

No evidence of body size awareness in the Hermann's tortoise (*Testudo hermanni*)

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Abstract

Navigating structurally complex environments often requires assessing whether an opening affords safe passage, a task that presupposes relying on an internal representation of body size. Evidence for such awareness has been reported in mammals and birds and may also occur in other vertebrates and invertebrates. We investigated this ability in the tortoise *Testudo hermanni*, a species that often encounters dense vegetation and narrow passages. We first assessed the tortoises' ability to distinguish between 2 apertures of different widths. Surprisingly, they discriminated only when one aperture was twice as wide as the other, a performance markedly lower than that reported in other species. We then examined whether tortoises chose an aperture based solely on its suitability for their body size rather than by comparing the 2 apertures. However, tortoises chose the narrower opening at similar rates regardless of whether it was passable and persisted in attempting passage even when it was inadequate. When examined in a different context, food quantity discrimination, tortoises exhibited the same lack of selectivity. Overall, our findings suggest that *T. hermanni* does not rely on body size when negotiating obstacles, possibly reflecting poor visual discrimination capacities or the evolution of alternative strategies for overcoming physical barriers.

Keywords body size awareness, cerebral lateralization, comparative cognition, obstacle negotiation, size discrimination

Graphical abstract



Tortoises discriminate between two apertures only if one is at least twice as wide as the other.

Tortoises do not distinguish between passable and non-passable apertures. After selecting a non-passable opening, they rarely switch choice and instead persist in attempting to force passage



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Numerous species routinely navigate environments cluttered with physical obstacles that must be overcome. Such obstacles are often dense, irregularly distributed, and may form clusters that force individuals to pass through narrow gaps. In these circumstances, an organism must decide whether to attempt passage or to seek an alternative route, which requires assessing whether an opening is sufficiently wide to allow transit without becoming trapped or slowed. This ability implies that an animal possesses some level of internal representation of its own body dimensions, particularly given that in many species, body size can change over time.

Body size awareness has been investigated in detail in humans, mostly from the perspective of its ontogenetic development. In our species, this capacity develops gradually, emerging during the first year of life and continuing to refine throughout early childhood. By the preschool years, children begin to make increasingly accurate judgments about the relationship between their body and environmental constraints, although systematic errors persist until middle childhood. The ability to integrate multisensory information to represent one's own body size reaches levels comparable to adults by adolescence (Brownell et al. 2007; Franchak et al. 2010; Franchak and Adolph 2012).

Awareness of one's own body dimensions and the ability to use this information when deciding whether to pass through a gap appear to occur in only a few other species across taxonomically diverse groups. Evidence of decision-making related to body size has been reported in species such as ferrets, crows, and dogs (Khvatov et al. 2021, 2023; Pongrácz et al. 2023). For instance, in dogs, body size awareness has been demonstrated through a narrow-gap task, requiring them to choose between a detour and a shortcut of variable size. When faced with an aperture that was too small relative to their body dimensions, dogs typically avoided attempting passage and instead opted for the longer detour, whereas they confidently used the shortcut when the aperture was sufficiently large (Pongrácz et al. 2023).

Experiments conducted on 2 invertebrates, bumblebees, and hermit crabs, suggest that they may also have some awareness of one's own body dimensions (Sonoda et al. 2013; Ravi et al. 2020). Additional species have shown behaviors that, although not providing direct evidence of body size awareness, offer suggestive indications that such a capacity may be present. Among teleosts, both adult and newly hatched zebrafish consistently choose larger gaps, and this preference becomes stronger as the smaller gap approaches the fish's own body width (Santacà et al. 2020a, 2020b). A similar observation was made in guppies, in which it was also shown that gap choice is affected by visual illusions that make an opening appear larger or smaller than it actually is (Santacà et al. 2022). As for reptiles, no studies have yet investigated body size awareness using paradigms comparable with those used to study mammals and birds. In a recent study, rat snakes (*Elaphe radiata*) were allowed to reach a shelter through holes of different diameters. At the beginning of the experiment, there was no evidence that individuals avoided apertures too small for their body size. However, over the course of about 20 trials, they gradually learned to avoid the smaller openings. Interestingly, in a further condition, snakes were able to acquire the same skill even after their body diameter had been experimentally increased by feeding them a large prey item (Khvatov et al. 2019). This indicates that snakes can learn to adjust their behavior based on their body dimensions; however, it remains unclear whether they acquire any

awareness of their own size or simply learn to avoid holes below a certain threshold. Several authors have proposed that body size awareness represents one of the most basic forms of self-awareness (Lenkei et al. 2020; Khvatov et al. 2023; Dobos and Pongrácz 2025). Clarifying how widespread this ability is across taxa is therefore essential for reconstructing the evolutionary history of self-representation. In this context, it becomes crucial to determine which other species—beyond mammals and birds—use knowledge of their own body dimensions when deciding whether to attempt or avoid passing through an opening.

To address this gap, we investigated this phenomenon in a chelonian model, the Hermann's tortoise (*Testudo hermanni*). In this species, the ability to visually estimate the size of an opening and attempt passage only when it is sufficiently large to accommodate the body is expected to be selectively advantageous. In fact, in their natural habitats, tortoises often encounter physically complex environments where physical obstacles may pose navigational challenges. Rocks, roots, fallen branches, and dense thickets can form barriers that are difficult to traverse and potentially dangerous for an animal that is broader than tall and possesses a rigid, non-deformable shell. Becoming trapped within a narrow opening can be costly, both in terms of time lost from other activities and increased exposure to environmental extremes, starvation risk, and predation. Evidence of entrapment, injury, and even mortality caused by becoming stuck in natural obstacles has indeed been reported for some tortoise species (Bourn and Coe 1978).

As reviewed above, the vertebrate species studied so far show the ability to discriminate between apertures of different sizes and tend to preferentially select the larger opening. To date, there is no empirical evidence on whether tortoises, including *Testudo hermanni*, show comparable abilities. Specifically, it remains unclear whether they can discriminate between apertures of different widths and whether they rely on information about their own body size when deciding whether to attempt passage.

In this study, we first examined tortoises' ability to discriminate between 2 apertures of different widths when both were passable, using a series of two-choice tasks in which subjects were required to select between apertures to access an adjacent compartment containing a food reward. Based on previous findings in other vertebrates, we predicted that tortoises would preferentially select the larger aperture and that their discrimination accuracy would increase as a function of the ratio between aperture widths.

We then observed tortoises in a narrow-gap task to determine whether they relied on body size awareness when deciding whether to attempt passage through a given opening, predicting that individuals would modulate their choices according to the relationship between aperture size and their own body dimensions.

Finally, we compared performance in the aperture discrimination task with that observed in a different, ecologically relevant context, food quantity discrimination, an ability for which extensive comparative data are available across species (Langen and Gibson 1998; Aïn et al. 2009; Miletto Petrazzini et al. 2017; Loconsole et al. 2023). In this case, we made a similar prediction, namely that tortoises would preferentially select the larger quantity, with performance modulated by the ratio between quantities.

Materials and methods

Experiment 1

Subjects

The subjects were 24 tortoises (*Testudo hermanni*), comprising 12 males and 12 females. Sex was determined based on tail and carapace morphology (Willemssen and Hailey 2003). All tortoises originated from the pet trade. They were either confiscated by the Regional Forest Service or recovered after being found abandoned and were subsequently entrusted by the competent authorities to the SperimentArea, an open-air facility of the Civic Museum Foundation of Rovereto (Trento, Italy), which is responsible for their long-term care. All individuals used in the present study had been housed in this facility for at least 12 months prior to testing. All individuals had previous experience with cognitive testing, though none of the prior tasks involved stimuli or procedures similar to those used in the present study. The experiment took place in a wooden hut within SperimentArea. During the months in which they are active, tortoises are maintained in a large outdoor enclosure (~300 m²) containing natural vegetation, shelters, and water sources.

