Learning to find the center of symmetric and asymmetric spatial layouts by the house cricket, *Acheta domesticus*

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Abstract

There is heavy debate about the mechanisms of spatial navigation by insects. Researchers tend to focus mainly on vision-based models, neglecting non-visual modalities. The capacity to navigate by layout symmetry has been reported in vertebrate species. Nevertheless, there has been no direct evidence for such an ability in insects, especially regarding center finding. To provide novel insight into the ongoing debate, we developed a non-visual paradigm for testing navigation by layout geometry. We tested the house cricket's (*Acheta domesticus*) to find a cool spot positioned centrally in heated arenas of different shapes. We found that the symmetry of the arena significantly facilitates how crickets learn to find the center of the arena, both in terms of time spent on the cool spot and the latency of locating it. We argue that due to the lack of visual cues, visiocentric models cannot directly address this observation, therefore we explore alternative explanations.

Keywords: comparative cognition, geometric cognition, house cricket (*Acheta domesticus*), insect behavior, spatial learning, spatial navigation

Introduction

Spatial navigation plays a vital role in lives of animals, allowing them to successfully and repeatedly forage for food, find their way back to nesting sites, or localize mating spots. To this end animals use a spectrum of strategies allowing them to return to the memorized locations despite the obsolescence of egocentric knowledge caused by unforeseen circumstances or disturbing stimuli (Dudchenko, Goodridge, Seiterle, & Taube, 1997; Gallistel, 1990; Ponticorvo & Miglino, 2009; Thinus-Blanc, Chabanne, Tommasi, Peruch, & Vauclair, 2010; Tomassi, Chiandetti, Pecchia, Sovrano, & Vallortigara, 2012). Due to the prevalence of the phenomenon of spatial navigation across the animal kingdom, as well as clear characteristics of navigational behavior that can be relatively easily measured in terms of movement in space and time, it is not surprising that navigation has become a model for comparative cognition as a whole (Wystrach & Graham, 2012).

Geometry-driven spatial navigation

In order to navigate in space, animals use various kinds of cues received via multiple modalities (Webb & Wystrach, 2016). Nevertheless, the contribution of vision seems to be examined much more than any other modality (regarding studies involving both vertebrate and invertebrate species) constituting a rather "visiocentric" predisposition in spatial navigation studies (Hohol, Baran, Krzyżowski, & Francikowski, 2017). Numerous vision-based behaviors, originally discovered in vertebrates, have also been revealed in insects using similar experimental setups. Making rotational errors in rectangular enclosures during attempts to recover spatial knowledge (after disorientation) using visually perceived layout geometry serves as a well-known example. Initially, Cheng (1986) discovered such a behavior in rodents, and in the subsequent decades, it was found in other vertebrate species as well (Gouteux, Thinus-Blanc, & Vauclair, 2001; Hermer & Spelke, 1996; Sovrano, Bisazza, & Vallortigara, 2002; Vallortigara, Zanforlin, & Pasti, 1990). More recently, this behavior has even been documented in insects such as ants (Wystrach & Beugnon, 2009) and bumblebees (Lee & Vallortigara, 2015; Sovrano, Rigosi, & Vallortigara, 2012).

Using layout geometry as a visual cue for navigation is not task dependent, since vertebrates (Gray, Spetch, Kelly, & Nguyen, 2004; Tomassi & Thinus-Blanc, 2004; Tomassi, Vallortigara, & Zanforlin, 1997) are able to localize the center of an arena on the basis of its overall geometric

shape and are capable of transferring this knowledge to other geometrically regular enclosures. Although the above-mentioned insect studies are not the only examples suggesting that miniature nervous systems are able to process geometric properties, such as symmetry (Giurfa, Eichmann, & Menzel, 1996; Rodríguez, Gumbert, De Ibarra, Kunze, & Giurfa, 2004), to the best of our knowledge, insects have not yet been tested using the searching for the center experimental model (Tomassi et al., 1997).

Mechanisms of spatial navigation

Sensitivity of vertebrates to layout geometry and their tendency to employ it during place finding have been explained mostly in reference to the hardwired high-level computational mechanism called the geometric module (GM; Cheng, 1986). This cognitive structure is thought to be implemented in the hippocampus and surrounding areas of the brain (Czajkowski et al., 2014; Moser, Moser, & McNaughton, 2017; O'Keffe & Nadel, 1978). GM is specialized in the processing of a narrow scope of information from visual input in order to build a distinctive, robust, and computationally inexpensive mental representation of the environment (Spelke & Lee, 2012; Spelke, Lee, & Izard, 2010; Vallortigara, 2012).

