripes). There was no disruption from activating both core systems – infants succeeded in detecting numerical ordinal relations between small and large sets (e.g., 2 vs. 4 and 3 vs. 6). Although this study does not inform us about the presence of ratio-based responding, at the very least this study suggests that it is easier for infants to construct and compare representations from the two core systems when associative learning is involved.

A second explanation for the divergent pattern of results obtained between infants and non-human animals is a developmental one. The evidence suggests a developmental progression in the ability of infants to process and compare sets when making numerical ordinal judgments. This is illustrated in the finding that infants are not able to process and represent numerical order with sequences that contain both large and small sets until 11-months of age. Although differences across human and non-human species have been investigated, changes across development within non-human animal species have not been thoroughly examined. Therefore it remains to be seen whether this developmental pattern is uniquely human or whether a similar developmental trajectory is mirrored in non-human animals. It is known that guppies show an ontogenetic progression from relying on object-based individuation to relying on both object-based individuation and approximate-magnitude systems when making RQJs (Bisazza et al., 2010). So it may be that non-human animals show a similar progression from greater reliance upon the object individuation system early in development (as has been observed in human infants) to later fluency with integrating representations across the analog-magnitude and parallel individuation systems when number is the only relevant cue. Attempts should be made to investigate developmental patterns in the way that non-human animals understand numerical order to determine if representations of small sets are similarly granted a privileged status early in the development of non-human species (Buhusi and Cordes, 2011).

Despite the differences in the way that infants and non-human animals process and represent numerical order, both preverbal infants and non-verbal organisms understand numerical order in a way that follows the patterns that exist in the natural world. Two sorts of evidence support this claim. First, in nearly all studies reviewed, non-verbal subjects acquired an ordinal rule with one set or series of numerical values and readily apply that rule to novel numerical values without further feedback or training (e.g., Brannon and Terrace, 2000; Brannon, 2002; Cantlon and Brannon, 2006; Picozzi et al., 2010). In other words, infants and animals abstracted ordinal relationships. This generalization of ordinal knowledge reveals that non-verbal organisms appreciate the intrinsic ordinal relationship amongst cardinal values (e.g., $4 < 8 < 12$), an ability which goes above and beyond the sequential ordering of numerical sets within the sequence (e.g., $4 \rightarrow 8 \rightarrow 12$).

Second, non-human animals and infants are less apt to acquire numerical sequences that violate this inherent order, even with repeated trials. This is exemplified in the finding that non-human primates cannot learn to arbitrarily order numerical sets (e.g., $3 \rightarrow 1 \rightarrow 4 \rightarrow 2$; Brannon and Terrace, 2000) and infants do not detect inverse number-line length ordinal interrelations (e.g., small numerical sets paired with long lines; de Hevia and Spelke, 2010). This suggests that non-verbal subjects rely upon the "less than" and "greater than" relationships inherent to numerical sequences when abstracting numerical ordinality. In sum, evidence strongly suggests that responding across these tasks was not the result of arbitrary sequence learning, but a function of the numerical values presented.

Interestingly, these findings can be juxtaposed against experiments that show that non-human animals and human infants detect serial order; that is, they readily learn arbitrary orderings of non-quantitative things. For example, non-human animals learn to select the yellow box followed by the blue box followed by the green box, etc. (Gillan, 1981; Boysen et al., 1993; Terrace, 1993; Beran et al., 2004; Merritt et al., 2007). Even infants as young as 4-months of age detect changes in the serial order of moving and sounding objects (Gulya et al., 1998; Lewkowicz, 2004; Lewkowicz and Berent, 2009)[13]. Furthermore, children and non-human animals learn non-monotonic quantitative serial orderings (e.g., medium box → medium-small box → large box → small box → medium-large box) more poorly than monotonic ones (Terrace and McGonigle, 1994; Ohshiba, 1997; Kundey et al., 2010). The intrinsic order of numerical quantities is salient. Although both infants and animals are capable of learning arbitrary sequences, they are less apt (or possibly unable) to do so when the sequences violate numerical ordering. This pattern not only speaks to the shared evolutionary basis of ordinal understanding about number and quantities, but also tells us that numerical order holds a privileged status above mere sequence learning.

