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Domestic dogs show flexible left-to-right spatial-numerical association

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Abstract

The Spatial Numerical Association (SNA) is a form of spatial representation of numerosities, which associates small numerosities with the left and large ones with the right. SNA has been reported across phylogenetically distant species, suggesting that its biological origin is independent of language, education, and symbolic number systems. However, research on SNA in domesticated mammals remains sparse.

Here, we investigated SNA in domestic dogs, a domesticated mammal characterized by heterogeneous individual experiences and prolonged interactions with humans. We trained 49 pet dogs to circumnavigate a central panel displaying eight dots. Then, in an unrewarded test, they were presented with two identical lateral panels displaying either a smaller (4) or a larger (16) numerosity. To account for individual lateralization, dogs were classified as SNA-consistent only if they chose the left panel in the smaller test and the right panel in the larger test. The number of dogs showing flexible SNA-consistent responses exceeded chance expectations and persisted when continuous variables (perimeter, density and area) were unreliable.

To assess whether SNA correlated with performance in a visual numerical discrimination task, some dogs also underwent comparisons between numerosities ranging from 4 to 16. Remarkably, dogs showing a consistent SNA outperformed the others in the discrimination with more difficult ratio (> 0.70).

Our results show a left-to-right-oriented SNA in adult dogs, suggesting that numerical spatialization in non-human animals persists despite potentially extensive differences in individual experience and may be related to the efficiency of the Number Sense.

INTRODUCTION

Numerical information is ubiquitous in the environment, and the ability to process numerosity is widespread among vertebrates (Piantadosi and Cantlon 2017). To interact effectively with their environment, animals must not only identify relevant stimuli, but also estimate their numerosity, an ability that likely confers direct fitness benefits by maximizing food intake and reducing predation risk (Giurfa 2019; Nieder 2020; Regolin et al. 2025).

Numerical abilities in non-huma animals, ranging from numerical discrimination to proportional reasoning, are thought to rely on two systems: the Object File System (OFS) which precisely represents small numerosities (up to four items), and the Analogue Magnitude System (AMS), which approximately represents larger numerosity. The OFS is an object-based attentional mechanism that creates discrete files in working memory for each perceived object. Although the OFS evolved to represent objects, it also implicitly tracks their numerousness (Trick and Pylyshyn 1994).

Estimates of larger numerosities rely on the AMS, which is characterized by distance and magnitude effects: performance improves as numerical distance increases and declines as numerical magnitude increases, respectively. As a consequence, discrimination depends on the ratio between the numerosities being compared, rather than on their absolute difference, becoming progressively more difficult as the ratio approaches 1, in accordance with the Weber's law (Gallistel and Gelman 1992; Dehaene 2011). Similar effects reported across species (Cantlon and Brannon 2007; Scarf et al. 2011; Garland et al. 2012; Rugani et al. 2013, 2014b) suggest that there is a shared, ancient, non-symbolic mechanism for number comprehension, called Number Sense (Feigenson et al. 2004; Cantlon and Brannon 2007; Dehaene 2011). Number Sense is an evolutionarily ancient system, available early in development, that allows animals to represent and compare quantities approximately, without the use of symbols or language (Feigenson et al. 2004; Dehaene 2011). Beyond advancing our understanding of numerical cognition, investigating the cognitive mechanisms underlying numerical representations across species provides insights into the evolutionary origins of Number Sense and of the selective pressures that shaped its emergence (Rugani 2018; Regolin et al. 2025).

A distinctive feature of numerical representation is the so-called Mental Number Line, a Spatial-Numerical Association (SNA) whereby smaller numbers are associated with the left side of space and larger ones with the right (Galton 1880). The Mental Number Line was first described in humans and was initially thought to be a cultural artifact, shaped by reading and writing direction (Dehaene et al. 1993; Zebian 2005; Shaki et al. 2009). The most compelling challenge to the cultural origin of SNA comes from comparative research (Brugger 2015; Vallortigara 2018; Felisatti et al. 2026a; Eccher et al. 2026). Seminal evidence was reported in birds that were trained to identify an item by its ordinal position and then tested with the same array rotated by 90°. Their preference for the left item, rather than for the right one, suggested that numerical ordinality is represented along a left-to-right spatial axis (Rugani et al. 2007, 2010). Cross-species applications of this paradigm revealed a consistent left-to-right proto-counting tendency across phylogenetically distant vertebrates, including day-old domestic chicks (Rugani and Regolin 2020, 2021; Rugani et al. 2025), adult Clark’s nutcrackers (Rugani et al. 2010), adult rhesus monkeys (Drucker and Brannon 2014) and preschool children (West and McCrink 2021; Rugani et al. 2022b). So far, pigs represent the only known exception, exhibiting a right-side bias, possibly because, unlike other species, they relied on spatial rather than numerical cues (Brosche et al. 2026). Although this paradigm established the existence of a spontaneous left-to-right proto-counting bias across species, the reported bias is unidirectional. It therefore does not capture the defining feature of the human Mental Number Line, i.e. the relative spatial organization of numerical magnitude, in which smaller numbers are associated with the left and larger ones with the right. Crucially, whether a number is represented as "small" or "large" depends on the numerical context rather than its absolute value. Thus, the same number can be represented as either small or large depending on the reference set. For example, the number 8 is represented as large when compared with 2, but as small when compared with 32 (Dehaene 2011; Rugani and de Hevia 2017; Vallortigara 2018; Felisatti et al. 2026a; Eccher et al. 2026).

Clear evidence for a smaller-left and larger-right association comes from a spatial-numerical congruency paradigm (Rugani et al. 2015). Following training to locate a food reward behind the central panel displaying five elements, chicks were tested with two identical panels, both depicting the same numerosity, either smaller (2 vs. 2) or larger (8 vs. 8) than the training numerosity. Birds preferentially approached the left panel when the test numerosity was smaller than the training numerosity and the right panel when it was larger. Crucially, this spatial bias was relative to the reference numerosity: the same numerosity (8) was associated with the right side after training with five elements, but with the left side after training with 20 elements. Remarkably, the observed SNA could not be explained by continuous physical variables, including cumulative area, overall perimeter, and element density (Rugani et al. 2015), nor by individual lateralization biases (Rugani et al. 2020).

This evidence renewed interest in the evolutionary origins of spatial-numerical associations (Brugger 2015; Rugani and de Hevia 2017; Vallortigara 2018; Giurfa et al. 2022; Felisatti et al. 2026a; Eccher et al. 2026)) and provided a valuable framework for investigating SNA in non-verbal subjects. The spatial-numerical congruency paradigm (Rugani et al. 2015) has subsequently been applied across different species, yielding mixed results. Studies that closely replicated the original chick paradigm in cleaner fish (*Labroides dimidiatus*), rhesus monkeys (*Macaca mulatta*), and capuchin monkeys (*Sapajus apella*) generally failed to detect SNA (Triki and Bshary 2018). In contrast, studies that preserved the underlying rationale of the paradigm while adapting the experimental design to the biological and ecological characteristics of the tested species successfully demonstrated SNA in human newborns (de Hevia et al. 2014; Di Giorgio et al. 2019), zebrafish (*Danio rerio*)(Potrich et al. 2026), and honey bees (*Apis mellifera*) (Giurfa et al. 2022). Overall, this evidence, together with findings obtained using different paradigms across species (de Hevia and Spelke 2010; Rugani et al. 2014a, 2022a, b, 2024; Adachi 2014; de Hevia et al. 2014; Bulf et al. 2016; Gazes et al. 2017; McCrink et al. 2020; de Hevia 2021; Loconsole et al. 2023; Eccher et al. 2025; De Hevia et al. 2025; Decarli et al. 2025; Straulino et al. 2026; Volpi and De Hevia 2026; Felisatti et al. 2026b), indicates that numerical spatialization is a common feature of brains endowed with a Number Sense (Giurfa et al. 2022). Whereas studies in newborn animals address whether SNA emerges before extensive experience, adult domesticated animals provide a complementary model for examining whether these associations persist or are reshaped by prolonged individual learning and interaction with humans. Nevertheless, to date, the only study conducted in a domesticated mammal, the pig, did not provide evidence of numerical spatialization, as the animals relied on spatial rather than ordinal numerical cues (Brosche et al. 2026). The domestic dog (*Canis familiaris*) therefore represents a valuable comparative model for investigating whether SNA is also present in domesticated mammals with variable experiences.