The experimental subjects were collected from the enclosure and were measured. To test subjects of similar size, only individuals whose carapace width fell within the predetermined range (maximum shell width: 12–15 cm; shell length: 15–20 cm) were selected. Males (16.56 ± 0.78 [15.50; 20.00] cm × 14.09 ± 0.99 [12.70; 15.00] cm; shell length × width) and females (17.46 ± 1.22 [14.80; 17.1] cm × 13.33 ± 0.87 [12.00; 15.00] cm) did not differ in shell width (two-sample *t* test: *t*₂₂ = 2.013, *P* = 0.057). They were housed in small semi-natural outdoor enclosures (~16–25 m²). Females were housed in small groups, whereas males were housed either individually or in pairs, provided that no aggressive interactions occurred (assessing behavioral compatibility between the 2 tortoises). Each subject was marked with a non-toxic paint pen to allow reliable individual identification. In these enclosures, tortoises had unrestricted access to water and shelter, but not food. Food rewards were provided during testing sessions, and the total amount of food given across all trials was sufficient to meet the animals' daily nutritional requirements and was comparable to their regular feeding regime. For logistical reasons related to the daily time required to complete all trials, the 24 subjects were divided into 2 groups of 12 (6 males and 6 females) and observed at 2 different times (July and August, respectively).

Apparatus

The apparatus used in this experiment was placed inside a wooden hut at the SperimentArea to ensure a controlled environment. It consisted of a white rectangular wooden box (163.0 cm × 83.0 cm × 41.3 cm; L × W × H; Fig. 1a), whose base was covered with a green corrugated polypropylene sheet. A layer of wood pellets was spread on the floor to improve traction and facilitate exploration by the tortoises. The first section of the apparatus was a corridor (60.0 cm × 20.0 cm × 20.0 cm; L × W × H). At the end of the corridor was a V-shaped choice area, closed by a wooden panel with 2 rectangular apertures positioned in front of the subject. To create the experimental apertures, we used a wooden support (48.0 cm × 80.0 cm × 40.0 cm; L × W × H)

attached to the apparatus and fitted with 2 large base apertures. Different masks made of double sheets of green corrugated polypropylene sheet were then applied to this support to obtain the desired aperture sizes (Fig. 1b).

Beyond this area, the tortoises could access a rectangular compartment (50.0 cm × 80.0 cm × 40.0 cm, L × W × H), where a feeder box was positioned in the center (6.9 cm × 8.0 cm, L × W) and filled with preferred food items (fresh vegetables and small pieces of tomato). The box was not visible from the choice area. A 400-watt halogen lamp was placed 100 cm above the apparatus to provide light and heat. The trials were recorded using a camera (Microsoft LifeCam Studio) mounted 120 cm above the apparatus on the same wooden frame supporting the lamp.

Inside the hut, there was a box (90.0 cm × 90.0 cm, 60.0 cm, L × W × H) lit with a halogen lamp (100 cm high). We used it on days when the weather was unfavorable, to warm up subjects before experiments.

Stimuli

In Experiment 1, stimuli consisted of 2 apertures of 25 cm, in height but differed in width (Fig. 1c1–4, d1–3). In Experiment 1A, 4 different masks were used. The wider aperture was kept constant, 25 cm wide, whereas the narrower one varied in width, yielding 4 width ratios in which the narrower aperture measured 60% (Fig. 1c1), 70% (Fig. 1c2), 80% (Fig. 1c3), or 90% (Fig. 1c4) of the wider one. In Experiment 1B, we used a single type of mask with a 50% ratio (Fig. 1d1). In Experiment 1C, we had 2 conditions, both with the same width ratio (60%). One condition presented the same apertures of 60% condition of Experiment 1A and acted as a control (Fig. 1d2). In the other condition, we proportionally reduced both apertures so that the narrower one was smaller than the width of the smallest subject (wider 20.0 cm; narrower 12.0 cm; hereafter ratio “60%R”; Fig. 1d3). For each stimulus, we constructed a series of different masks using double sheets of corrugated polypropylene (Poliplak®) glued together with silicone.

Trial procedure

At the beginning of each trial, the experimenter placed a mask (according to the daily sequence) against the wooden support in order to create 2 apertures of different widths. The tortoise was then gently placed at the beginning of the corridor and allowed to move toward the choice area. Once the tortoise had chosen an aperture and reached the box containing the food reward, a corrugated polypropylene sheet (Poliplak®; 80.0 cm × 60.0 cm, L × H) was positioned in front of the apertures to prevent it from returning to the choice area. During food consumption, the mask was replaced with a new one for the next trial according to a pre-planned scheme. Tortoises were allowed approximately 3 min to feed before being returned to the start of the corridor, and the procedure was repeated until the subject completed its daily sequence of trials. The apparatus was then reset, and the next subject was observed. All trials were recorded using a camera positioned above the apparatus. Recording started when the tortoise approached the end of the corridor and stopped once at least half of its body had passed through the chosen aperture. During each trial, the experimenter noted which aperture was selected; these observations were later verified by reviewing all video recordings.

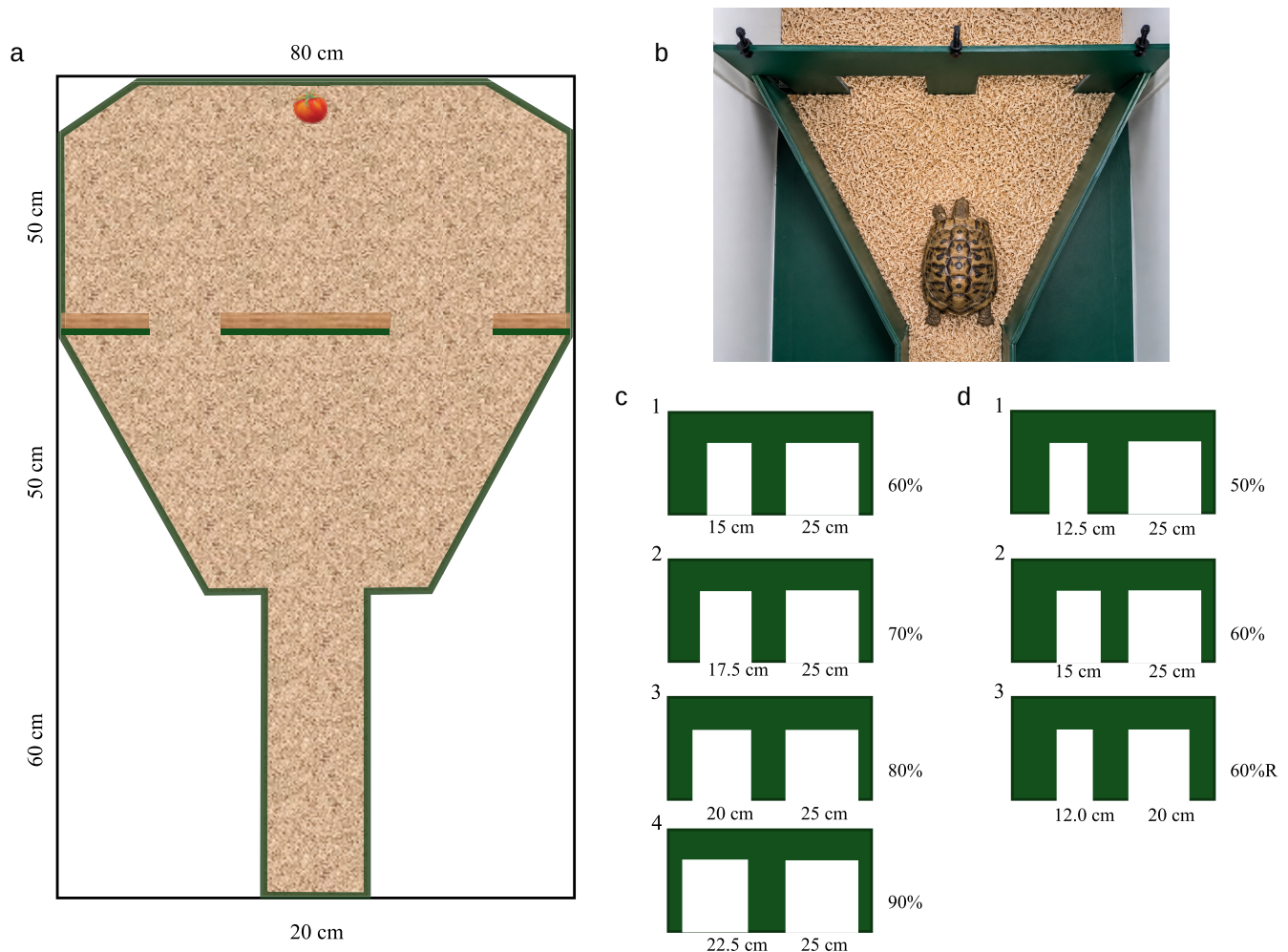


Figure 1 a) Aerial view of experimental apparatus used in Experiment 1. b) Aerial photograph of a tortoise within the apparatus's choice area during Experiment 1A–C. c, d) View of stimuli mask consisted of 2 apertures differing in width used in Experiment 1A and Experiments 1B, C, respectively.