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[13] Ibid footnote 9, p. 9.

DISCUSSION

From free-ranging dogs deciding whether to retreat from a rival pack (Bonanni et al., 2011) to young human infants reaching for the most bits of cereal (Feigenson et al., 2002), tasks requiring ordination of quantities provide a wealth of evidence showing that both preverbal human infants and non-human animals are sensitive to ordinal relationships. Single-trial experiments assessing spontaneous ordination reveal a robust set size signature in both non-human animals (but, see, Krusche et al., 2010) and preverbal infants. On the other hand, when non-human animals are given repeated attempts to order quantities, set size limitations diminish, and analog-magnitude representations play a primary role. As such, non-verbal understanding about number-related order depends upon both object-based individuation and analog-magnitude systems. Whether a similar pattern holds for repeated trials in RQJ tasks with infants remains an open question ripe for investigation.

Given that number is naturally confounded with other quantitative variables in RQJ tasks, these types of experiments cannot distinguish whether this non-linguistic sensitivity to ordinality is based upon number, surface area, volume, hedonic value, and/or a combination of these quantities. Our examination of numeric appreciations of ordinality (i.e., when non-numerical quantities like surface area, contour length, inter-element distance, and density are prevented from systematically covarying with the cardinality of sets) reveals less similarity between infants and non-human animals. When sequential responses to numerical order are reinforced, the representations that non-human animals form are not limited by set size, but are ratio-dependent (Brannon and Terrace, 1998, 2000; Smith et al., 2003; Judge et al., 2005; Brannon et al., 2006; Cantlon and Brannon, 2006; Scarf et al., 2011).

In contrast, the ability of young human infants (under 9 months) to detect changes in numerical order primarily continues to reveal a set size signature. It is not until the end of the first year of life (∼11 months) that infants reliably detect changes in numerical order regardless of the size of the sets involved (Brannon, 2002). Thus, evidence suggests that the ability to integrate numerical representations generated from the exact (object individuation) and approximate (analog-magnitude) systems increases across development in human infancy. More work is needed to clarify this discrepant pattern of findings across infants and non-human animals, though. Specifically, whether methodological differences (employing associative learning vs. passive observation) may account for these observed differences remains to be determined. That associative learning activates a continuous, broadly applicable system for understanding small and large numerical values (i.e., analog-magnitudes) is a compelling idea. For one, it could inform the creation of educational tools and efforts designed to stimulate an infant's understanding of number. Further, more work is needed to determine whether the developmental trajectory, an increased ability to integrate numerical representations generated from the exact and approximate systems, is mirrored in the lives of non-human animals. Discovering that the cognitive development of non-human animals follows the trajectory shown by human infants would provide strong evidence to support a shared evolutionary basis of numerical cognition.

Even after our review, many questions remain about the evolutionary origins and adaptive significance of ordinal knowledge and its relation to other cognitive abilities. Surprisingly, although human infants appear capable of detecting ordinal relationships across small and large sets by around 11 months of age (Brannon, 2002), they continue to fail to discriminate changes in set cardinality crossing the small/large set size boundary as late as 23 months of age (i.e., they fail to discriminate a set of two from four; Barner et al., 2007). What is it about ordinality that allows infants to overcome the set size limitations imposed by the employment of two distinct representational systems? One way to shed light on this question is to evaluate the role of individual differences (in terms of plasticity and stability over time) in the development of ordinal abilities. For example, early understandings of numerical order may be correlated with, or predicative of, greater precision in analog-magnitude representations, an ability to detect all kinds of order in the world, and/or mathematical skills. Future research should explore these possibilities. Similar questions may also be addressed with non-human species to shed light on when and why such abilities have emerged and if they are immune to set size limitations early in development.