Dogs (*Canis familiaris*) have recently emerged as a valuable model for non-invasive comparative neuroscience (Bunford et al., 2017) and evidence in their numerical cognition are growing (Bonanni et al. 2011; Miletto Petrazzini and Wynne 2016). Dogs (*Canis lupus familiaris*) and wolves (*Canis lupus*) can discriminate between sequentially presented quantities of food when food items are dropped one at a time into two opaque containers, demonstrating the ability to maintain and compare internal representations of non-visible quantities. Control conditions using stones ruled out the possibility that

dogs relied on simple non-numerical cues, such as presentation time or the number of insertion events (Range et al. 2014). Nevertheless, when numerosity and the total amount of food were experimentally dissociated, dogs preferentially selected the option containing the greater amount of edible food rather than the larger number of food items, indicating that, in food choice contexts, the amount of food outweighs numerosity (Miletto Petrazzini and Wynne 2016). In a computerized simultaneous discrimination task, dogs and wolves successfully discriminated visual quantities. However, both species relied not only on numerical information but also on continuous visual cues, such as stimulus size and shape (Rivas-Blanco et al. 2020). Moreover, dogs' performance followed Weber's law: they spontaneously discriminate numerosities at ratios up to 0.67 (Lõoke et al. 2020), with performance improving to ratios of 0.80 following training (Rivas-Blanco et al. 2020). Together, these findings support previous evidence that dogs rely on an approximate representation of numerical magnitude like that described in other species (Ward and Smuts 2006; Cantlon and Brannon 2006, 2007; Rugani et al. 2013, 2014b; Macpherson and Roberts 2013; Range et al. 2014; Miletto Petrazzini and Wynne 2016; Lõoke et al. 2020). Dogs also exhibit some perceptual biases affecting numerical estimation. In particular, they are susceptible to the connectedness illusion, underestimating the numerosity of arrays composed of interconnected items (Lõoke et al. 2020) similarly to humans (He et al. 2009; Anobile et al. 2017; Fornaciai and Park 2021). Moreover, dogs show serial dependence in numerical judgments, with previously presented numerosities biasing the estimation of subsequent stimuli (Lõoke et al. 2024) which suggests the involvement of a high-level processing stage, similarly to what has been reported in humans (Fornaciai and Park 2022). However, dogs showed no evidence of numerosity misperception in the Solitaire illusion (Lõoke et al. 2020), in which the spatial arrangement of identical items induces an over- or under-estimation of their numerosity, suggesting that only some perceptual mechanisms underlying numerical estimation are shared with humans (Agrillo et al. 2014; Byosiere et al. 2020; Lõoke et al. 2020). Together, these findings suggest that dogs possess flexible numerical representations that are influenced by perceptual organization, raising the question of whether numerical magnitude is also spatially represented, as observed in several other vertebrate species. Despite this growing evidence for numerical competence, research on spatial–numerical associations in dogs remains unexplored.

Here, we investigated whether domestic adult dogs exhibit spontaneous numerical spatialization by associating smaller numerosities with the left and larger numerosities with the right.

In Experiment 1, we adapted the spatial–numerical congruency paradigm previously validated in chicks, human newborns, honeybees, and zebrafish. Dogs were first trained to locate a food reward hidden behind a central panel depicting a reference numerosity of eight dots. At tests, where no trials were rewarded, dogs faced two identical lateral panels displaying either a smaller (4 vs. 4) or a larger (16 vs. 16) numerosity. Because dogs show substantial tendency to develop side bias when facing choice tasks (Kis et al. 2025), only dogs that circumvented the central panel from both the left and the right during training were included. Moreover, we assessed SNA using a stringent within-individual criterion: dogs were classified as SNA-consistent only if they chose the left panel in the smaller-than trial and the right panel in the larger-than trial. If dogs spatialize numerosity according to the SNA, we expected them to

exhibit a flexible response pattern, choosing the left panel in the smaller-than trial and the right panel in the larger-than trial.

In Experiment 2, we investigated whether individual performance in the spatial–numerical congruency task was associated with quantity discrimination abilities. To this aim, dogs were tested in a simultaneous numerical comparison task involving discriminations of increasing difficulty, using ratios of 0.50 (4 vs. 8 or 8 vs. 16) and 0.73–0.75 (6 vs. 8 or 8 vs. 11). Although evidence for spontaneous numerical spatialization across species is steadily increasing, whether Spatial–Numerical Associations confer any functional advantage for numerical processing remains unknown. Spatial organization of numerical magnitude has been hypothesized to facilitate access to and comparison of numerical representations, thereby increasing the efficiency of quantity processing (Loconsole et al. 2023; Rugani et al. 2025; Felisatti et al. 2026a). However, this hypothesis has yet to be directly tested in non-human animals. If numerical spatialization facilitates numerical processing, we expect dogs showing a congruent SNA to outperform the others, particularly in the more demanding discriminations involving ratios close to Weber's threshold.

In Experiment 3, we controlled for the possible influence of continuous visual variables on SNA using the spatial-numerical congruency paradigm, by equating density and total perimeter across numerosities while cumulative area and element size varied inversely with numerosity. If dogs use discrete numerosity rather than continuous visual variables, we expect them to continue to exhibit the predicted flexible response pattern, choosing the left panel in the smaller-than trial and the right panel in the larger-than trial.

MATERIALS AND METHODS

Subjects

A total of 49 dogs together with their owner were enrolled for this study. Twenty-five of them were male and 24 were female, with an average age ± standard deviation of 7.1 ± 3.6 years. Dogs were of various breed: 3 Australian shepherd, 2 Shetland, 2 Border collie, 2 Golden retriever, 2 Schnauzer, 2 French bulldog, 2 Poodle, 2 Cavalier king Charles Spaniel, 1 Bichon, 1 Beagle, 1 Pomeranian, 1 Shi-tzu, 1 Labrador retriever, 1 German shepherd, 1 Whippet, 1 Dachshund, 1 Hovawart, 1 Italian Bloodhound, 1 Fox Terrier, 1 Lagotto Romagnolo, 1 Belgium shepherd, 1 English setter, 1 Yorkshire, 1 American akita, 1 Basenji, 1 English bulldog, 1 Cocker Spaniel, 13 mix breed. The dog-owner dyads consisted of employees or students of the University of Padua, or were recruited through the volunteer participant database of the Laboratory of Applied Ethology of the University of Padua. The inclusion criteria for the dogs were being adult dogs at least one year old, having no known visual or motor impairments, and being comfortable with their owner in unfamiliar laboratory environments.

The required sample size was determined using G*Power for a two-tailed exact binomial test, assuming an expected proportion of 0.55, a chance level of 0.25, $\alpha = 0.05$, and 80% power. The analysis indicated a

minimum sample size of 22 subjects. Therefore, out of 49 dogs, 24 took part in Experiment 1, 14 of which were also available to participate in Experiment 2, while the remaining 25 took part in Experiment 3.

Experiment 1

Experimental Setting

The tests took place in an experimental room measuring 420 x 290 cm. In order to provide a distraction-free area for the dogs, inside the experimental room, a smaller area measuring 200 x 250 cm was created, framing it with white panels. Along one of the longer sides, the panels left an 80-cm-wide opening that served as the dog's starting position. Here, the owner sat on a stool while the dog was positioned between the owner's legs and gently held by the shoulders. In front of the dog, a movable curtain could be raised or lowered by the first experimenter to either reveal or occlude the testing scene during the different phases of the experimental session. During the training trials, the visual stimulus was presented on a support placed on the floor, 150 cm in front of the dog. Immediately behind the stimulus support, a bowl containing a food reward for the dog was placed. During the test trials, two identical stimuli were presented simultaneously on separate supports positioned on the floor, 170 cm to the left and to the right of the dog's starting position, respectively. To ensure a clear left–right choice, the testing area was divided into two symmetrical parts by a white plastic partition (130 × 30 cm) extending in the centre of the room. Along the opposite longer side of the testing area, a second curtain concealed the second experimenter (Fig. 1). Two cameras (AVer TR311HWV2, Taipei, Taiwan) were recording the whole experiment. One camera was mounted on the ceiling to have an overhead view of the testing area and record the dog's choices. The second camera was positioned on the rear wall of the room, facing the dog, and was used to record the dog's orientation while being held at the starting position before release.