While there is still no consensus about the exact mechanism responsible for the observed behavioral patterns of layout geometry-driven navigation in vertebrates (Cheng, 2008; Cheng, Huttenlocher, & Newcombe, 2013; Duval, 2019; Hohol, 2020; Sutton & Newcombe, 2014; Vallortigara, 2018; Wystrach & Graham, 2012), in the case of insects, it is widely accepted that view matching (VM) is the core mechanism behind this mode of spatial navigation (Cartwright & Collett, 1983; Collett, Chittka, & Collett, 2013; Judd & Collett, 1998; Wehner, Michel, & Antonsen, 1996; Wehner & Räber, 1979; Wystrach, Cheng, Sosa, & Beugnon, 2011). The VM approach assumes that the animal records a snapshot of the area surrounding the goal, and then moves so as to minimize the discrepancy between the snapshot and the actual view, wherein the memorized "view" is not simply understood as a mental image, but instead as a set of encoded parameters including depth, motion, edges, or specific features. On the other hand, even though the neuroanatomy of different insect species appears relatively similar, particular species significantly differ in terms of spatial scale, occupied ecological niche, evolutionary pressures, neural complexity, and primary perceptual modality. Therefore, one can expect that even significant behavioral convergence in geometry-driven navigation may be constituted by different perceptual and cognitive mechanisms, depending on the species. For instance,

Gigantiops destructor, a neotropical formicine ant tested by Wystrach and Beugnon (2009) for the presence of rotational errors, is a highly visual animal equipped with sizeable eyes. Therefore, the VM-based explanation of its navigational behavior in geometrically regular arenas is convincing. Nevertheless, this does not automatically imply that the navigation of other insects, such as adult house crickets, which are predominantly nocturnal animals, in the aforementioned enclosures would also be driven by VM.

Moreover, it has recently been argued that VM is able to explain any complex navigational behavior, to the exclusion of other mechanisms (assuming sufficient capacity of memory to store the views), which calls its explanatory value into question (Duval, 2019; Hohol et al., 2017). Aside from navigation by visual cues (Doria, Morand-Ferron, & Bertram, 2019; Wessnitzer, Mangan, & Webb, 2008), crickets have been tested in experiments involving auditory cues (Hedwig & Poulet, 2005; Reeve & Webb, 2003). Nevertheless, none of the existing studies allow us to infer their ability to use layout geometry for spatial learning and navigation.

Objectives and hypotheses of the present study

In the present study, we tested whether house crickets (*Acheta domesticus*) are able to find a target positioned centrally in an arena, and if so, whether the symmetry of the spatial layout facilitates learning of a place-finding task. To this end, we employed a variant of the center-finding task, where the goal of the animal is to find an invisible cool spot positioned at the center of the following experimental enclosures: circular, square, triangular, and asymmetric quadrilateral. Originally, the task was developed by Tomassi, Vallortigara, and Zanforlin (1997) to test the spatial cognition of chickens, and later it was used to investigate other vertebrate species, namely pigeons (Gray et al., 2004) and rats (Tomassi & Thinus-Blanc, 2004). However, to the best of our knowledge, the task has never been applied in studies on insects.

We also aimed to explore possible non-visiocentric cognitive mechanisms of insect spatial navigation based solely on layout geometry. As the VM generally explains navigational behavior in a low-level way, namely, the overall encoding of the layout geometry is not required, we prevented the insects from using view-based place finding. For this purpose, we employed a non-visual paradigm modeled on the Tennessee Williams (TW) setup (Wessnitzer

et al., 2008), which is a “dry” analog of the Morris (1981) water maze (MWM) test commonly used for assessing navigational capabilities. Additionally, the setup was controlled for other (olfactory and auditory) modalities, which could provide insects with a readily viable cue for reorientation. Furthermore, the non-visual testing conditions were carefully selected to meet the ecological validity standard (De Gelder & Bertelson, 2003) as the house cricket imagoes are predominantly active at night (Cymborowski, 1973; Górska-Andrzejak & Wojtusiak, 2003).

We expected to find that the behaviors observed in this study would converge with those previously reported in vertebrates. We hypothesized that crickets would find the center. Our second hypothesis is that they would learn to find the center more efficiently in conditions with symmetric arenas compared to the asymmetric one. This corresponds with the expectation that geometrically regular environments are easier to navigate.