Familiarization and training

Before the testing phase began, the subjects underwent a 3-day familiarization and training phase. On the first day, subjects were allowed to familiarize themselves with the apparatus. Food was placed in the feeding box of the apparatus, and no masks were placed on the wooden frame. A subject was collected from the enclosure, measured and marked, and then released at the beginning of the corridor and allowed to explore freely. Once the tortoise had found and consumed the food, this was replenished, and the subject was collected and released again into the corridor, until a total of 3 trials had been completed. The subject was then returned to its housing enclosure, and the next individual was introduced to the apparatus.

On the 2 following days, subjects underwent a training phase in which they learned to pass through one of 2 apertures to reach the food. The procedure was identical to that of the test phase, except that a mask with 2 apertures of identical width (25.0 cm) was used. Each individual performed 8 trials per day (16 in total). On the fourth day, the experimental phase began.

Tests

Experiment 1 was composed of 3 different series of trials (Experiments 1A, 1B, and 1C), differing in their aims.

Experiment 1A

This series aimed to determine whether Hermann's tortoises exhibit, like other species previously examined, a preference for negotiating larger openings. To assess their ability to discriminate, the ratio between the widths of the 2 apertures was varied across 4 levels (60%, 70%, 80%, and 90%), which fall within the range typically employed in aperture discrimination studies with other vertebrates (Maeda and Fujita 2010; Khvatov et al. 2021; Santacà et al. 2020a, 2020b, 2022).

The series consisted of 48 trials and was conducted over a period of 6 days, with each of the 12 animals performing 8 trials per day in immediate succession within the same session. The 4 width ratios were presented in a semi-random sequence, with each ratio presented twice daily. By the end of the experiment, each animal had encountered each ratio 12 times. The sequence was designed so that the narrower aperture appeared equally often on the right and on the left.

Experiments 1B and 1C

Because in Experiment A, tortoises did not show a consistent preference for the larger aperture, even at the easiest ratios, we conducted a follow-up test using a more pronounced size difference (Experiment 1B). In this second phase, we further tested

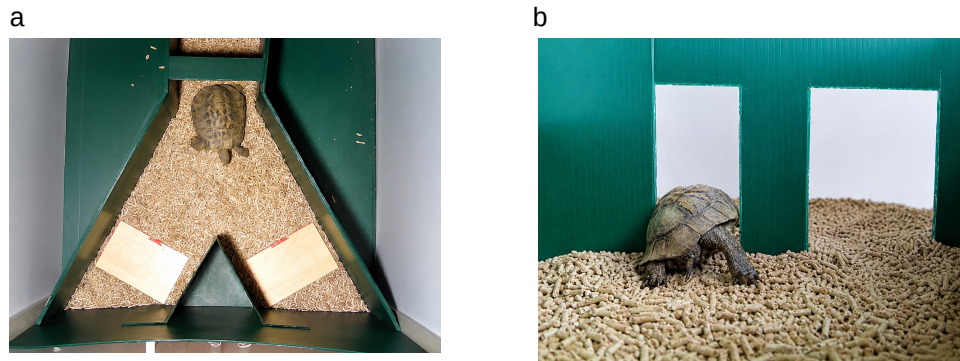


Figure 2 a) Aerial photograph of a tortoise within the apparatus' choice area during Experiment 2. b) Photograph of a tortoise attempting to pass through the apertures that was too narrow for its body size.

the hypothesis that tortoise choices might be guided by body size awareness (Experiment 1C), such that individuals would preferentially select the larger aperture only when the smaller one was too narrow to allow safe passage.

Experiments 1B and 1C were conducted on the same subjects following the completion of Experiment 1A. In this phase, tortoises underwent 6 additional days of testing, completing 9 trials per day (for a total of 54 trials), with trials from the 2 experiments intermingled within each daily session. Each day, every tortoise completed 3 trials from Experiment 1B and 6 from Experiment 1C (3 per condition). As before, a semi-randomized sequence balanced for the left–right position of the smaller opening was used.

In all 270 trials of Experiment 1C in which tortoises chose the narrower, impassable aperture, they nonetheless attempted to pass through it. To do so, they struggled vigorously, pressing against the corrugated polypropylene sheet mask or using the edges of the aperture to twist their bodies sideways and reduce their effective width. In 269 of these trials, they eventually succeeded in crossing after varying periods of effort through the narrowed apertures, whereas in a single case, the subject desisted, retreated, and ultimately corrected its choice. To quantify this phenomenon, in all trials of Experiment 1C, we measured crossing time for both the wider and narrower apertures, defined as the interval between the moment the tortoise's head passed the door line and the moment its entire body cleared the opening. A few videos ended before the tortoise had fully crossed the aperture and were excluded from analyses.

Experiment 2

To assess whether the low performance observed in the aperture task reflected a specific limitation in aperture size discrimination or a more general difficulty in processing continuous size differences, we conducted a second experiment in a different, ecologically relevant context, i.e., food quantity discrimination. Using an apparatus similar to that employed in the aperture task, subjects were presented simultaneously with 2 food portions of different sizes. The size ratios matched those used in the aperture discrimination experiment.

Subjects

The subjects in this experiment were the same individuals observed in Experiment 1, and testing commenced 3 days after the completion of the previous experiment.

Apparatus

For Experiment 2, the apparatus was slightly modified from the one previously described. A sheet of corrugated polypropylene was attached to the wooden support, closing the 2 apertures that, in Experiment 1, provided access to the compartment containing the feeder (Fig. 2a). The 2 slices of tomato that subjects were required to choose between were each placed on a wooden platform (19.6 cm wide, 12.5 cm long) positioned on the ground and fixed with silicone glue. The posterior part of the platforms was elevated by 2.6 cm above the ground by a corrugated polypropylene support, in order to facilitate the visibility of the food. The tablets were placed 37.0 cm away from the corridor exit. A triangular-shaped divider (base: 21.0 cm, sides: 20.0 cm, height: 20.0 cm) was placed in the center of the apparatus, separating the 2 stimuli so that tortoises were required to make a clear choice between them.

Stimuli

In Experiment 2, the stimuli consisted of 2 rectangular slices of tomato (San Marzano variety) of equal cross-section (1 cm × 1 cm) but differing in length, corresponding to the same width ratios used in Experiment 1A. The larger slice measured 5.0 cm in length, whereas the smaller slices measured 3.0 cm (60%), 3.5 cm (70%), 4.0 cm (80%), and 4.5 cm (90%). The slices were placed horizontally so that the difference in length was clearly visible to the subjects. Slices were prepared a few minutes before each trial to avoid delays between successive trials.

Trial procedure

The procedure of Experiment 2 was substantially identical to that of Experiment 1. Each tortoise was placed at the start of the corridor and, upon entering the choice area, faced 2 tomato slices of different sizes positioned on wooden platforms (Fig. 2a). A trial ended when the tortoise consumed one of the slices. At this point, the subject was temporarily held for 30 s in the compartment that, in Experiment 1, contained the feeder, to allow removal of any remaining food and placement of new stimuli. The subject was then returned to the start of the corridor, and the procedure was repeated until the subject completed its daily sequence of trials. The apparatus was then cleaned and reset to its initial conditions, and the next subject was observed.

Tests

As subjects were already familiar with the apparatus and handling procedures, no additional familiarization or training phase was conducted in this experiment. The testing phase was identical to that of Experiment 1A. The experiment lasted 6 days, with each subject completing 8 trials per day, and followed the same semi-randomized sequence of stimulus presentation. In some trials, tortoises showed no interest in approaching or eating either food item. These were recorded as “null trials” and repeated at the end of the testing sequence or, more rarely, on the following day. Nevertheless, 4 individuals failed to complete the full set of 48 trials and were omitted from the analysis. All sessions were video recorded from the moment the tortoise approached the corridor exit until it bit the tomato slice.