Stimuli

The stimuli consisted of printed sheets (30x42 cm) attached to the support through magnets positioned both on the back of the stimuli and on the support itself. Stimuli were generated in MATLAB (R2024b, MathWorks, Natick, USA) and consisted of a black background displaying a set of white dots, each with a radius of 1.5 cm (Fig. 2). To ensure a homogeneous spatial distribution of the dots, a MATLAB script virtually divided each stimulus into four equal quadrants. An equal number of dots was allocated to each quadrant, while the exact position of each dot within its quadrant was random. The number of dots varied according to the experimental phase and testing condition. For the training phase 10 stimuli depicting the numerosity of 8 white dots were created, each of which was presented sequentially during the 10 training trials. During the test phase, dogs were presented with two identical stimuli simultaneously. In the *more-than condition*, the stimuli displayed 16 dots, in the *less-than condition*, the stimuli displayed 4 dots.

Procedure

The experiment involved two sessions, made at least one week apart. Each session was composed of 10 training trials, plus a test trial. Upon arrival at the laboratory, dogs were given time to familiarize with the environment and settle down, while an experimenter explained the testing procedure to the owner. The owner was instructed to enter the experimental room with the dog and sit on the stool located at the starting position between the panels. The dog was positioned between the owner's legs, facing straight toward the centre of the testing area, and was gently held by the shoulders. Owners were instructed to remain silent generally throughout the session and to avoid interacting with or influencing the dog's behaviour. Experimenter 1 entered the experimental room together with the dog-owner dyad and positioned herself behind them. Experimenter 2 was already concealed behind the rear curtain and had prepared the first training stimulus, placed a food reward in the bowl, and lowered the front curtain so that the testing scene was hidden when the dog and owner entered the room. Once everyone was in position, the first training trial began. Experimenter 1 raised the front curtain, allowing the dog to see the stimulus. As soon as the curtain was fully raised, Experimenter 1 started a stopwatch and, after 5 seconds, touched the owner's shoulder as a signal to release the dog. The dog was then allowed to explore the testing area and to retrieve the food reward located behind the stimulus. Once the reward had been found, the owner was allowed to verbally praise the dog and call it back to the starting position. Experimenter 1 then lowered the front curtain, after which Experimenter 2 removed the previous stimulus, placed the next one, and replaced the food reward. This procedure was repeated for all 10 training trials. If some dogs did not spontaneously explore the testing area or seek the food reward, Experimenter 1 instructed the owner to gradually encourage the dog using a sequence of prompts: first, giving a familiar search-related verbal cue (e.g., “search”, “find”, or another word commonly used by the owner to encourage the dog to locate reward); if the dog still did not approach the stimulus, the owner could stand up and take a step forward; if necessary, the owner could then point toward the stimulus. If a dog failed to independently approach the stimulus and retrieve the food reward after five training trials, he/she was excluded from the study. The 11th trial consisted of the test trial and followed the same general procedure as the training trials. However, the testing area was arranged by the second experimenter so that, on the left and on the right side of the room, two stimuli were presented simultaneously. Consequently, after Experimenter 1 raised the curtain and the dog was released, the dog was required to make a choice by approaching either the left or the right stimulus first. To avoid reinforcing side preferences, no accessible food reward was provided during the test trial. However, to maintain the same olfactory conditions as during training trials, an inaccessible piece of food was hidden behind each test stimulus. The side of the first stimulus approached by the dog was recorded as dog's choice. After making this choice, the dog was allowed to continue exploring the testing area and inspect the opposite stimulus. This procedure ensured that the dog could verify that no food reward was available behind either stimulus, thereby minimizing the possibility that a learning by exclusion strategy could influence the subsequent testing session. At the end of the test trial, the session was concluded and dogs and owner were invited for the second testing session at least one week later.

The second session was identical to the first except for the stimuli presented during the final test trial so that each dog was exposed in one test trial to the *more-than* stimuli and in the other to the *less-than* stimuli. The order of presentation of the two test conditions was counterbalanced across subjects. Only at the end of both sessions, owners were debriefed regarding the aim of the experiment and the theoretical background of the study.

Data collection

The side chosen by the dog in the test trials was manually recorded form the videos of the test sessions. Data about the dog's eyes orientation during the training trials were collected with Observer XT (version 12.5, Noldus, Wageningen, The Netherlands), with a continuous sampling technique. Orientation toward the stimulus or elsewhere were collected from the moment the eyes of the dog became visible from the curtain being pulled up, until the dog was released by the owner. Similarly, dog's orientation towards the right stimulus, the left stimulus or elsewhere was collected during the test trials. Orientation was coded for 30% of the videos by a second observer to assess interobserver reliability (Pearson correlation coefficient ranging from 0.82 to 0.89). Data of dog's orientation were computed as the mean percentage of time looking at the training stimulus and the percentage of time looking at the left or at the right stimulus during the test trials.

Data analysis

The SNA assumes that smaller numerosities are associated with the left side, while larger ones are associated with the right side. Hence, dogs' choices in the test trials were coded as 'correct' when they conformed to such assumption (i.e. dog chose the left stimulus when presented with the *less-than condition* or the right stimulus in the *more-than condition*). Dogs were then classified as "SNA-consistent" if they choose the side consistent with SNA assumptions in both conditions, and "SNA-inconsistent" otherwise. Then, a two-tailed binomial test was run to determine whether dogs conforming to the SNA assumptions were more numerous than what predicted by chance (i.e. 25% chance of choosing the correct stimulus on both the *less-than* and the *more-than* test trials).

A Generalized Estimating Equation (GEE) model was implemented to assess whether choices in the test trials were explained by attention paid by dogs to either the reference stimulus during the trials of the training phase, or either of the two stimuli in the test trials. The outcome of each test trial (correct/wrong) was included in the model as a dependent variable, assuming a binomial distribution. The mean percentage of looking at the stimulus during training trials and the percentage of looking at both the left and at the right stimulus during the test trials were included as continuous predictors. The identity of the dogs was included as the subject variable to account for repeated measurements within individuals. All statistical analyses were performed with SPSS (v. 28, IBM, Armonk, NY). The level of statistical significance was set at 0.05.

Experiment 2

Experimental Setting

The test was conducted in an experimental room measuring 420 x 290 cm. The dog starting position, market by a T on the floor, was located 130 cm away from the two stimuli supports, one of which was placed on the right side of the room and the other on the left side. The two stimuli were on the floor 80 cm apart. In between the two stimuli, Experimenter 1 was located, whose task was to place the stimuli on the stands and signal to the owner to release the dog. Behind Experimenter 1, at the back of the room, there was a table used by a second experimenter to prepare the new stimuli for each trial. This back area was made inaccessible to the dog by the presence of two panels (Fig. 3). One ceiling camera (AVer TR311HWV2, Taipei, Taiwan) was used to have an overhead view of the dog's choices.

Stimuli

Stimuli of the Experiment 2 consisted in a square shape of black polycarbonate panels measuring 30x30 cm, on top of which dots of commercial turkey ham slices (1 cm diameter, 0.1 cm thick) or polymer clay were evenly arranged (Fig. 3). Three sets of 2 stimuli were used. The first set of 2 stimuli were used for the training phase and consisted in one positive stimulus displaying 5 food dots, and one negative stimulus displaying 2 dots of polymer clay, the same colour and size as the real pieces of food. The second and the third set of stimuli were used for the test phase. In one set the two stimuli presented were displaying either 4 vs 8, or 8 vs 16 (ratio of 0.5) dots of food. In the other, stimuli with a numerosity of 6 vs 8 (ratio of 0.75), or 8 vs 11 (ratio of 0.73) dots of food were used.