Materials and methods

Experimental setup

In the presented study, the center-finding task (Tomassi et al., 1997), combined with the non-visual variation of the TW setup (Wessnitzer et al., 2008), was used. The paradigm was implemented as an experimental apparatus (Fig. 1) that consisted of a leveled, matted, white glass sheet and variously shaped arenas (circular, square, triangular and asymmetric quadrilateral) all of the same height (25cm) and adjusted to approximately the same area (709±3%cm^2 - circular d=30, square: a=27, triangular: a=40 asymmetric quadrilateral: a=37 b=24 c=23 d=26 α=67° β=80° γ=100° δ=113° [cm]). The arenas were made of solvent-welded white Lucite and devoid of any visual cues. The surface of the glass was uniformly heated to 50±1°C with IR heating lamps (4 x 250W bulbs, heat distribution evaluated with the FLIR T640 thermal camera) with the exception of a centrally localized cool spot that was maintained at a constant temperature of 25±1°C by a water-cooling block (⌀60mm). All experimental trials were performed in a soundproofed dark room. Arenas were illuminated with a red LED ring (24x WS2812B) (see Worldsemi, 2019 for product card) emitting at a wavelength of 620-625nm, which is beyond the detection threshold of the retinal receptors of crickets (Herzmann & Labhart, 1989), and thus was chosen in order to ensure a lack of visual cues. Before each trial the enclosures of the arenas were rotated by 45° and, along with the glass plate, were thoroughly wiped with 70% (v/v) denatured ethyl alcohol to eliminate olfactory clues.

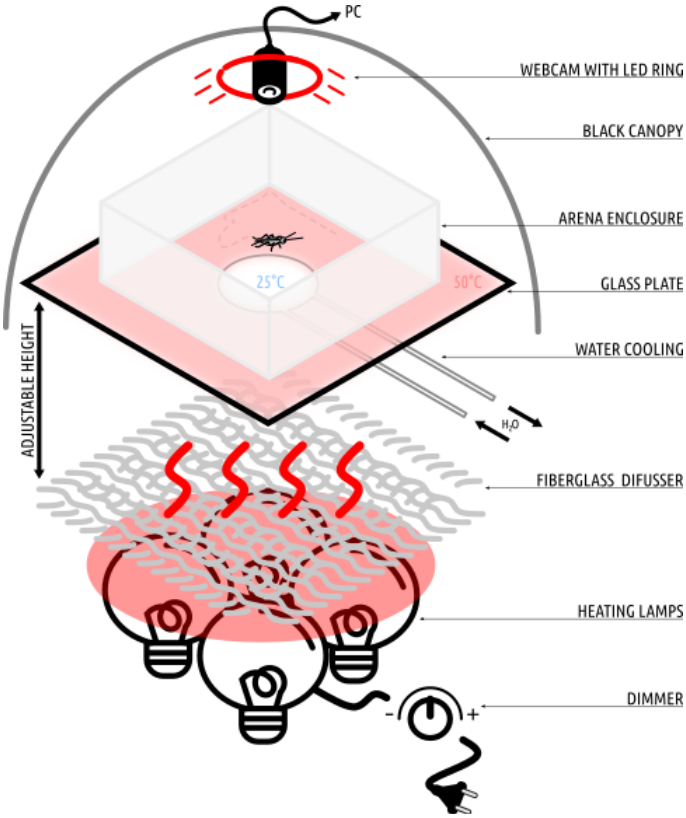

Figure 1. The applied experimental setup iterates the TW model, namely a spatial learning task similar to the MWM, where the insect explores a plate heated to an aversive temperature to find the invisible cool spot on which it can rest (Mizunami, Okada, Li, & Strausfeld, 1998). Our apparatus consisted of 4 x 250W dimmable heating lamps with a fiberglass cloth diffuser mounted above them. Thermal radiation generated by the lamps uniformly heated the bottom side of the glass plate (500x500x4mm), painted with two layers of heat resistant enamel—the first layer was made of white enamel (to provide a contrasting background for insect tracking), and the second was painted black (for thermal absorption). On the backside of the plate, the 3D printed water cooler (⌀60mm) was attached with a gecko pad and connected to a constant flow of cool water adjusted to ensure a constant temperature on a cool spot on the surface of the plate. The glass was chosen due to its low thermal conductivity, which created a sharp thermal boundary around the cool spot. The upper surface of the glass was matted to ensure sufficient traction for the insects. Differently shaped arena enclosures were placed on the surface of the glass. The setup was calibrated with the aid of thermal imaging to provide stable temperatures of 50±1°C on the hot part and 25±1°C on the cool spot (Fig. 2). Prior to every training session, the setup was warmed to the desired temperatures.