Statistical methods

Data analysis was performed in RStudio (version 2022.02.3 Build 492; Integrated Development for R. RStudio, PBC, Boston, MA, USA; <http://www.rstudio.com/>). Descriptive statistics are reported in the main text as average $\pm$ standard deviation. The statistical tests were two-tailed and the threshold for statistical significance was set at $P=0.05$. All data were checked for normality (Shapiro–Wilk test).

Performance

In all experiments, we used one-sample t -tests to investigate whether the observed preference for the larger aperture (Experiments 1A, B, and C) or food (Experiment 2) calculated for each ratio or for total trials differed from that expected by chance (50%), differed by chance. We calculated the performance as the percentage of correct responses, each coded as 1, over the total number of trials. We checked for the normality of data (Shapiro–Wilk test). The one-sample t -test is robust in case of deviation from normality (de Winter 2013). For each experiment, sex differences in the total performance were assessed via a two-sample t -test. Homogeneity of variance was checked (Levene Test). For both Experiments 1A and 2, the total performance was compared among ratios via a linear mixed-effects model (“lmer” function from the “lmerTest” R package) fitted with ratio as a fixed factor, and subjects as a random effect. The significance of the model parameters was assessed via Satterthwaite’s approximation method for the calculation of degrees of freedom (“anova” function from the “lmerTest” R package).

In Experiment 1B, we investigated whether the accuracy of performance, i.e., the preference for the larger aperture as a response variable was predicted by the time spent making the decision. The general hypothesis of the speed-accuracy trade-off suggested that individuals who spend more time making a decision show higher performance (Chittka et al. 2009). We first tested this hypothesis using a generalized linear mixed-effects models (“glmer” function from the “lme4” R package) with a binomial distribution on the binary scored response for each trial (coded as 1 when individual selected the larger aperture, or 0 when subject selected the smaller aperture) fitted with time (log-transformed) as covariate, and subject as random effect. The significance of the model parameters was assessed via the Wald chi-squared method (“Anova” function from the “car” R package). Secondly, we tested this hypothesis on

the average performance and time observed within individuals via Spearman’s rank correlation analysis.

In Experiment 1C, the comparison between the 2 ratios 60% was performed using paired 2 sample t -tests. As no difference was found between the 2 ratios 60% from the analysis, we calculated the approximate Bayes Factor (BF) to directly test for the non-significant results, a robust approach even though for a small dataset (Wagenmakers 2007; Dienes 2014). To interpret the absence of effect, we calculated the Bayes Factor in favor of the null model, i.e., no difference between the 2 ratios 60%, as $1/BF$ from the output of the “ttestBF” function from the “BayesFactor” R package. We used the same approach to quantify the difference in the crossing time between the smaller apertures and all others.

To investigate the effect of learning on the performance across testing days, we fitted a generalized linear mixed-effect model with a Binomial distribution on the responses observed for each trial with day as a covariate, numerical ratio as a fixed factor, and subject as a random effect. The model included the interaction between the covariate and the fixed factor. We used this approach to study the effect of learning in Experiments 1A, 1C, and 2.

We compare the performance across ratios observed in multiple experiments (i.e., Experiment 1A vs. 1C, Experiment 1B vs. 1C) using a linear mixed-effects model on the total performance fitted with ratio as a fixed factor and subject as a random effect. Significant differences among ratios were further investigated by performing Tukey post hoc tests via “emmeans” R package.

Lateralization

For all Experiments, we assessed whether there was a population-level bias in both the direction and strength of lateralized behavior. We calculated a relative lateralization index as the proportion of right-turn choice over the total number of trials. This index ranged from -1 (left-turn bias) to $+1$ (right-turn bias), indicating the direction of the bias. First, we evaluated whether the distribution of the relative lateralization index showed a normal distribution via Shapiro–Wilk Test. Then, we assessed whether the average of this index was significantly different from 0 using a one sample t -test that, in case of significance, indicated a lateralization bias at population level. Third, we assessed sex differences in the relative lateralization index using 2 sample t -tests. The same approach was used for analyzing the relative lateralization index calculated considering only the incorrect choices. The strength of the lateralization bias was calculated as the absolute value of the relative lateralization index calculated considering either all trials or only the incorrect choices. We described the distribution of this index by using the same approach.

To calculate the repeatability of the lateralization bias across Experiment 1A, Experiment 1B, and C, we performed Spearman’s rank correlation analysis.

Predictors affecting performance

For both Experiments 1 and 2, we evaluated the effect of 3 different predictors on the performance. We fitted a linear mixed-effect model with sex and ratio as fixed factors,

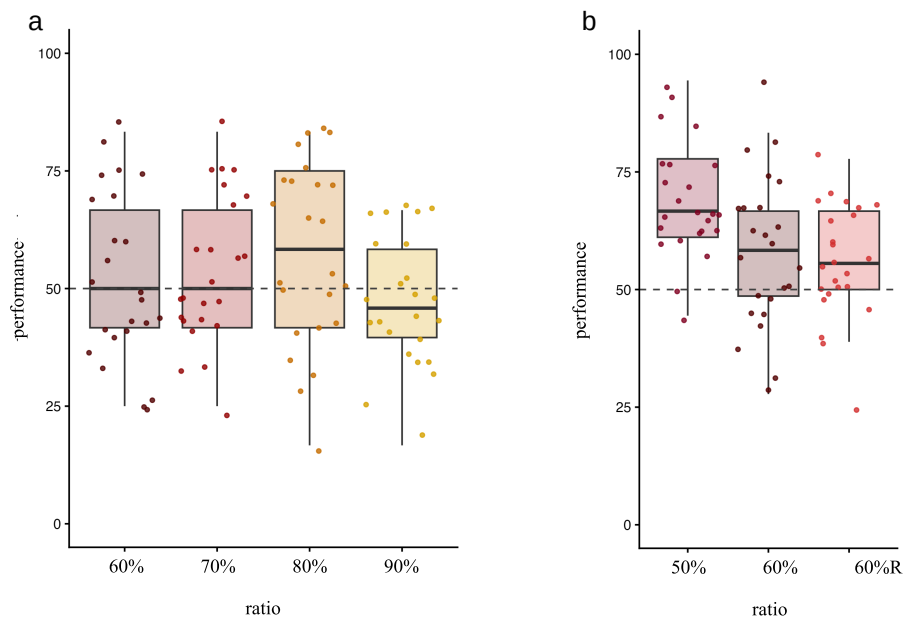


Figure 3 a) Preference for larger apertures as a function of the numerical ratio in Experiment 1A. The black bars inside each box represent the median value at the population level. b) Preference for larger apertures as a function of the numerical ratio in Experiment 1B and 1C. The black bars inside each box represent the median value at the population level. The dots represent individuals' scores. The dashed line represents the preference expected by chance (50%).

lateralization index as a covariate, and subject as a random effect. We performed 4 different models that contained one of the 4 lateralization indices, i.e., the relative or absolute lateralization index calculated on all trials or on the incorrect trials.

Comparison between Experiment 1A and Experiment 2

To compare the overall performance between Experiment 1A and Experiment 2, we used the same approach as previously described by fitting a model with ratio and experiment as fixed factors, and subject as a random effect. The model included the interaction between the 2 fixed factors.

The repeatability of the lateralization bias within individuals was assessed via Spearman's rank correlation analysis. We used this approach for the 4 calculated lateralization indexes.

Results

Experiment 1

Performance

Experiment 1A

Tortoises did not significantly select the larger aperture in any of the 4 numerical ratios (ratio 60%: 51.74 ± 18.22 ; $t_{23} = 0.467$, $P = 0.645$; ratio 70%: 54.17 ± 15.54 ; $t_{23} = 1.313$, $P = 0.202$; ratio 80%: 57.99 ± 20.19 ; $t_{23} = 1.938$, $P = 0.065$; ratio 90%: 46.88 ± 14.08 ; $t_{23} = 1.088$, $P = 0.288$; Fig. 3a). Preference for the larger aperture did not differ among numerical ratios ($F_{3,92} = 1.763$, $P = 0.160$).

A significant preference for the larger aperture emerged when averaging the performance of each subject across the 4 ratios

(52.69 ± 5.75 ; $t_{23} = 2.294$, $P = 0.031$). There was no sex difference in performance (female: 54.34 ± 6.31 ; male: 51.04 ± 4.82 ; $t_{22} = 1.439$, $P = 0.164$).