In conclusion, evaluating the shared basis of ordinal numerical knowledge helps us construct a complete picture about the development and evolution of numerical cognition. Although much has been learned about the signatures of numerical ordinal behavior in both human infants and non-human animals, open questions remain. A stronger parallel between infant and animal paradigms will provide greater insight into the developmental and evolutionary origins of these sophisticated abilities. Ordinal knowledge about number is an evolutionarily ancient, developmentally early, non-linguistic capacity that spans a species' social system and ecological niche. Because developmental psychology is about comparison and comparative psychology is about development, our fields must continue to track age-related changes in the way that all species understand numerical order.

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Subitizing and visual short-term memory in human and non-human species: a common shared system?

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Numerical competence is widely spread across human and non-human species. Here we discuss the possibility that the similarities shown in the processing of small sets of items might be due to the characteristics of basic cognitive abilities for the processing of visual items, common to both human and non-human living beings.

Several species show a fast and accurate performance in judging the numerosity of small sets of items, an ability termed "subitizing" (Tomonaga and Matsuzawa, 2002; Agrillo et al., 2012). Regardless of whether one or two systems for the processing of non-symbolic magnitudes exist, the similar performances often observed across such diverse species have led to the hypothesis that there may be shared core systems supporting numerical abilities of non-human species and non-verbal numerical abilities of humans (Beran et al., 2011). A challenging question is whether these similarities in non-symbolic numerical information processing are due to numerical competences or if they are caused (in both human and non-human species) by the limits of the systems devoted to the processing of visual sets of items (visual short-term memory, VSTM). VSTM can retain a limited amount of information at one time and, in humans, it is typically investigated by means of change detection paradigms. In contrast, most of the paradigms investigating the neural mechanisms of VSTM in animals required the retention of just a single memorandum and, until recently, no study provided a direct comparison between humans and primates of VSTM capacity in a change detection task. This issue was addressed by Elmore et al. (2011) by testing humans and rhesus monkeys with the same change detection paradigm. A memory array (composed by colored circles or clip arts figures), was presented and, after a retention interval, a test array with two items appeared; the response consisted in choosing the "changed" item. Task difficulty was manipulated by varying the number of items presented in the memory array (i.e., the VSTM load). The authors were able to show that animals can perform a change-detection task with the same procedures/stimuli used for humans, and also succeeded in highlighting the qualitative similarities between the performance of monkeys and humans. This comparative study, as the one by Beran et al. (2011), is an interesting example suggesting that the use of identical procedures for humans and animals might provide fruitful insights on humans' cognitive performance: indeed, it strongly suggests the possibility to enlarge the research field of numerical cognition with truly multidisciplinary approaches, where conclusions made for one (non-human) species can be informative also for a second one (e.g., human).

To address the point we want to raise here, namely the fact that subitizing range cannot be considered as independent from VSTM capacity limits, the bridge across species needs to be complemented by a further bridge across cognitive abilities. The latter bridge has been provided by an influential behavioral experiment on humans (Piazza et al., 2011) which addressed the relation between the processing of non-symbolic magnitudes and VSTM. Beginning with the naïve observation that in humans the behavioral limits of subitizing and VSTM are strikingly similar (around 3–4 items), the authors adopted a sophisticated dual-task paradigm to determine whether these similar capacity limits are subserved by the same cognitive mechanisms and recruit the same resources. In each trial, participants performed two tasks: a counting task and a change detection VSTM task. Participants were first presented with a memory array of either two or four colored circles (low vs. high VSTM load), briefly replaced by a counting set ranging from one to eight items. This set was then masked and the participants were asked to report its numerosity (primary task). Finally, they were presented with a test array (same number of colored circles of the memory set) and performed a same–different judgment with respect to the memory set (secondary task). The amount of VSTM load selectively impaired performance in the counting task, by reducing the individual subitizing range, but had no effect on the estimation of large quantities; furthermore, the interference between the two tasks exhibited a predictable pattern, in line with the idea of a common capacity limit. This result suggests the presence of a domain general mechanism (i.e., multiple object individuation) shared by subitizing and VSTM; by recruiting the core resources that are characterized by a limited capacity, even an apparently basic ability like subitizing can be significantly impaired. From a broader perspective there is one main question that can be intuitively addressed: what is the comparison of non-symbolic magnitudes, if not the active maintenance of information conveyed by stimuli which are no longer in view?