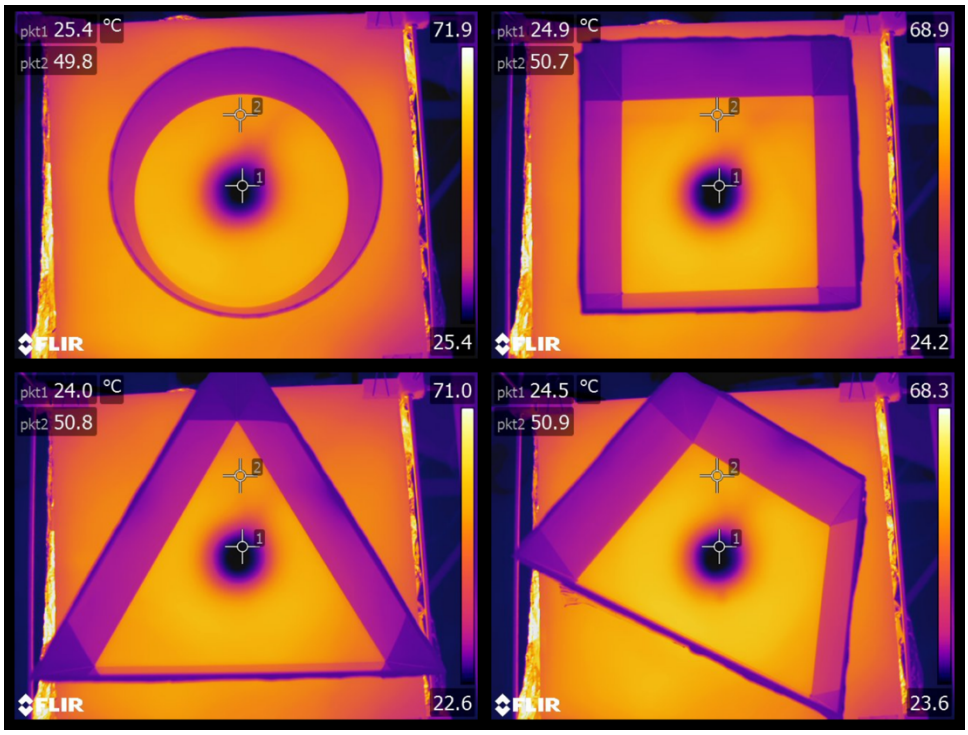

Figure 2. Thermal imaging of the heat distribution on the surfaces of the arenas. Two measurement points, ptk1 and ptk2, indicate the temperatures of the cool spot and the rest of the arena, respectively. Images were acquired with a FLIR Systems AB high-performance thermal camera FLIR T640 (640x480px IR resolution, sensitivity 0.04˚C at 30˚C).

Animals

House crickets (*Acheta domesticus*, wild type) used in the study were acquired from a stock colony maintained at the Institute of Biology, Biotechnology and Environmental Protection. Insects were reared under constant conditions of 30±2°C, 40±10% RH, and a 12:12 light:dark photoperiod with water and food pellet *ad libitum*. In all trials, adult male crickets were used 1-2 days after imaginal molt and in perfect conditiond. For each arena shape, 15 crickets were tested (n=15 x 4).

Procedure

Prior to the experimental procedure, each insect was removed from the general colony and underwent initial habituation in order to familiarize it with the transfer container (black film roll case - ⌀30mm h50mm). After that, the insect was released in a random spot of the arena and left undisturbed for a 5-minute trial (Fig. 3) while a recording was captured. Between

subsequent trials, the cricket was removed from the apparatus for a 5 min rest. Each session consisted of 10 trials (Wessnitzer et al., 2008) per arena. The procedure of each trial was analogous to a typical MWM test. The cricket was released at a random location in the arena and had to find the centrally localized, invisible cool spot that allowed it to escape the aversive heat stimuli.

Figure 3. Experimental timeline was based on a study done by Wessnitzer, Mangan and Webb (2008) consisting of 10 x 5 min long trials alternating with 5 min rests. Duration of the rest time was adjusted from 2 min used by Wessnitzer et al. (2008) to reduce elevated erratic escape behavior which was observed in a pilot study conducted prior to the primary experiment.

Data acquisition

All recordings were captured with a Microsoft LifeCam Studio webcam and VirtualDub (v1.10.4.35491) software. Movement trajectories of tested insects were extracted with SwissTrack 4 software (Lochmatter et al., 2008) and further processed in R (ver. 3.6.1; R Core Team, 2013) with the trajr package (McLean & Skowron Volponi, 2018).

Statistical analysis

For statistical data analysis, R (ver. 3.6.1; R Core Team, 2013) was used. To test whether the proportion of time spent at the center of the arena increases with trial repetitions (i.e., to assess learning curve), and to test whether this time proportion changes in a similar manner in the different arena types, mixed effects linear regression models were fitted using the package MCMCglmm (Hadfield, 2010). Four separate models were fitted, one for each arena type, because in each arena a different group of crickets was used. In the models, the proportion of time spent at the center of the arena was the response variable, while trial number was used as

a continuous predictor variable. The response variable was square root-transformed in order to normalize the distribution. In each model, we controlled for between-individual differences in intercept and slope estimates (random intercept and slope model), by defining the variable with the individual codes of the crickets as a random factor.