Procedure

Dogs initially underwent a training phase to familiarize with the experimental procedure. During the first trial, the experimenter stood in front of the dog and presented a stimulus containing 3 food dots. The experimenter attracted the dog's attention by calling its name and pointing to the food dots. The owner, seated on the stool at the starting position and holding the dog gently by the shoulders between their legs, released the dog, allowing it to approach the stimulus and consume the food dots. This trial was done in order to allow the dog experiencing that the dots presented on the stimuli were actual food. After this, the discrimination training began. For each trial, the experimenter presented two stimuli, a positive stimulus with five food dots and a negative stimulus with two fake food dots. After attracting the dog's attention by calling its name, the experimenter placed the two stimuli on their supports, one on the left and one on the right side of the testing room. Following a 5s delay, the owner released the dog upon the experimenter's signal. If the dog approached the positive stimulus, it was allowed to consume the food dots and received verbal praise. If it approached the negative stimulus, no reward was available. At the end of each trial, the owner called the dog back to the starting position. The side of the positive stimulus was alternated across trials. The training phase made in order to familiarize with the procedure, consisted of 10 trials, after which the dog proceeded directly to the test phase. The test phase consisted of two test trials, one for each discrimination ratio, and followed the same procedure as the training trials. In contrast to the training phase, both stimuli contained real food rewards, so that dogs were

rewarded regardless of their choice. The first test trial assessed discrimination at a ratio of 0.50. Dogs were presented with either a 4-versus-8 or an 8-versus-16 food-dot discrimination, with the stimulus sets counterbalanced across participants. The second test trial assessed discrimination at a ratio of 0.73–0.75. In this trial, dogs were presented with either a 6-versus-8 or an 8-versus-11 dot discrimination, again counterbalanced across participants. The side of presentation of the positive stimulus was counterbalanced across subjects: for half of the subjects, it was presented on the right side in the first test trial and on the left side in the second test trial, whereas the opposite was done for the other half.

Data collection and analysis

For each test trial, choices were coded as a binary variable, depending on whether the dog selected the stimulus representing the larger (correct) or the smaller (wrong) quantity.

For each test trial, performance, i.e., the frequency of correct/wrong choices, was compared against chance level using a one-tailed exact binomial test, for both the 0.5 ratio condition and the 0.7.

To assess whether the presence of a Spatial Numerical Association was associated with the performance in Quantity discrimination, a GEE model with a binomial logistic distribution was fitted. The outcome of each test trial of the Experiment 1 (correct/wrong) was entered as the dependent variable. The outcomes of the 0.5 ratio trial, of the 0.7 ratio trial and of the first training trial of Experiment 2 were included as categorical predictors. The rationale for including the outcome of the first training trial was to assess whether the presence of SNA was associated with a spontaneous response to the presentation of different quantities. Dog ID was specified as the subject variable to account for repeated measurements within individuals.

All statistical analyses were performed with SPSS (v. 28, IBM, Armonk, NY). The level of statistical significance was set at 0.05.

Experiment 3

Experimental Setting and Procedure

Experiment 3 was designed as a control for the potential influence of continuous, non-numerical visual cues. While in Experiment 1 changes in numerosity were associated by changes in other stimulus properties, in Experiment 3 density and total perimeter were controlled so that the stimuli differed only in numerosity (see Stimuli section for details). The experimental setting and procedure implemented in the third experiment was the same as the one used in Experiment 1.

Stimuli

The stimuli consisted of square printed sheets (30x30 cm) attached magnetically to the support as for Experiment 1. Stimuli were created using GeNEsIS in Matlab (R2020a Version ; (Zanon et al. 2022) and displayed a black background with a set of white squares. The number and the dimension of the white squares varied according to the experimental phase and testing condition; however, stimuli were created

in order to keep density and total perimeter constant across numerosities. The density, defined as the number of elements divided by the total occupied area, was set as = 0.03; the total perimeter, defined as the sum of the perimeters (contours) of all elements, was set as = 64. For the training trials, 10 stimuli depicting a numerosity of 8 white squares were created, resulting in elements with the size of 2×2 cm. For the test trials, depending on the condition (*more-than* or *less-than*), two stimuli were presented simultaneously depicting either 16 white squares (1x1 cm) or 4 white squares (4x4 cm; Fig. 4).

Data collection and analysis

The data of Experiment 3 were collected and analysed in the same way as for Experiment 1.

Therefore, data about the of the outcome of each test trial (correct, wrong) of two experiments on the SNA were pooled, in order to see if there was a potential effect of the Experiment (one and three) and of the Condition (more-than, less-than). To this aim, a GEE model with a binomial logistic distribution was implemented, with the outcome of each test trial (correct/wrong) included in the model as a dependent variable, and Experiment and Condition as categorical predictors.

Dog ID was included as the subject variable to account for repeated measurements within individuals. All statistical analyses were performed with SPSS (v. 28, IBM, Armonk, NY). The level of statistical significance was set at 0.05.

RESULTS

Experiment 1

The two-tailed binomial test against the chance level of 25% showed that dogs performed above chance level (k = 11 “correct” out of n = 24, p = 0.042).

The dogs’ orientation in relation to the performance outcome is shown in Fig. 5. The GEE model used to assess the potential effect of the dog’s looking time at the stimuli on the performance outcomes, did not reveal any effect (mean percentage of time looking at the training trials: Wald $\chi^2 = 0.205$, p = 0.651; percentage of looking time at the left stimulus during the test trial: Wald $\chi^2 = 2.198$, p = 0.138; percentage of looking time at the right stimulus during the test trial: Wald $\chi^2 = 1.595$, p = 0.207).

Experiment 2

The dogs’ percentage of correct choices of the two test trials are reported in Fig. 6. The one-tailed binomial test against the chance level of 50% showed that dogs performed above chance level in the 0.5 ratio test (k = 11 “correct” out of n = 14, p = 0.028) but not in the 0.7 ratio test (k = 8 “correct” out of n = 14, p = 0.39).

The GEE model implemented to assess if performance in Experiment 1 could be explained by performance in Experiment 2, revealed an effect only related to the 0.7 ratio test (Wald-Chi square = 4.962, p = 0.026, Odds ratio = 9.696), with dogs having a successful outcome in the Experiment 1 performing better than dogs who failed (Estimated Means ± Standard Error: “Correct” Experiment 1 outcome = 0.90 ± 0.089; “Wrong” Experiment 1 outcome = 0.49 ± 0.191). Performance of dogs in the first training trial (Wald-Chi square = 3.048, p = 0.081) and in the 0.5 ratio test (Wald-Chi square = 0.181, p = 0.671) did not have an influence.

Experiment 3

The two-tailed binomial test against the chance level of 25% showed a performance of the dogs above the chance level (k = 12 “correct” out of n = 25, p = 0.022).

The dogs’ orientation according to the test result is shown in Fig. 7. The GEE model used to assess the potential effect of the dog’s orientation on the performance outcomes, showed no effect (mean percentage of time looking at the training trials: Wald χ^2 = 0.049, p = 0.824; percentage of time looking at the left stimulus during the test trial: Wald χ^2 = 2.006, p = 0.157; percentage of time looking at the right stimulus during the test trial: Wald χ^2 = 0.372, p = 0.542).

The GEE model run to explore a possible influence of the Experiment (one and three) and of the Condition (*more-than* and *less-than*) on the outcome of each test trial (correct/wrong) of Experiment 1 and 3, revealed no effect (Experiment: Wald χ^2 = 0.003, p = 0.957; Condition: Wald χ^2 = 0.530, p = 0.467). However, running the intercept-only model, it showed a significant intercept (Wald χ^2 = 6.339, p = 0.012).