Interestingly, the integrated view provided by the two investigations presented here sheds light on the advantages that a comparative study on VTSM and numerical cognition might grant both across and within species. Importantly, VSTM provides an essential link between perception and higher cognitive functions, and the role played by capacity limits of VSTM should not be neglected when investigating the basic numerical abilities both in humans and animals. In conclusion, given the mounting evidence that non-symbolic numerical processing and VSTM are intimately related, and given their qualitative similarities in humans and non-humans, we can argue that a comparative investigation on the relation between non-symbolic numerical processing and VSTM might provide dramatic advances in the understanding of the bases of numerical processing. This type of approach can open to the broader idea of an assessment of cognitive abilities and capacities in non-human species. It could also open to a fine-grained analysis of the ability to flexibly deploy attentional resources/capacity limits in such cognitive abilities. Finally, this approach might help to solve outstanding questions such as to discover whether subitizing and large numerosity estimation are related to two different mechanisms or whether they are only the two extremes of the same continuum, and whether non-symbolic numerical abilities and VTSM can be dissociated in animals.

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Minds without language represent number through space: origins of the mental number line

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During the last decades, extensive research has investigated both the developmental origins and the representational format of numerical information. A crucial contribution to these issues comes from recent studies on non-verbal populations, such as non-human animals and preverbal infants, which suggest that number is intuitively and fundamentally spatial in nature, that a predisposition to relate numerical information to spatial magnitude emerges very early in life, and that the association of numbers to different spatial positions critically depends on biologically determined processing and attentional biases.

Various sources of evidence suggest that when representing numbers human adults translate them into corresponding spatial extensions and positions (Restle, 1970; Galton, 1880; Dehaene et al., 1993; Fias et al., 1996). This phenomenon is referred to as number-space mapping and accounts for various systematic behavioral effects in numerical and visuo-spatial tasks. For instance, numerical processing modulates spatial representation according to a cognitive illusion, whereby small numbers induce a compression and large numbers an expansion of spatial extent (de Hevia et al., 2006, 2008; Stöttinger et al., 2012). In particular, adult's bisection of a line flanked by two numbers is biased toward the larger one (Fischer, 2001; de Hevia et al., 2006; Ranzini and Girelli, 2012), and the reproduction of a spatial extension is underestimated when delimited by two small numbers, and overestimated when delimited by two large numbers (de Hevia et al., 2008). Other observations, such as the interference between numerical and physical size in Stroop-like tasks and cross-dimensional mapping tasks (Stevens, 1970; Girelli et al., 2000; Pinel et al., 2004; de Hevia et al., 2012), support the existence of a mapping between symbolic and non-symbolic numbers and spatial magnitude.

The idea we would like to put forth is that the number-space mapping appears to be fundamental, spontaneous, and present very early in life, as it might constitute an innate trait of human, and possibly non-human, cognition. The notion that this mapping is universal and spontaneous is supported by neuroanatomical evidence showing that common parietal structures are engaged in both numerical and spatial tasks (Dehaene et al., 2003; Fias et al., 2003). Critically, electrophysiological studies have revealed that the posterior parietal cortex in primates, which includes quantity-selective neurons, contains accurate information about discrete (number of items) and continuous (length) quantity, with the same neurons coding for both non-symbolic number and spatial length (Tudusciuc and Nieder, 2007). Therefore, in line with the well-known ATOM (A Theory Of Magnitude) model proposed by Walsh (2003), numbers, as well as other magnitudes, might not be represented in isolation but spontaneously connected to space representation.