There was no variation in the performance across testing days ($\chi^2_1 = 0.034$, $P = 0.854$) nor a significant interaction day $\times$ numerical ratio ($\chi^2_3 = 3.695$, $P = 0.296$), suggesting the lack of learning by subjects during the tests.

Experiment 1B

When one aperture was double wider than the other (ratio 50%), subjects showed a significant preference for the larger one (68.75 ± 12.24 ; $t_{23} = 7.505$, $P < 0.001$; Fig. 4). There was no sex difference in performance (female: 67.13 ± 14.11 ; male: 70.37 ± 10.42 ; $t_{22} = 0.640$, $P = 0.529$).

Performance of ratio 50% significantly differed from the average performance of Experiment, as well as for each of the 4 ratios separately ($F_{4,115} = 6.124$, $P < 0.001$; post hoc average ($P < 0.001$); single ratios all $P < 0.025$).

Performance of ratio 50% also differed from that of both conditions of experiment 1C ($F_{2,46} = 7.785$, $P = 0.001$; Post hoc ratio 50 vs ratio 60%: $P < 0.004$; ratio 50 vs ratio 60%R: $P < 0.001$).

For this experiment, we investigated whether there was a tradeoff between speed and accuracy of the choice (i.e., preference for the larger aperture). In each trial, decision time (log-transformed) did not significantly predict whether the response was correct ($\chi^2_1 = 0.002$, $P = 0.962$). Contrary to the general hypothesis of a speed-accuracy tradeoff, on average, individuals who chose more frequently the larger aperture were faster to make the choice; however, this negative relationship did not reach statistical significance (Spearman's rank correlation: $\rho = -0.360$, test statistic $S = 3,128$, $P = 0.084$; Supplementary Figure S1).

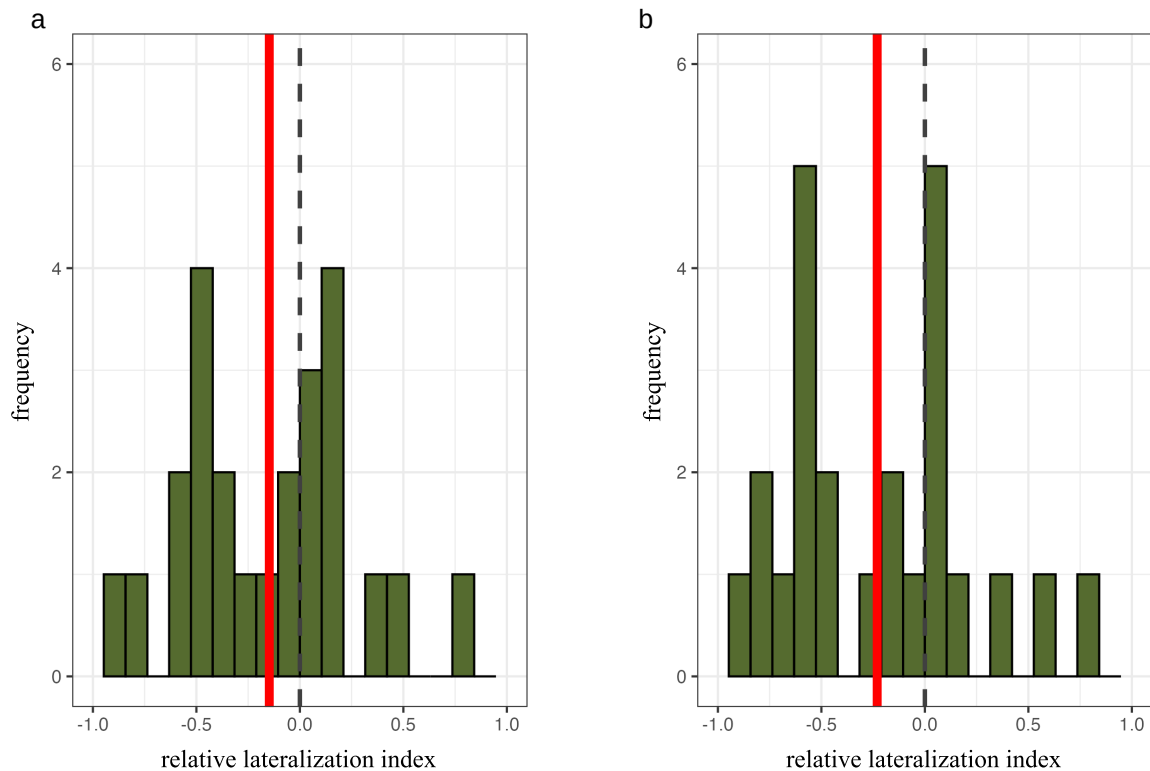


Figure 4 Density distribution of the relative lateralization index calculated using either (a) all trials or (b) only the incorrect trials, in Experiment 1. The red line represents the average index at population level. The dashed line represents the absence of lateralization bias (index = 0).

Experiment 1C

Performance did not differ significantly between the 2 conditions (ratio 60%: $57.87 \pm 15.79\%$; ratio 60%R: $55.79 \pm 12.42\%$; paired t -test: $t_{23} = 0.614$, $P = 0.545$; Fig. 3b). The Bayes Factor indicates that the null hypothesis was 3.92 more likely than the alternative, confirming that subjects behaved similarly regardless of whether the smaller aperture allowed passage or not.

There was no variation in the performance across testing days ($\chi^2_1 = 0.183$, $P = 0.669$), nor a significant interaction day $\times$ numerical ratio ($\chi^2_1 = 0.346$, $P = 0.556$), suggesting the lack of learning by subjects during the tests.

When selecting the aperture that was too narrow for their body size, tortoises nevertheless attempted to pass through (see Fig. 2b and Supplementary Video S1s). They typically engaged in prolonged struggling behaviors, including pressing against or bending the plastic material and rotating their bodies sideways to reduce effective width. Despite these difficulties, all but one individual ultimately succeeded in crossing to the other side. The time required to traverse non-navigable apertures averaged 17.54 s (± 6.45 ; range 7.44–32.00 s), which was significantly longer than the 4.75 s (± 1.34 ; range 3.2–8.2; $t_{23} = 10.010$, $P < 0.001$) needed to pass through the wider, navigable apertures.

Lateralized response

There was a general tendency to choose the left aperture more frequently, but this effect reached significance only at the 50% ratio, where discrimination was most accurate (Supplementary Table S2). However, many individuals showed a marked preference

for one direction over the other, resulting in a strongly platykurtic distribution of the relative lateralization index. The individual directional bias in gap choice was consistent across experiments, confirming the reliability and stability of this measure.

When considering the entire Experiment 1, the relative lateralization index followed a normal distribution ($W = 0.976$, $P = 0.820$). The mean value did not differ significantly from zero (-0.15 ± 0.41 ; $t_{23} = 1.787$, $P = 0.087$), indicating no overall left-right bias in aperture choice (Fig. 4a). On average, the 2 sexes did not differ in their degree of lateralization ($t_{22} = 0.203$, $P = 0.841$). However, a lateralization bias emerged when analyzing turning preferences only for the incorrect trials (Fig. 4b). In this case, the relative lateralization index also followed a normal distribution ($W = 0.952$, $P = 0.303$), but at the population level, subjects showed a significant left-turning preference (-0.23 ± 0.45 ; $t_{23} = 2.524$, $P = 0.019$). No sex differences in laterality were detected ($t_{22} = 0.136$, $P = 0.893$).

Analyzing all trials, the distribution of the absolute lateralization index did not differ from a Gaussian distribution ($W = 0.928$, $P = 0.088$; Supplementary Figure S2a). On average, the 2 sexes did not differ in absolute lateralization ($t_{22} = 1.495$, $P = 0.149$). Conversely, for incorrect trials, the distribution of this index significantly deviated from normality ($W = 0.908$, $P = 0.032$) and was platykurtic (kurtosis = -1.48), indicating an excess of highly lateralized and non-lateralized individuals, and a scarcity of mildly lateralized ones (Supplementary Figure S2b). No sex differences were detected ($W = 53.000$, $P = 0.285$).