DISCUSSION

In this study, we explored whether domestic dogs associate relative numerical magnitude with space and whether this spatial organization is related to proto-numerical discrimination abilities. To assess Spatial Numerical Association (SNA), we used a spatial-numerical congruency paradigm, which required dogs learning to find a food reward behind a panel displaying a reference numerosity eight. In unrewarded test trials, dogs faced two identical panels, one on the left and one on the right, depicting the same numerosity, either smaller or larger than the reference. To assess relationship between spatial-numerical association and quantity processing, we also use a simultaneous numerical comparison task between two numerosities of food rewards characterized by a ratio of 0.50, or 0.70.

Our first main finding is that domestic dogs associate relative numerical magnitudes with space. In Experiments 1, the number of dogs showing the complete SNA-consistent pattern (selecting the left panel in the smaller-than condition and the right panel in the larger-than condition) exceeded chance expectations. In Experiment 3, the SNA-consistent pattern persisted when continuous variables were controlled. Specifically, density and total perimeter were held constant, whereas cumulative area and individual element size varied inversely with numerosity. Consequently, the smaller numerosity was composed of larger elements and occupied a greater cumulative area, whereas the larger numerosity

was composed of smaller elements and occupied a smaller cumulative area. If dogs had mapped physical extent or element size onto space, these cues should have induced a pattern opposite to the numerical prediction. Instead, dogs continued to associate the smaller numerosity with the left and the larger numerosity with the right.

Remarkably, the pattern observed in Experiments 1 and 3 cannot be explained by preferences for one side of space. This issue is particularly relevant in dogs, in which behavioral lateralization has been documented across motor and sensory domains (Siniscalchi et al. 2017; Stiller et al. 2024). Moreover, dogs are known to develop side biases when facing two-choice tasks, especially when the choice is uncertain (Kis et al. 2025). For these reasons, to minimize the influence of individual side biases, only dogs that circumvented the central panel from both the left and the right during training were included. Additionally, we also adopted a stringent within-individual criterion and we limited each kind of trial to one. Each dog underwent only one smaller-than and one larger-than test trial (unlike previous studies using multiple trials and group-level analyses; (Giurfa et al., 2022; Potrich et al., 2026; Rugani et al., 2015, 2020, but see Di Giorgio et al., 2019, for a single-trial adaptation). We then classified dogs as SNA-consistent only when they selected the left panel in the smaller-than condition and the right panel in the larger-than condition. A stable leftward or rightward preference would have produced the same choice in both conditions and could therefore not result in an SNA-consistent classification. Nevertheless, dogs' side responses appear to reflect the relation between the test numerosity and the previously experienced reference rather than a fixed lateral bias.

This result extends evidence obtained in human infants and newborns, gorillas, orangutangs, monkeys, day-old domestic chicks, adult Clark's nutcrackers, zebrafish, and honeybees (de Hevia and Spelke 2010; Rugani et al. 2010, 2015, 2020, 2024; Drucker and Brannon 2014; Adachi 2014; de Hevia et al. 2014; Gazes et al. 2017; Di Giorgio et al. 2019; Giurfa et al. 2022; Volpi and De Hevia 2026; Potrich et al. 2026; Felisatti et al. 2026b), showing that discrete numerical magnitudes can also be associated with space in a domesticated mammal. Moreover, the present results strengthen the hypothesis that SNA appears to be present even in animals with heterogeneous life histories and extensive experience with their owners, as it is for family dogs.

Our second main finding is that numerical spatialization correlates with the efficiency of magnitude processing. Although evidence for spontaneous numerical spatialization across species is steadily increasing, and SNA has been proposed as a hallmark of all brains endowed with a number sense, independently of their complexity (Giurfa et al. 2022; Rugani et al. 2025), whether Spatial–Numerical Associations confer any functional advantage for numerical processing remains unknown. Spatial organization of numerical magnitude has been hypothesized to increase the efficiency of numerical processing (Loconsole et al. 2023; Rugani et al. 2025; Felisatti et al. 2026a). In humans, studies in which participants classify symbolic numbers using left- and right-sided responses, typically responding faster to smaller numbers with the left hand and to larger numbers with the right hand, have not consistently found a correlation between the strength of SNA and arithmetic performance (Cipora and Nuerk 2013; Cipora et al. 2020; He et al. 2021). Importantly, these studies mainly focused on symbolic mathematical

skills rather than elementary non-symbolic quantity discrimination. Whether SNA is associated with the efficiency of basic numerical processing has not yet been tested in non-human animals and therefore remains unknown. This was the aim of Experiment 2, which showed that dogs discriminated quantities differing by a 0.50 ratio but not those differing by the more demanding 0.73–0.75 ratio, thus supporting previous evidence that quantity discrimination in dogs is ratio-dependent (Rivas-Blanco et al. 2020; Lõoke et al. 2020). However, the key innovative finding of our study is that performance in the more difficult discrimination was associated with performance in the spatial–numerical congruency task (Experiment 1).

Remarkably, performance in the spatial–numerical congruency task was correlated only with the more demanding quantity discrimination. One possible interpretation is that the spatial organization of numerical magnitude facilitates magnitude estimation when the task is difficult. When two quantities are clearly different, the advantage provided by spatial coding might not emerge. By contrast, when the ratio approaches the discrimination threshold, organizing magnitudes along an oriented spatial continuum may increase processing efficiency. This correlational result should nevertheless be interpreted with caution: only 14 dogs, which participated in Experiment 1, completed both experiments, due to the owners' availability to return for an additional session. Although preliminary, this finding paves the way for future studies with larger samples and repeated trials to directly test whether SNA facilitates quantity discrimination.

These data may support the Right Hemisphere Dominance Model (Rugani et al. 2015, 2016, 2025; Rugani and de Hevia 2017; Rugani and Regolin 2020; Giurfa et al. 2022), one of the three models proposed to explain the neural basis of the SNA, together with the Brain's Asymmetric Frequency Tuning Model (BAFT; (Felisatti et al. 2020) and the Emotional-Valence Model (Vallortigara 2018; Rugani et al. 2020). The BAFT model is based on hemispheric specialization for spatial-frequency processing, with spatial frequencies being low-level visual features extracted from visual scenes to create a coherent percept (Gazzaniga 2000; Kauffmann et al. 2014). Smaller numerosities, typically characterized by lower spatial-frequencies, preferentially engage the right hemisphere and induce a leftward bias. Conversely, larger numerosities, typically characterized by higher spatial-frequencies, preferentially engage the left hemisphere and induce a rightward bias. However, BAFT does not directly predict an association between SNA and numerical performance. The Emotional-Valence Model postulates that smaller numerosities are intrinsically associated with negative emotions, which engage the right hemisphere and induce leftward behavior, whereas positive emotions engage the left hemisphere and drive responses toward the right. This model also explains the SNA's origin but does not directly predict an association between SNA and numerical performance. The Right Hemisphere Dominance Model proposes that SNA is rooted in the functional lateralization of the brain, with the right hemisphere specialized in both spatial and numerical processing. This biological bias, acting as an anchor, leads organisms to explore the environment from left to right, resulting in an association between smaller magnitudes, encountered first, and the left side, and between larger magnitudes and the right side. Under this model, numerical spatialization is therefore intrinsically linked to numerical processing and may be associated with performance in numerical tasks.

Taken together, our findings show that domestic dogs associate small numerosities with the left and large numerosities with the right. This pattern persisted under control of the more relevant continuous physical variables and was not explained by individual lateral biases. Moreover, SNA-consistent performance correlated with more accurate discrimination of difficult quantity comparisons, providing preliminary evidence for a functional relationship between numerical spatialization and magnitude processing. These findings extend SNA to a domesticated mammal and support the hypothesis that the spatial organization of numerical magnitude is a widespread property of non-symbolic number representations that transcend individual experience.

Declarations

Competing interests:

The Authors declare no competing interests.

Ethics approval:

All procedures performed in this study involving client-owned animals were in strict compliance with the European Community Council Directive (2010/63/EU) and national legal requirements (Italian Legislative Decree D.Lgs. 26/2014) governing the care and use of animals for scientific purposes. The research protocol was approved by the Organism in Charge for Animal Welfare (Organismo Preposto al Benessere Animale, protocol nr. 20236) of the University of Padua. Written informed consent was obtained from all dog owners prior to participation. Adherence to veterinary care and behavioral standards was monitored by board certified veterinarians (P.M., L.M.)