Further support for an intuitive and universal number-space mapping comes from research conducted with preschool children, preverbal infants, humans in remote cultures, and non-human animals, where a spontaneous mapping between number and space has been observed through a variety of experimental paradigms. When bisecting a line flanked by two different, non-symbolic numbers, 3–5-year-old children show a signature bias toward the larger number, just as adults do (de Hevia and Spelke, 2009; Girelli et al., 2009). Through the habituation paradigm, infants at 8 months of age transfer the discrimination of an ordered series of numbers to an ordered series of line lengths, and learn and productively use a rule that establishes a positive relationship between number and length, while failing to do so with an inverse relationship (de Hevia and Spelke, 2010; see also Lourenco and Longo, 2010). Using the number line task, which explicitly requires the mapping of number onto space (Siegler and Opfer, 2003), adults living in an Amazonian remote culture, with little or no education, resemble children's mappings with non-symbolic numbers (Dehaene et al., 2008). These findings suggest that the number-space mapping takes place well before formal education, preceding language, and symbolic knowledge acquisition. Moreover, among other mappings between continuous dimensions the number-space mapping seems to have a privileged status. When preschool children create cross-dimensional matches between different instances from the dimensions of number, line length, and level of brightness, they reliably perform mappings between number and length, and only partially between brightness and length, but fail to map number and brightness (de Hevia et al., 2012). Also in adults, number establishes a stronger overlap, at both functional and neural levels, with the dimension of space than with the dimension of brightness (Pinel et al., 2004; but see Cohen Kadosh et al., 2008).

An instantiation of the number-space mapping is that ordered numerical magnitudes are associated to different spatial positions along a horizontal continuum. The classical finding for this phenomenon is the Spatial-Numerical Association of Response Codes (SNARC) effect: generally speaking, small numbers are responded faster with the left hand and large numbers with the right hand, suggesting a compatibility effect between the left and right sides of one's own body and a left-to-right oriented numerical representation (Dehaene, 1992; Dehaene et al., 1993; Fias et al., 1996). This phenomenon has been extended to a variety of scenarios; among others, priming with a small or large number leads to shifts of attention toward the left or right sides of the space, respectively (Fischer et al., 2003). Critically, SNARC-like effects have been described for non-numerical ordinal series: adults react faster using the left hand to the presentation of the initial letters of the alphabet (Gevers et al., 2003), initial tones of a musical scale (Rusconi et al., 2006), initial (or past) events (Santiago et al., 2007), and initial elements in a list of unrelated words (Previtali et al., 2010), while they are faster using the right hand for the final elements of these series. Therefore, ordinal information in general, and not only number, triggers the use of an oriented spatial code. Moreover, the association of number with spatial positions is amply malleable, so that by simply varying the task requirements or setting, like conceiving numbers as depicted in a clock-face (Bächtold et al., 1998) or exposing bilingual participants to reading different languages (Shaki and Fischer, 2008), the association changes. This suggests that associating numbers to spatial positions results from a task-dependent individual's mental strategy to organize information (Fischer, 2006), an instance of the spatial coding of ordinal information in working memory (van Dijck and Fias, 2011).

Contrary to what commonly hypothesized, the origins of this mapping might not be exclusively culturally based. In favor of a culturally based position, the SNARC effect is modulated by reading direction: in Western cultures, small numbers are associated to the left and large numbers to the right side, while in cultures with right-to-left reading/writing direction the association is weaker (Dehaene et al., 1993) or reversed (Shaki et al., 2009). However, although early attempts to trace the SNARC effect in children described its emergence at 9 years of age (Berch et al., 1999), recent studies using non-symbolic number and non-chronometric tasks found it in 4-year-old children not formally introduced to reading system (van Galen and Reitsma, 2008; Patro and Haman, 2012). Moreover, the 3- and 4-year-olds who exhibit a consistent left-to-right bias in tasks such as subtraction and addition of tokens and counting objects (e.g., counting from the left and proceeding rightwards) are more proficient at basic numerical knowledge (Opfer et al., 2010). These studies suggest that, much before entering school, early cultural factors engendered by activities such as counting or "reading" illustrated books (McCrink et al., 2011) may determine the specific orientation of children's number-space mapping.