Additionally, four other models were fitted to test whether the latency of center-finding decreased with the progression of trials. The models were prepared using linear regressions (separately for each arena) in which the response variable was the latency (in minutes) of locating the cool spot for the first time during each trial. The response variable was log-transformed before model fitting in order to normalize its distribution. Trial repetition number was used as a continuous predictor variable, and we also controlled for between-individual differences in intercept and slope estimates, by defining the variable with the individual codes of the crickets as a random factor.

For all the above-described models, both proper and non-informative priors were used. For the random variance estimation, we used parameter expanded priors to improve mixing of the Markov chains. For each model, we used 255 000 Markov Chain Monte Carlo iterations, from which the first 5 000 iterations were discarded as "burn-in." We saved parameter estimates from every 50th iteration, yielding posterior distributions with nominal sample sizes of 5 000.

To quantify arena-type differences in the fixed-effect slopes, we created contrast parameter distributions by subtracting each fixed-effect posterior distribution from the other three fixed-effect slope posterior distributions, corresponding to different arena types. Additionally, to check whether latency of finding the center of the arena differed between arena types in the last trial sessions, we re-fitted the latency-regression using the number of trials minus ten as a predictor (i.e. the range of this trial-variable was from -9 to 0, instead of being from 1 to 10). In these models, the regression curve intercepts would coincide with the latencies measured at the last trial. Using these intercept estimates, we compared whether there were arena shape-based center-finding latency differences in the last trial. We report parameter estimates of models and slope differences (contrasts) as the modal values of the posterior distributions. Credible intervals were quantified as the lower and upper cutoff values of the 95% highest posterior density intervals.

For each arena type, we used Mann-Whitney tests to compare the proportions of time spent in the centers of the arenas between the control group and the first trial of the treatment group.

Because multiple comparison tests were used on the same dataset, we applied Bonferroni's *post hoc* P-value adjustment on the P-values from the Mann-Whitney tests to reduce the probability of a type I error.

Results

As trials progressed, crickets tended to spend more time at the centers of the arenas regardless of arena shape, as indicated by the significant positive effect of the trial number on the proportion of time spent in the center (Table 1). We found no differences between the slopes of the learning curves of the circular, triangular, and square arenas. However, we found that the learning curve estimate (slope) was an order of magnitude lower in the asymmetric arena (Table 2 & Figs. 4 & 5). Furthermore, as the trials progressed, the latency of the crickets finding the center of the arena significantly decreased for all arena types (Table 1). No arena type differences were found between the slopes of the latency-reduction regressions (Table 2 & Fig. 6). Notably, even in the last trials, the crickets needed significantly more time to find the center of the asymmetric arena, as indicated by the significantly higher intercept estimate in the regression model of the asymmetric arena in comparison to the circular (ß = -1.643, HPD_{lower} = -2.168, HPD_{upper} = -1.160), triangular (ß = -1.534, HPD_{lower} = -2.255, HPD_{upper} = -0.698), and square (ß = -0.838, HPD_{lower} = -1.352, HPD_{upper} = -0.254) arenas.

Crickets from the control group spent significantly less time at the arena center in the circular ($P < 0.001$), triangular ($P = 0.016$), and square ($P = 0.032$) arenas than crickets in the first trial of the treatment group. However, no such difference was apparent in the case of the asymmetric quadrilateral arena ($P = 0.854$).

Response variable	***Arena shape***	***Slope estimate***	***HPD_{lower}***	***HPD_{upper}***
Proportion of time spent in arena center	Circular	0.025*	0.017	0.036
	Triangular	0.028*	0.014	0.043
	Square	0.022*	0.012	0.036
	Asymmetric	0.007*	0.002	0.015
Latency to find arena center	Circular	-0.185*	-0.253	-0.120
	Triangular	-0.242*	-0.341	-0.155
	Square	-0.132*	-0.207	-0.071
	Asymmetric	-0.169*	-0.219	-0.089

Table 1. Parameter estimates from the fitted models.

Slope estimates are the modal values of the posterior distributions, while HPD_{lower} and HPD_{upper} are lower and upper cutoff values of the 95% highest posterior density (credible) intervals, respectively; intervals not crossing zero indicate that the given parameter estimate significantly differs from zero (statistically significant estimates are marked with asterisks).

Response variable	***Arena shapes used to draw contrast slope estimate***		***Contrast estimate***	***HPD_{lower}***	***HPD_{upper}***
Proportion of time spent in arena center	Circular	Triangular	-0.005	-0.021	0.014
	Circular	Square	-0.001	-0.013	0.017
	Circular	Asymmetric	0.018*	0.006	0.030
	Triangular	Square	0.002	-0.014	0.025
	Triangular	Asymmetric	0.021*	0.006	0.037
	Square	Asymmetric	0.016*	0.002	0.029
Latency to find arena center	Circular	Triangular	0.070	-0.048	0.179
	Circular	Square	-0.028	-0.135	0.054
	Circular	Asymmetric	-0.043	-0.120	0.065
	Triangular	Square	-0.123	-0.219	0.010
	Triangular	Asymmetric	-0.081	-0.215	0.013
	Square	Asymmetric	0.022	-0.082	0.106

Table 2. Contrasts of slope estimates from the fitted models.