To study consistency of laterality measures, we correlated lateralization indexes measured in the first (Experiment 1A) and the second (Experiment 1B and C) series of trials. We found high

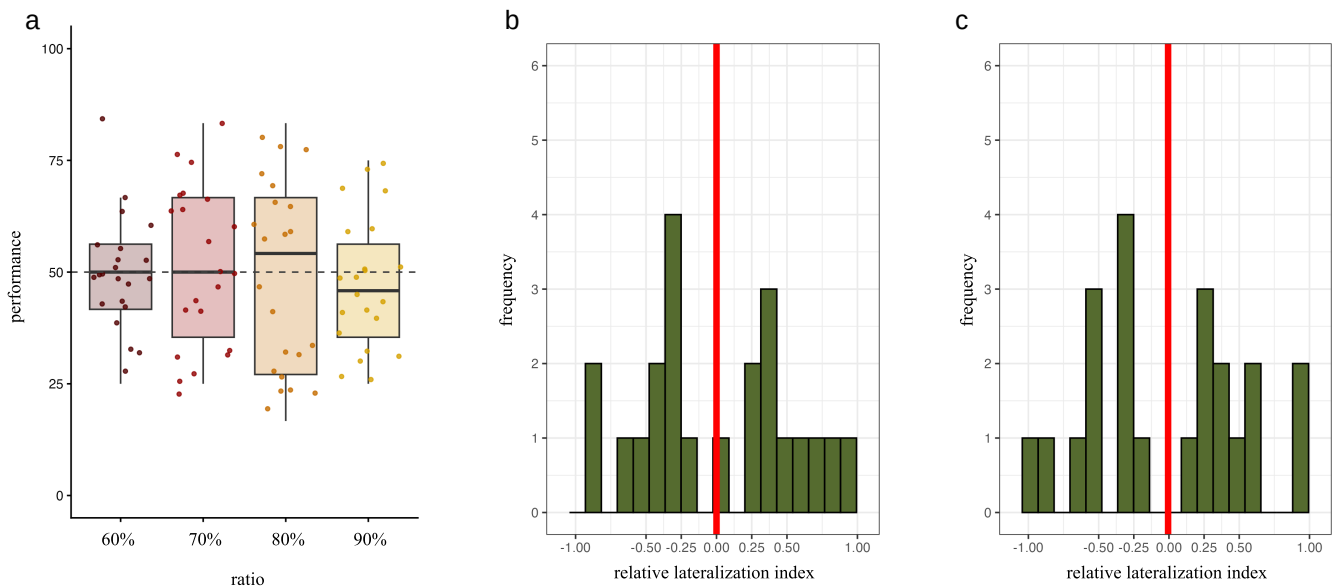


Figure 5 a) Preference for larger food as a function of the numerical ratio in Experiment 2. The black bars inside each box represent the median value at the population level. The dots represent individuals' scores. The dashed line represents the preference expected by chance (50%). b, c) Density distribution of the absolute lateralization index calculated using either (b) all trials or (c) only the incorrect trials, in Experiment 1. The red line represents the average index at population level.

correlation in both lateralization direction (Spearman's rank correlation test: $\rho = 0.789$, $S = 496.62$, $P < 0.001$) and strength ($\rho = 0.524$, $S = 1,094.6$, $P = 0.009$). Similar results were obtained considering only the incorrect choices (direction $\rho = 0.761$, $S = 550.62$, $P < 0.001$; strength ($\rho = 0.506$, $S = 1,135.00$, $P = 0.012$).

Predictors of discrimination performance

We ran on the whole dataset of Experiment 1 4 GLMM models (Supplementary Tables S2–S5). They included the same variables (width ratio and sex) but differed with respect to the lateralization measure used (absolute or relative lateralization index, calculated on all trials or on the incorrect ones; see next section). Overall, the analyses revealed a significant effect of ratio and no effect of sex. Of the 4 models, only the one that included the absolute index calculated on all trials found a significant effect of lateralization ($\chi^2_1 = 4.586$, $P = 0.032$; Supplementary Table S3), indicating that less lateralized individuals better discriminated between the 2 apertures. Adding the absolute lateralization index as predictor significantly improve the model fit (AIC full model: 3316.7; AIC model without the variable of interest: 3318.9; $\chi^2_1 = 4.194$, $P = 0.041$), however, the variance explained exclusively by the lateralization index, after accounting for the variance explained by other predictors (i.e., sex and numerical ratio), was extremely low (partial $R^2 = 0.002$; approx. 0.2% of variance) and the estimated CI of semi-partial R^2 include the zero [0.00; 0.016], suggesting a moderately low effect of lateralization on the performance.

Experiment 2

Performance

Tortoises did not significantly select the larger food item in any of the 4 numerical ratio (ratio 60%: 50.00 ± 12.60 ; $t_{21} < 0.001$, $P > 0.999$; ratio 70%: 51.52 ± 17.94 ; $t_{21} = 0.396$, $P = 0.696$; ratio

80%: 48.86 ± 20.94 ; $t_{21} = 0.255$, $P = 0.802$; ratio 90%: 47.35 ± 14.64 ; $t_{21} = 0.850$, $P = 0.405$; Fig. 5a). Preference for the larger food item did not differ among numerical ratios ($F_{3,84} = 0.2414$, $P = 0.867$).

No significant preference was observed even when averaging the performance of each subject across the 4 ratios (49.43 ± 5.31 ; $t_{21} = 0.502$, $P = 0.621$). There was no sex difference in performance (female: 48.11 ± 3.54 ; male: 50.76 ± 6.54 ; $t_{20} = 1.182$, $P = 0.251$).

There was no variation in the performance across testing days ($\chi^2_1 = 1.488$, $P = 0.223$) nor a significant interaction day $\times$ numerical ratio ($\chi^2_1 = 1.901$, $P = 0.593$), suggesting the lack of learning by subjects during the tests.

Lateralization

The relative lateralization index followed a normal distribution ($W = 0.953$, $P = 0.365$). There was no tendency to choose either the left or the right stimulus at the population level (proportion right choice 0.00 ± 0.54 , $t_{21} = -0.051$, $P = 0.960$; Fig. 5b).

In this experiment, we found a difference in the degree of lateralization between the 2 sex ($t_{20} = 2.572$, $P = 0.018$), because male displayed a left-side bias (-0.27 ± 0.47) whereas female a right-side bias (0.27 ± 0.50) which were however not significantly different from chance (male: $t_{10} = 1.865$, $P = 0.092$; female: $t_{10} = 1.776$, $P = 0.106$).

The results are similar when analyzing turning preferences only for the incorrect trials (Fig. 5c). The relative lateralization index followed a normal distribution ($W = 0.946$, $P = 0.264$), and the mean value did not significantly differ from zero (-0.01 ± 0.56 , $t_{21} < 0.001$, $P > 0.999$). The analysis confirmed a difference in the degree of lateralization between the 2 sexes (male: -0.29 ± 0.48 ; female: 0.28 ± 0.49 ; $t_{20} = 2.713$, $P = 0.013$) but no significant left-right bias in either sex (male: $t_{10} = 1.979$, $P = 0.076$; female: $t_{10} = 1.859$, $P = 0.093$).

Analyzing all trials, the distribution of the absolute lateralization index significantly deviated from normality ($W=0.909$, $P=0.044$) and was platykurtic (kurtosis = -1.05), indicating an excess of highly lateralized and non-lateralized individuals, and a scarcity of mildly lateralized ones (Supplementary Figure S3a). The 2 sexes did not differ in absolute lateralization ($t_{20}=0.289$, $P=0.775$). Similar results were obtained when considering only the incorrect trials (Supplementary Figure S3b). The distribution of this index significantly deviated from normality ($W=0.877$, $P=0.011$) and was platykurtic (kurtosis = -0.84). No sex differences were detected ($t_{20}=0.135$, $P=0.894$).

Predictors of discrimination performance

We ran on the 22 subjects that completed all trials of 4 GLMM models as in Experiment 1. None of the predictors resulted in a significant effect in any of the 4 models (Supplementary Tables S6–S9).

Comparison of Experiment 1A and Experiment 2

Overall, the analysis did not reveal a significant difference in the performance between the 2 experiments ($\chi^2_1=2.334$, $P=0.126$). There was no difference among the 4 ratios ($\chi^2_3=5.631$, $P=0.131$), nor the interaction experiment $\times$ numerical ratio ($\chi^2_3=2.828$, $P=0.419$). No effect of sex emerged ($\chi^2_1=0.046$, $P=0.831$).