Far from denying the strong impact of cultural conventions on the number-space mapping, we see these forces as playing a modulating and refining role, not a fundamental one. Our idea is that the association of numbers onto spatial positions along a spatial magnitude might root in early biases present in the processing of magnitude information, whether numerical or spatial, which, from early on in development, would concur in shaping the way infants attend and represent any ordinal information, such as number. Optimal candidates might be a biologically determined advantage for processing the left hemispace, and an advantage in the processing of increasing order. Across the lifespan, these biases would be modulated and refined by exposure to cultural conventions.

In fact, and of critical importance to our view, not all processing biases are determined by culture. Let us review the seminal studies on counting abilities in newly hatched chicks. In these studies, chicks are trained to peck at the 4th position in a series of ten identical, equispaced and sagittally oriented locations. Afterwards, when required to identify the correct location within a new series identical to the one used at training, but horizontally oriented, chicks are more accurate at identifying the 4th position from the left than from the right end, which is chosen at chance level (Rugani et al., 2010). While cultural conventions cannot account for these findings, basic attentional biases can. The left bias shown by chicks is thought to be due to right hemispheric dominance in visuospatial processing, resulting in the left hemifield guiding the birds' behavior. Chicks' hemispheric lateralization can be experimentally manipulated by controlling the rearing environment of the eggs, thus providing a promising animal model for investigating the neural bases of the oriented number-space mapping (Vallortigara et al., 2010). This manipulation has been also performed in fish by obtaining animals that differ in the direction of cerebral lateralization. When these animals solve a bisection task, i.e., choosing the central element in a row, strong spatial biases are found in opposite directions, either toward the right or the left, depending on the artificially obtained direction of cerebral lateralization (Dadda et al., 2009).

These findings from non-human, non-linguistic species substantiate the role of neural factors and visuo-spatial processing strategies in engendering attentional biases. One contribution to the emergence of a number-space mapping in humans is, in our view, the biologically determined attentional bias regulating the asymmetrical exploration of space. Although available infant literature does not clearly establish the presence and degree of such biases, hints for this phenomenon are nonetheless informative. First, classical studies on infants' visual exploration indicate that at birth horizontal scans are wider and more frequent than vertical scans (Haith, 1980), suggesting that visual exploration and stimulus detection are easier along the horizontal than the vertical orientation. Second, a timing asymmetry may exist in the maturation of cerebral hemispheres, with a temporal advantage for the right over the left hemisphere (Rosen et al., 1987).

Thus, spatio-temporal constraints on brain development may determine an advantage of the left over the right visual hemispace in early infancy. This leftward spatial bias might constrain both the exploration of external space and the organization of information along a representational space. In fact, attentional biases in visual space likely extend to the mental representation of information. For instance, patients with unilateral neglect not only fail to explore the left side of visual space, but also the left side of a mental image (Bisiach and Luzzatti, 1978), and fail to accurately bisect imagined numerical intervals, showing biases toward the larger number (Zorzi et al., 2002; Vuilleumier et al., 2004). A further processing bias relevant to our argument is the recently disclosed advantage for processing increasing magnitude information. Four-month-old infants discriminate increasing ordered sequences of an object progressively changing in size, but fail at detecting decreasing sequences (Macchi Cassia et al., 2012). These finding points to the existence of an asymmetry in the processing of ordinal information which, combined with a natural propensity to asymmetrically explore space, might constitute one of the building blocks of a mental mapping where numbers are associated to different spatial positions. From early on and across the lifespan, the advantage in the horizontal scanning of the left hemispace, and the advantage in the processing of ascending order might combine with culturally based factors, such as exposure to reading/writing habits and the associated scanning and ordering routines. These factors would either counteract a predetermined orientation or strengthen it, eventually giving rise to culturally dependent strategies to represent ordinal information, including, but not limited to, number.

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