Slope estimates are the modal values of the posterior distributions, while HPD_{lower} and HPD_{upper} are lower and upper cutoff values of the 95% highest posterior density (credible) intervals, respectively; intervals not crossing zero indicate that the given contrast estimate significantly differs from zero (marked with asterisks).

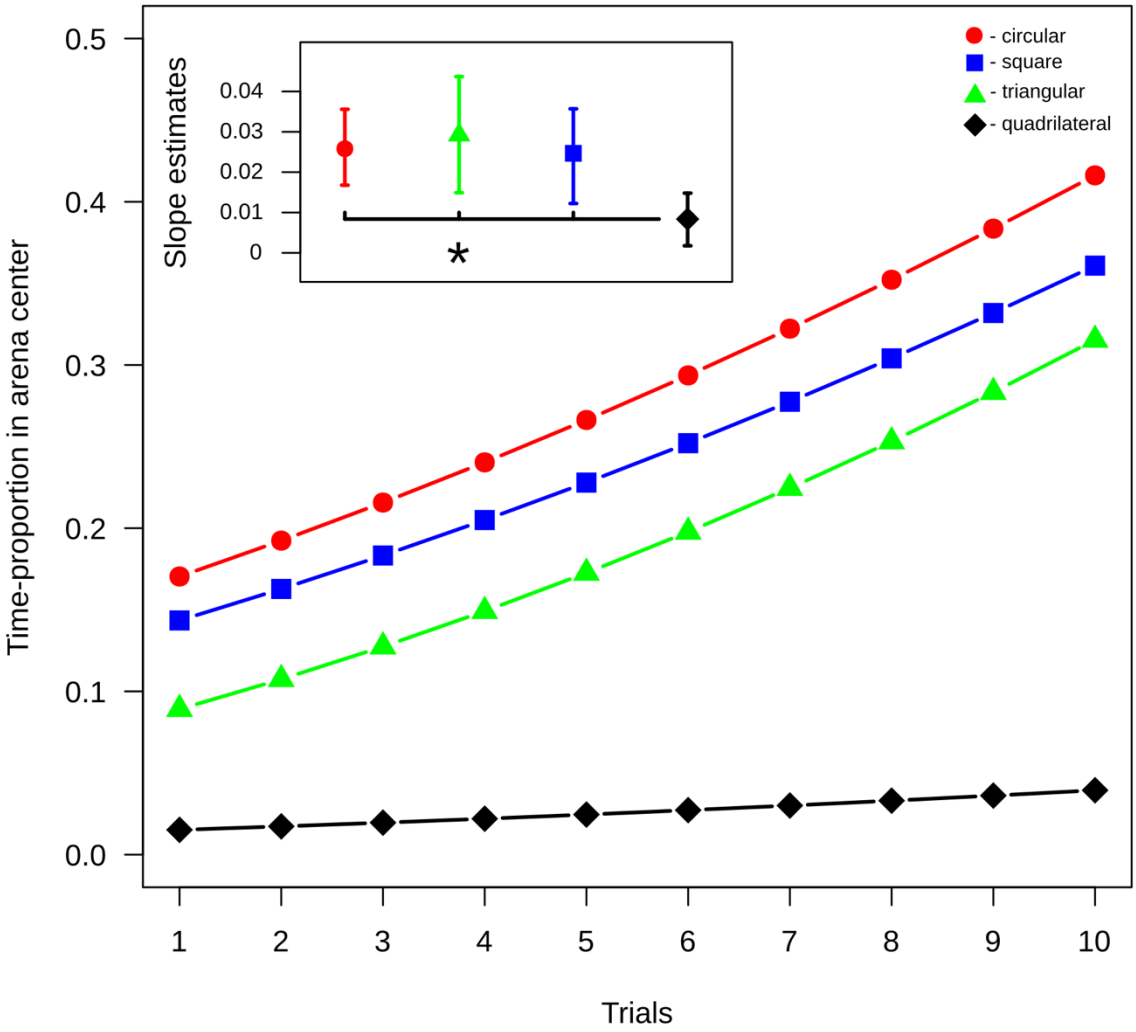

Figure 4. Association between progression in time (throughout successive trials) and the proportion of time spent in the center of arenas within trials. The sub-plot in the upper-left visualizes the slope parameter estimates from the fitted models, and the 95% credible intervals of the parameters. In both the main and the sub-plot, circles, triangles, squares, and diamonds represent data from circular, triangular, square, and asymmetric arenas, respectively. The slope of the learning curve from the asymmetric arena was significantly smaller than that of all the other arena types, while there were no significant differences between the slopes of the other three arenas.