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Author Contribution

AB: Investigation, Data Curation, Writing – Original Draft; LM: Conceptualization, Methodology, Writing – Review and Editing, Supervision; VB: Investigation, Data Curation; RR: Conceptualization, Methodology, Writing – Original Draft; PM: Conceptualization, Methodology, Formal Analysis, Writing – Review and Editing.

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Data Availability

Data are publicly available in the data repository of the University of Padua, at https://researchdata.cab.unipd.it/id/eprint/1896

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Figures

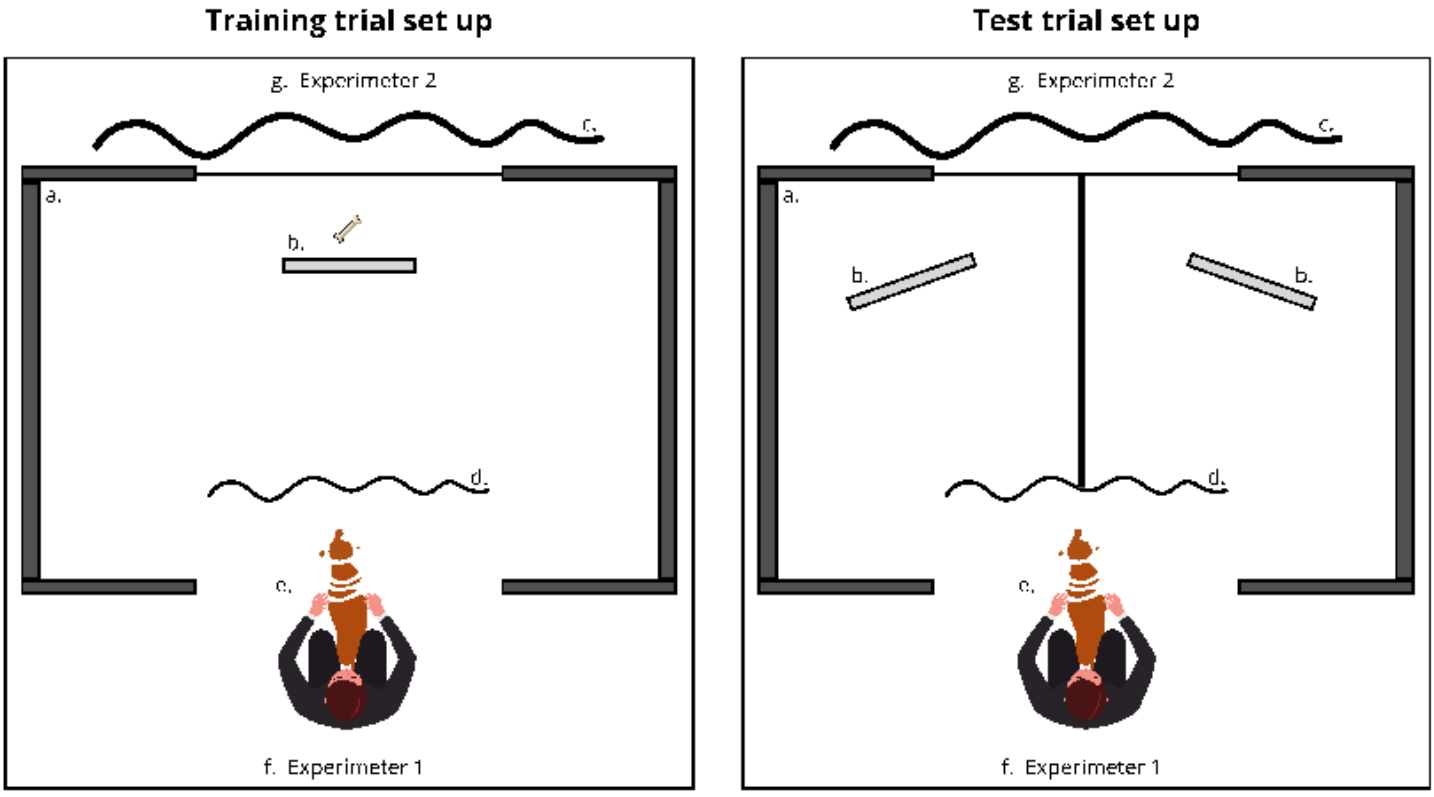


Figure 1

Graphic representation of the experimental setting during the training phase (on the left) and the test phase (on the right). The letters represent, respectively, a. panels that framed the smaller experimental

area; b. the stimuli supports and, only in case of training trials, the bowl placed behind containing the dog reward; c. the rear curtain that hide the second experimenter; d. the front curtain that could conceal the scene to the dog; e. the dog-owner dyad; f. the first experimenter; g. the second experimenter. The two recording cameras are not depicted. The elements of the represented figure are not scaled.

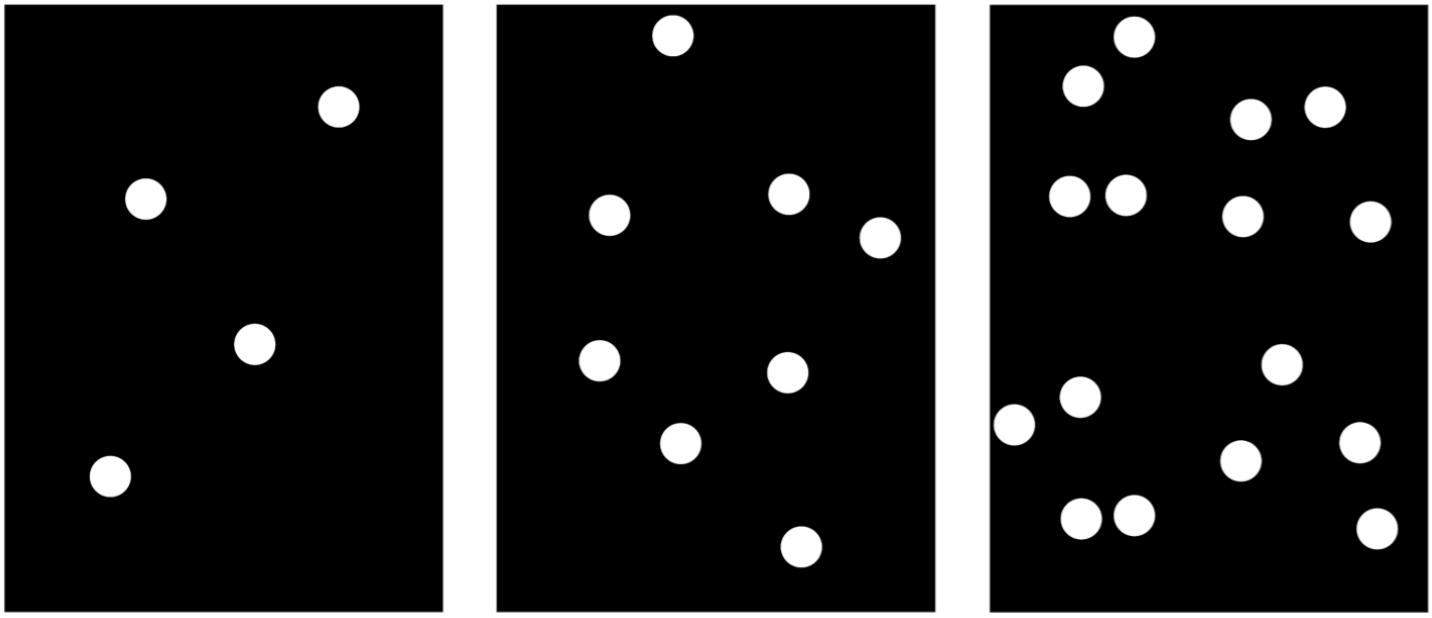


Figure 2

Examples of stimuli used in Experiment 1: a training stimulus (middle), displaying the reference numerosity of 8, and stimuli used in *less-than condition*, numerosity of 4 (left), and in the *more-than condition,* numerosity of 16 (right).