Lateralization indexes calculated in this experiment were not correlated with those of Experiment 1, either for direction ($\rho=0.182$, $S=1,448.7$, $P=0.418$) or the strength ($\rho=0.175$, $S=1,461.80$, $P=0.437$).

The results were similar when considering only the incorrect choices. No significant correlations were found either for direction ($\rho=0.095$, $S=1,602.90$, $P=0.674$) or strength of lateralization ($\rho=0.149$, $S=1,507.80$, $P=0.509$).

Discussion

Aperture size discrimination in *Testudo hermanni*

When tested with aperture size ratios commonly used in discrimination studies, Hermann's tortoises showed no consistent preference for the larger opening at any individual ratio, although a weak (52.7%) but significant preference emerged when data were combined across ratios. This pattern departs from the general trend observed across other species—both vertebrates and invertebrates—which typically show good abilities to discriminate continuous size differences, whether in tasks involving gap selection or in other perceptual contexts.

The ability to choose the wider of 2 openings has been reported in species as diverse as guppies, zebrafish, rats, dogs, and hooded crows (Krupa et al. 2001; Maeda and Fujita 2010; Santacà et al. 2020a, 2020b, 2022; Khvatov et al. 2021). In zebrafish, for instance, adults can discriminate between 2 openings differing by less than 10% in width, and similar accuracy levels are found already at 2 days post-hatching, suggesting that this perceptual ability develops very early and remains consistent across growth stages (Santacà et al. 2020a, 2020b). Consistent preferences for the larger resource have been reported in other ecologically relevant contexts. In fruit flies, beetles, toads, and mosquitofish, males prefer larger females—typically those

capable of producing more offspring (Bisazza et al. 1989; Marco et al. 1998; Byrne and Rice 2006; Jiron et al. 2025). Similarly, in guppies, angelfish, parrots, and horses, individuals tend to prefer the larger of 2 available food items (Ain et al. 2009; Lucon-Xiccato et al. 2015; Gómez-Laplaza et al. 2019; Cappellato et al. 2020). The minimum perceivable differences in these contexts tend to broadly align with the thresholds reported for obstacle-negotiation tasks.

Controlled operant conditioning experiments further confirm this sensitivity: zebrafish and pigeons, for example, can reliably discriminate between 2 visual objects when the smaller is approximately 85% the size of the larger, thus supporting the findings obtained through spontaneous choice paradigms (Blough 1986; Bisazza and Santacà 2022).

There are several possible explanations for our result. One is that tortoises may have a lower capacity to discriminate quantities compared with other vertebrate species observed, requiring larger differences to effectively distinguish between options. A second possibility is that, unlike other investigated species, for ecological reasons, tortoises have not been selected to prefer the more advantageous option. Results from Experiment 1B support the former hypothesis. When presented with a choice between 2 apertures where one is twice the size of the other, tortoises show a significant preference for the larger aperture. This suggests that, like other species, tortoises do have an intrinsic motivation to pass through the larger gap, but this motivation becomes evident only at relatively large size differences, possibly indicating a higher discrimination threshold and reduced sensitivity to continuous size differences compared with other vertebrates.

Lateralization as a confounding factor

A third factor that might account for the tortoises' poor discrimination performance is cerebral lateralization. Over the past 2 decades, numerous studies have shown that vertebrates across all major taxa—including reptiles—display hemispheric asymmetries in the localization of cognitive functions (Bisazza et al. 1998; Sovrano et al. 2018; Bisazza and Lucon-Xiccato 2025). These asymmetries often manifest as motor or sensory biases, such as a preference for using one eye or limb in specific tasks.

In general, lateralized animals tend to be advantaged across a range of ecological contexts, as they can simultaneously perform 2 competing cognitive functions, each managed by a different hemisphere (Rogers 2021). However, pronounced lateralization can also be ecologically costly under certain conditions, particularly when individuals must choose between 2 simultaneously available options located on opposite sides of the body, as perceptual biases may lead to consistent side preferences regardless of option quality. For example, strongly lateralized goldbelly topminnows are less efficient than non-lateralized conspecifics when integrating social information from both visual fields (Dadda et al. 2009), and in the common toad (*Bufo bufo*), hemispheric specialization can result in missed feeding opportunities or delayed responses to predators approaching from one side (Vallortigara et al. 1998; Lippolis et al. 2002). A distinct but related issue concerns side biases that emerge during experimental testing. Indeed, cognitive studies have long reported that, in binary choice paradigms with stimuli presented along the left–right axis, such biases can lead individuals to repeatedly

select one side, regardless of stimulus properties, thereby compromising discrimination performance (Mackintosh 1974; Topál et al. 1997; Andrade et al. 2001).

Both sensory and motor asymmetries have previously been reported in *T. hermanni* (Stancher et al. 2006; Sovrano et al. 2018; Santacà et al. 2025). In the present study, we did not find a strong directional bias at the population level. There was a general tendency to choose the left opening more frequently, an effect reaching significance only when considering incorrect trials. However, many individuals showed a marked preference for one direction over the other, resulting in a strongly platykurtic distribution of the relative lateralization index. The individual laterality was highly consistent across experiments in both strength and direction, confirming the reliability and stability of these measures. The analysis of the predictors of choosing the larger opening revealed that the degree of lateralization was inversely correlated with performance, whereas the direction of asymmetry had no significant effect. This result supports the hypothesis that poor performance may be linked to interference from motor or sensory biases. It should be noted, however, that the variance explained by this factor was low, suggesting that lateralization alone cannot account for the reduced performance of *T. hermanni* compared with other vertebrates.

Is aperture selection guided by body size awareness?

The present findings are also compatible with an alternative hypothesis, namely that tortoises may be capable of accurately discriminating the size of the apertures, but that this ability becomes relevant only when the smaller aperture prevents them from passing through. Such discrimination would presuppose that tortoises—like mammals, birds, and possibly other species—possess some form of body size awareness, allowing them to relate external constraints to their own body dimensions. Results of Experiment 1C suggest that this is likely not the case: at the same aperture ratio, the tendency to choose the larger opening remained at chance level, regardless of whether the smaller aperture allowed passage or not. Analysis of the passages in this experiment further shows that, in the condition where the aperture was narrower than their body size, tortoises struggled considerably to pass through, even when employing strategies such as forcing the plastic material or orienting their bodies sideways to reduce their width. It is clear, however, that passing through in this manner entails a notable disadvantage, as the time required to negotiate the narrower openings was substantially longer—on average 4-fold longer—that needed to traverse the wider ones. In their natural habitat, such behavior could carry considerable costs, including the loss of time and energy that could be allocated to other activities, as well as the risk of becoming trapped, exposing them to extreme environmental conditions, prolonged starvation, or increased vulnerability to predators.

Body size awareness versus learning-based strategies

There are 2 ways in which an animal may solve the narrow-gap task used here. The first involves assessing the size of the

opening prior to attempting passage, in relation to an internal representation of its own body dimensions. In this case, correct responses are expected to occur from the very first encounters with the problem. The second possibility is that individuals learn through trial and error to avoid gaps below a certain threshold size—a strategy that does not require any knowledge of one's own body size. This learning-based pattern would be characterized by initially random responses, followed by a gradual improvement in performance across trials.

Not all existing studies allow a clear distinction between these 2 mechanisms. Experimental evidence supports the presence of body size awareness in humans, dogs, ferrets, rats, and crows (Khvatov et al. 2021, 2023, 2024). Conversely, in the rat snake (*Elaphe radiata*), individuals initially chose gaps randomly but gradually increased their avoidance of openings that were too small, indicating that they relied on a learning-based strategy rather than on an internal representation of their own body size (Khvatov et al. 2019). Sonoda et al. (2013) studied aperture-size selection in wild-caught hermit crabs, which likely had extensive prior experience with such tasks, making it difficult to determine whether their performance reflected learning or a pre-existing body-size awareness. In guppies and zebrafish, performance has been measured over extended periods, encompassing hundreds of passages, making it unclear whether they select the appropriately sized opening from the outset or learn to do so after early failed attempts (Santacà et al. 2020a, 2020b, 2022). Social insects also show the ability to avoid apertures that are too narrow, but the underlying strategy remains uncertain (Jakobi et al. 2025).