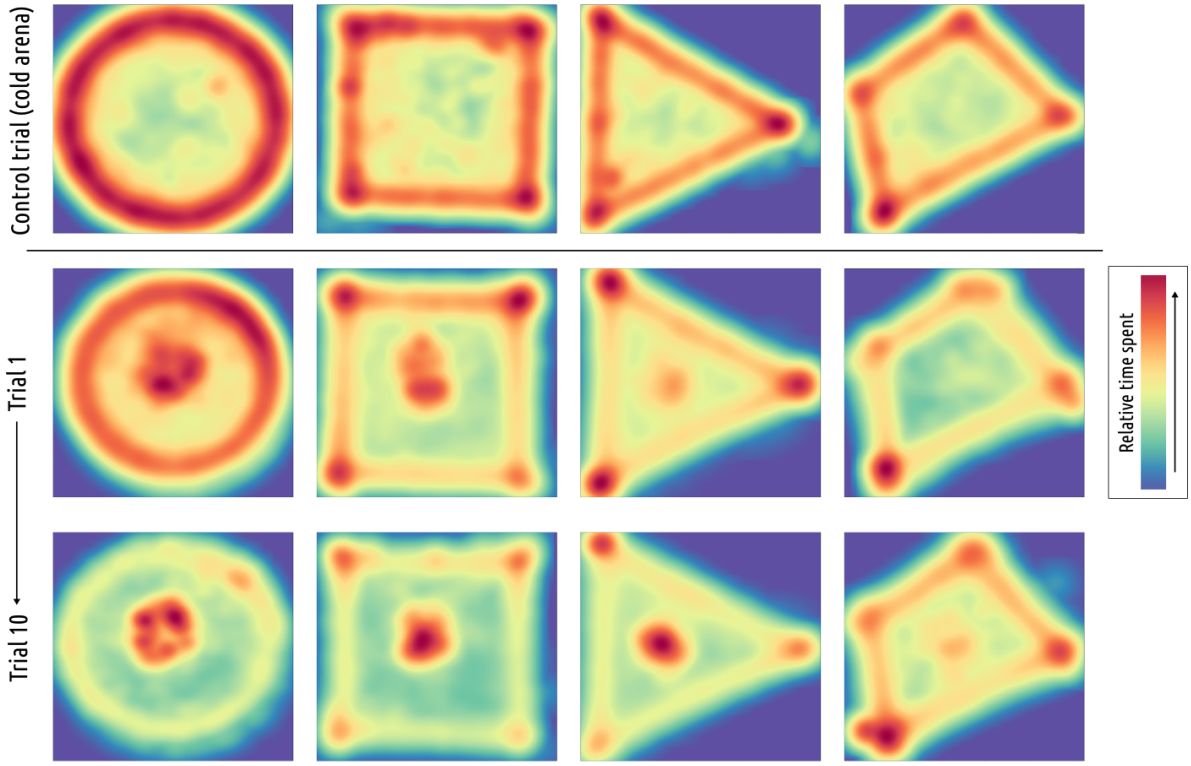

Figure 5. The cumulative heatmaps (for each of the conditions) represent the proportion of time spent by the insects in particular places of each arena in the control condition without thermal stimuli (upper row), the first trial (middle row), and the final trial (bottom row) of the study.