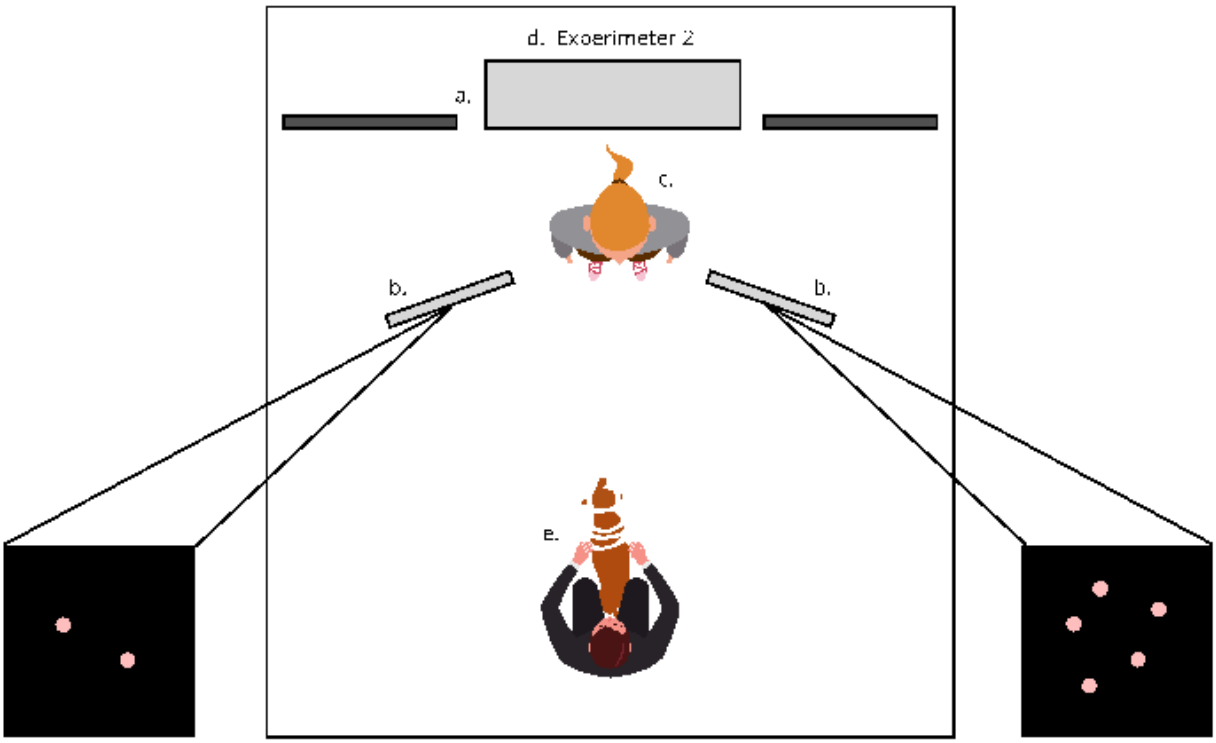


Figure 3

Graphic representation of the experimental setting. The letters represent, respectively, a. table and panels that framed the back area where Experimenter 2 prepared the stimuli; b. the stimuli supports displaying in this case training stimuli; c. Experimenter 1; d. Experimenter 2; e. the dog-owner dyad. The recording camera is not depicted. The elements of the represented figure are not scaled.

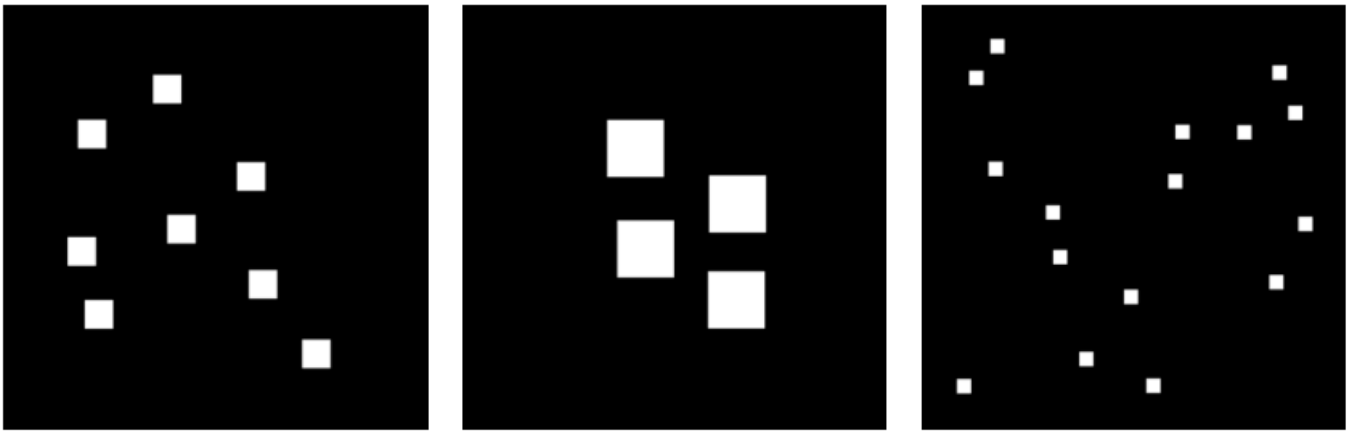


Figure 4

Examples of stimuli used in Experiment 3. On the left, an example of training stimulus, displaying the reference numerosity of 8. In the middle, a stimulus used in the *less-than*condition, displaying the numerosity of 4. On the right, a test stimulus used in the *more-than* condition, displaying the numerosity of 16.

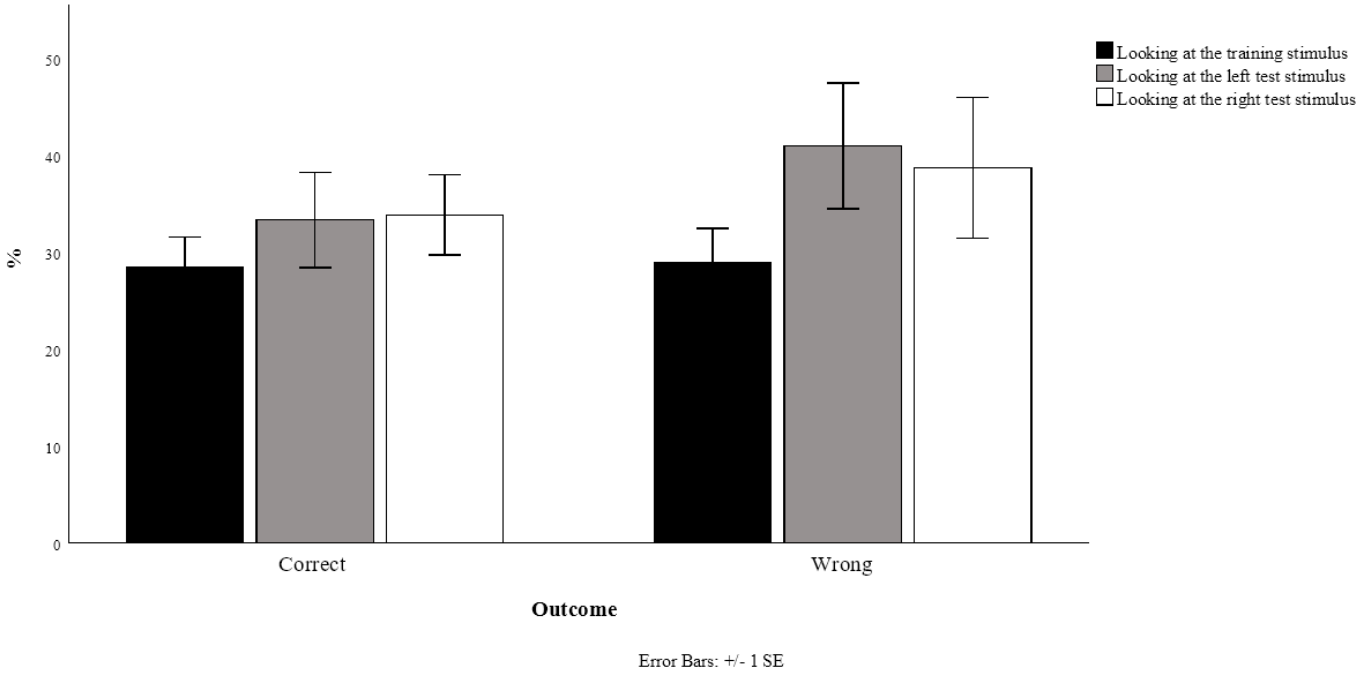


Figure 5

The mean percentage of time looking at the training stimulus, at the left stimulus during the test trial, and at the right stimulus during the test trial, by outcome of the test.