In Experiment 1C, only one reversal was observed across the 270 trials in which tortoises selected the narrower, non-passable aperture, with individuals consistently persisting with their initial choice. Moreover, choices for the smaller opening did not decrease over trials despite repeated ineffective attempts to pass through and becoming stuck (Fig. 2b, Supplementary Video S1), a likely aversive experience. Taken together, these findings suggest that tortoises not only show no evidence of body size awareness, failing to anticipate when an opening is too small but also appear unable to learn from inappropriate choices.

Is poor performance task-specific?

In sum, Experiment 1 indicates that tortoises are motivated to pass through the larger aperture but do so only when the difference in size is substantial. This does not necessarily imply that their visual discrimination abilities are generally inferior to those of other vertebrates. Rather, it is possible that their poor performance is specific to this context, whereas tortoises may be accurate in discriminating continuous quantities in other functional domains. For example, tortoises may have evolved specific motor strategies to cope with obstacles of this kind. In discussing the poor performance of tortoises relative to other reptiles and vertebrates in the transparent barrier detour task, Santacà et al. (2025) suggested that the typical strategy of this species involves physically forcing obstacles rather than circumventing them. Similarly, Golubović et al. (2013) observed that tortoises tend to use their body strength to climb or push over steep steps instead of seeking alternative routes. Together, these findings support the idea that Hermann's tortoises adopt a “bulldozer-

like” strategy when confronted with barriers, relying on persistence and physical force rather than flexible problem-solving. A second, non-exclusive explanation is that, in their natural environment, tortoises rarely face situations in which 2 distinct detour options are simultaneously available, which may have relaxed selective pressure on decision-making mechanisms in this context.

To determine whether the poor performance observed in the aperture discrimination tasks was specific to that context, we examined tortoises in a domain where spontaneous preferences for larger quantities have been extensively documented: food choice. According to optimal foraging theory, selecting larger food items increases foraging efficiency by maximizing energy gain and reducing time, effort, and risk, especially when alternative resources may become unavailable through consumption or loss, as in the case of prey (Mittelbach 1981; Pyke 1984). Indeed, a wide range of species across diverse taxonomic groups, including ants, lizards, marine turtles, dogs, parrots, and jays, have been shown to prefer the larger of 2 food quantities (Langen and Gibson 1998; Mailleux et al. 2000; Aïn et al. 2009; Fossette et al. 2012; Miletto Petrazzini et al. 2017; Loconsole et al. 2023). Using the same apparatus and size ratios as in Experiment 1A, Experiment 2 tested whether tortoises showed a spontaneous preference for larger food quantities when simultaneously presented with 2 food items differing in length. No significant preference emerged at any ratio, and performance closely mirrored that observed in the aperture discrimination task. Lateralization did not predict performance.

Using the same apparatus and size ratios as in Experiment 1A, Experiment 2 tested whether tortoises showed a spontaneous preference for larger food quantities when simultaneously presented with 2 food items differing in length. No significant preference emerged at any ratio, and performance closely mirrored that observed in the aperture discrimination task. Neither the strength nor the direction of lateralization significantly predicted performance in this experiment.

Gazzola et al. (2018) reported a moderate preference for larger food items in Hermann's tortoises, but methodological differences likely account for the discrepancy. In our study, the 2 options were spatially separated, requiring a directional choice from a distance prior to approach, whereas in Gazzola et al.'s setup, the items were placed very close together at the corridor exit. Given the strong reliance of chelonians on olfaction during foraging (Fitch 1965; Chelazzi and Delfino 1986; King et al. 2008; Rowland et al. 2015), such proximity may have allowed olfactory cues to influence decisions (i.e., through increased odor release from the larger food item), despite attempts to saturate the environment with food odor. In any case, performance was also modest in Gazzola et al. (2018), where tortoises showed a clear preference for the larger food item only at a 4:1 ratio, but performance declined rapidly at ratios of 0.5 or higher.

The lack of preference for the larger food piece might also be specifically related to the ecology of *T. hermanni*. In natural conditions, opportunities to choose between 2 simultaneously available food items might be rare, which may have relaxed selective pressures on decision-making mechanisms in this domain, too. Moreover, being a predominantly solitary forager, this species is unlikely to face direct competition over food; when encountering 2 nearby resources, an individual could probably in most cases, consume both. Interestingly, the lacertid lizards *Podarcis siculus*

and *Egernia stokesii* have been found to perform more accurately when discriminating sets of discrete items differing in number than when distinguishing individual items differing in area, and 2 freshwater turtles, *Mauremys sinensis* and *Trachemys scripta*, have shown numerical discrimination abilities comparable to, or even exceeding, those of many endotherms (Miletto Petrazzini et al. 2018; Szabo et al. 2021; Lin et al. 2024). These findings might suggest that reptiles, in general, are more attuned to visually assessing the number of food items within a patch, perhaps relying on other sensory modalities when evaluating the size of individual items. This interpretation is further supported by the observation that *Podarcis siculus* performed much more accurately when discriminating item size than item number when observed with dead housefly larvae, which may have provided additional olfactory cues, rather than with artificial two-dimensional stimuli (Miletto Petrazzini et al. 2017).

Concluding remarks

Overall, our results suggest that *T. hermanni* does not appear to be aware of its own body dimensions when deciding whether a gap is passable. However, the question remains as to why this species exhibits remarkably low selectivity in 2 ecological contexts where all other species observed to date show clear preferences for the more advantageous option. Perhaps body rigidity plays a decisive role: on one hand, inflexibility increases the risk of wasting time or even getting stuck, as the animal cannot adapt to the passages; on the other hand, it allows the displacement of obstacles, thereby widening the gaps—making discrimination unnecessary, especially when only small movements are required.

Further research is needed to determine whether *T. hermanni* truly exhibits lower-level cognitive abilities compared with other ectothermic vertebrates studied to date, or whether its poorer performance in cognitive tasks primarily reflects the species' distinctive ecological and life-history traits. Distinguishing between these 2 possibilities is crucial for understanding not only the evolutionary origins of quantitative abilities in reptiles but also the extent to which ecological specialization can shape cognitive performance. Interestingly, Hermann's tortoises perform well in spatial cognition tasks, particularly when using environmental geometry and landmarks to locate salient sites (Baratti et al. 2026), with abilities comparable to those observed, for example, in fish (Baratti et al. 2022, for a review). The ecological context and the nature of the task likely play a key role in shaping their performance.

Future investigations should aim to expand spontaneous choice paradigms to other functional domains beyond foraging and locomotion—for instance, by examining sexual selection contexts, such as male and female preferences for mate size. In addition, applying classical or operant conditioning paradigms—widely used in studies of other vertebrates—could help determine whether *T. hermanni*'s apparent insensitivity to continuous differences arises from perceptual limitations, motivational factors, or task-specific constraints.

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Authors' contributions

AB, GS, and VAS conceived and designed the research. TDP and VAS conducted the behavioral experiments and video analysis. AB and EG performed the data analysis and wrote the first version of the manuscript. All authors discussed the results, reviewed, edited the manuscript, and approved the submitted version.

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Conflicts of interest

The authors declare no conflicts of interest.

Ethics statement

Animal husbandry and experimental procedures complied with European Legislation for the Protection of Animals (Directive 2010/63/EU) and adhered to Italian and European Community laws regarding protected wild species (Art. 8/bis 150/92 all. A Reg. (CE) 338/97). The experimental protocol was approved by the internal Ethics Committee of the Civic Museum Foundation of Rovereto (Prot. A N. 0000238). The number of animals used was consistent with the "Reduction" principle, ensuring the minimum number necessary to obtain statistically valid results. During the experiments, every effort was made to minimize stress by conducting the experiments in accordance with the tortoises' daily rhythms, monitoring each tortoise until the end of the working day after the sessions, and re-housing the tortoises in familiar open-air enclosures at the end of all their experimental sessions, where they were provided with fresh vegetables, wild plants, and water.

Data availability

The datasets are available on request from the corresponding author.

Artificial intelligence (AI)-assisted technologies

During the preparation of this manuscript, the authors used ChatGPT for language editing. The authors reviewed all the AI-generated suggestions and edited as needed, and assume full responsibility for the content of the published article.

Supplementary material

Supplementary material can be found at <https://academic.oup.com/cz>.

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