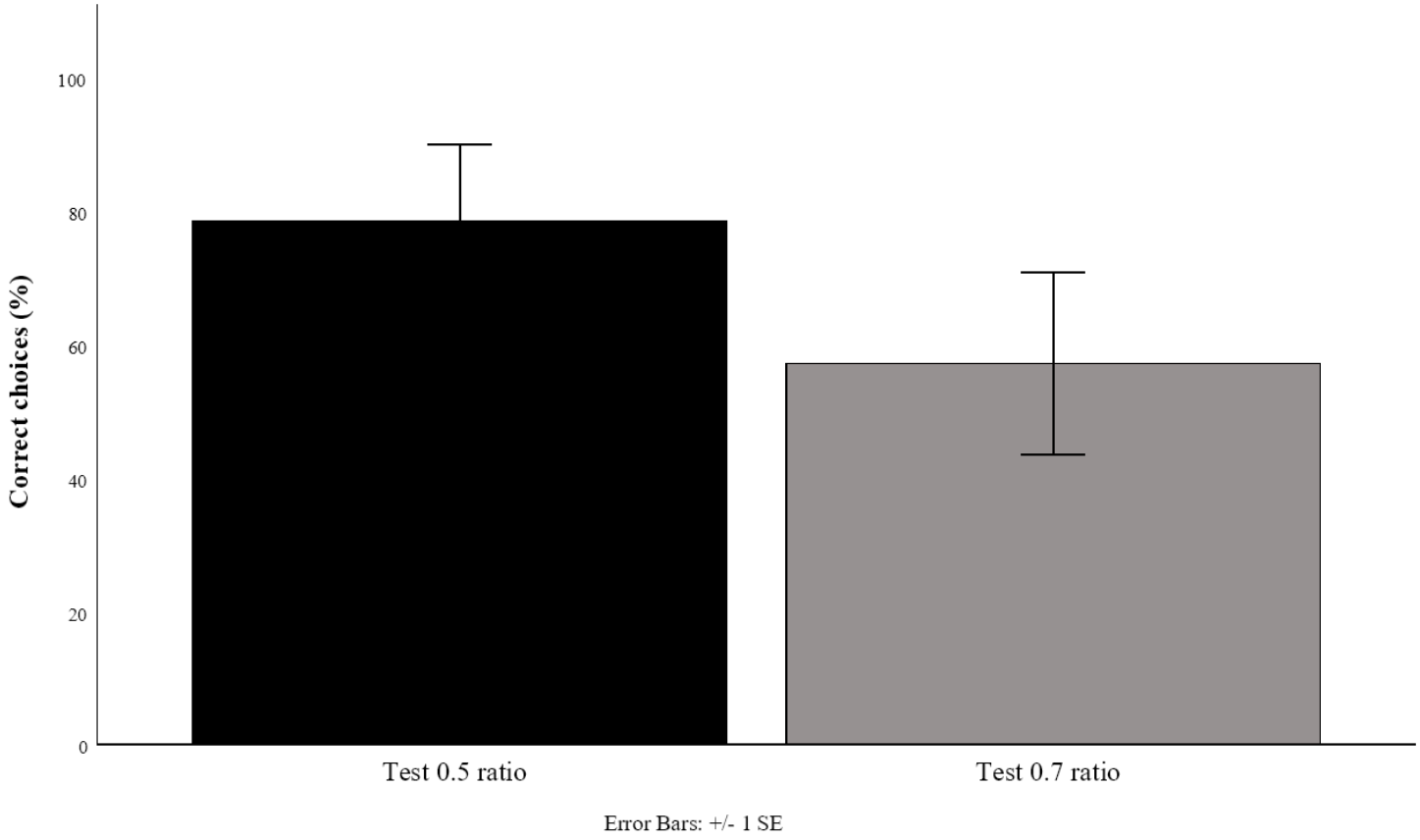


Figure 6

The percentage of correct choices of the 0.5 ratio and of the 0.7 ratio discrimination trials.

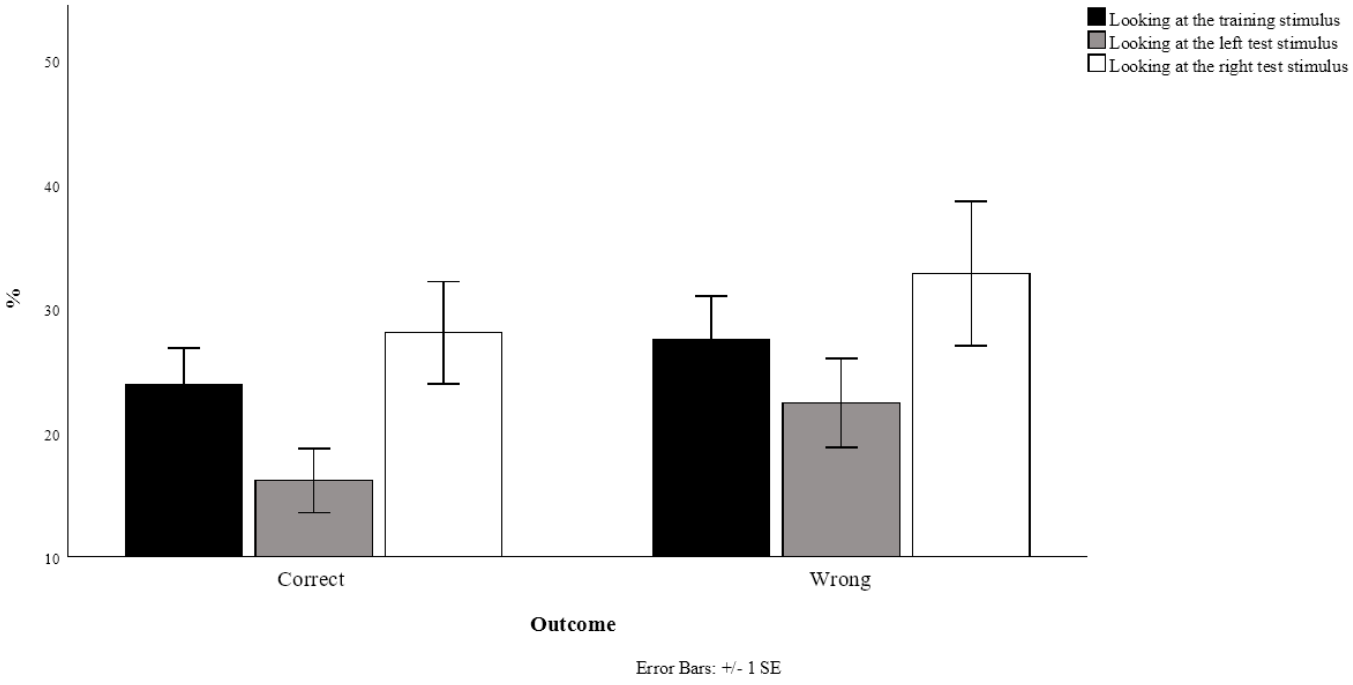


Figure 7

The mean percentage of looking time at the training stimulus, at the left stimulus during the test trial, and at the right stimulus during the test trial, by outcome of the test.