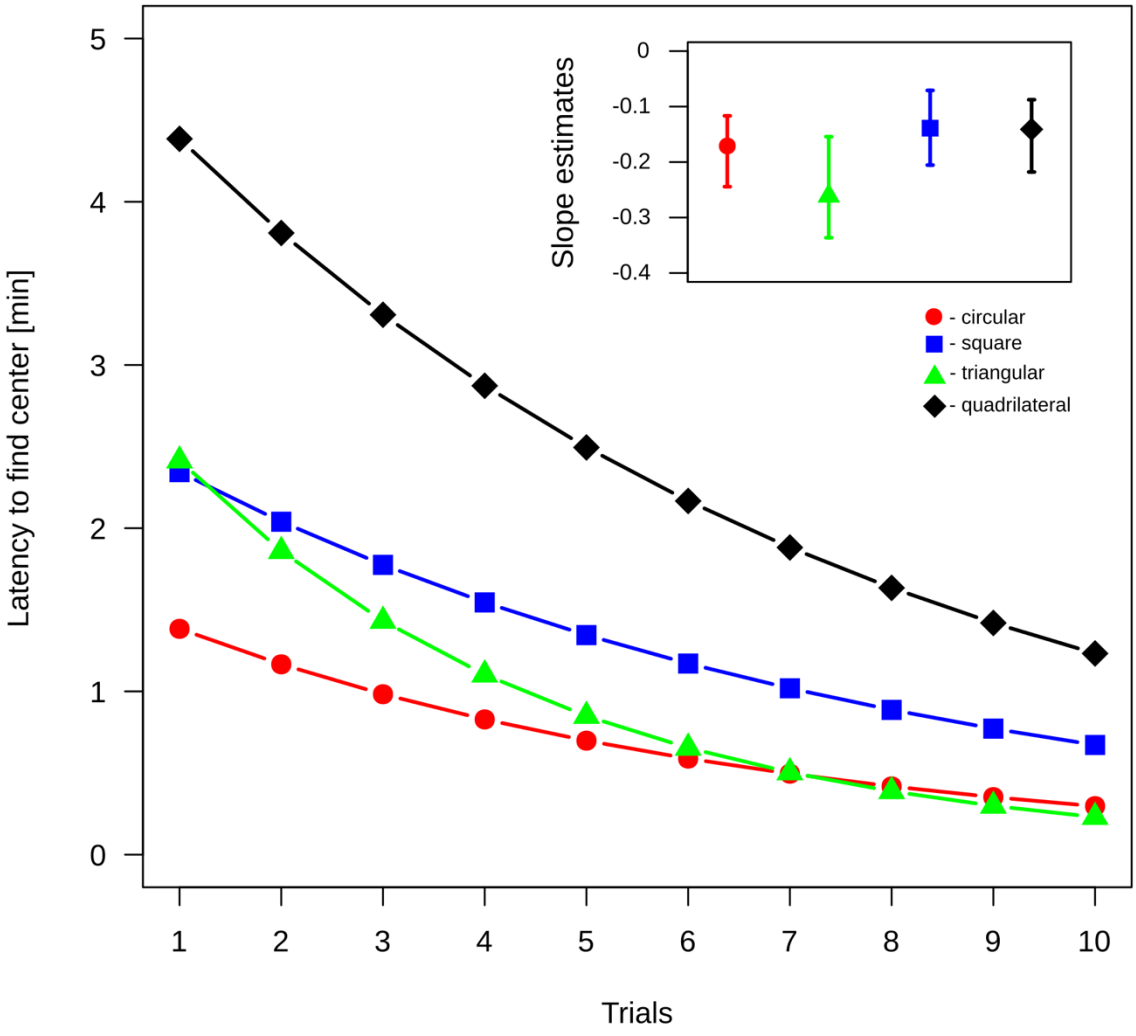

Figure 6. Association between progression in time (throughout successive trials) and latency of the crickets to find the center of the arena. The sub-plot in the upper-right visualizes the slope parameter estimates from the fitted models, and the 95% credible intervals of the parameters. In both the main and the sub-plot, circles, triangles, squares, and diamonds represent data from circular, triangular, square, and asymmetric quadrilateral arenas, respectively. No significant differences were observed between slope parameter estimates from the different arena types.

Discussion

The present study aimed to test two hypotheses. Firstly, we hypothesized that crickets are able to localize a centrally positioned, invisible cool spot. Secondly, we expected that the learning of a place-finding task would be more efficient in all the symmetric arenas in comparison to the asymmetric one. Therefore, we expected to replicate the observations commonly seen in studies on vertebrates (Gray et al., 2004; Tomassi & Thinus-Blanc, 2004; Tomassi et al., 1997).

Despite the lack of previous insect research conducted with the center-finding task, our hypotheses were driven by the general theoretical claim that sensitivity to layout geometry increases the adaptive value of animals. Layout geometry generally constitutes a distinctive, robust, and computationally inexpensive cue that can be used in place finding (Gallistel, 1990; Hohol, 2020; Spelke & Lee, 2012; Spelke et al., 2010; Vallortigara, 2012). This claim alludes to distal evolutionary origins of sensitivity to layout geometry, which imply that it should be observed in various animal phyla. Nevertheless, the mechanisms behind it could differ among the species. Our hypotheses were further substantiated by previous findings that insects exhibit sensitivity to object symmetry (Giurfa et al., 1996; Rodríguez et al., 2004). Additionally, they exhibit good navigational performance in other tasks where spatial layout is geometrically regular (Lee & Vallortigara, 2015; Sovrano et al., 2012; Wystrach & Beugnon, 2009), and finally, they are capable of swift conceptual learning, involving development of spatial concepts (Avargues-Weber, Dyer, Combe, & Giurfa, 2012; Avargues-Weber & Giurfa, 2013; Giurfa, 2013; Loukola, Perry, Coscos, & Chittka, 2017).

We found that crickets are able to localize the centrally positioned, invisible cool spot. The efficiency of learning a place-finding task is significantly more robust in all the symmetric arenas (namely circular, square, and triangular) in comparison to the asymmetric quadrilateral one. More specifically, the learning curve estimates were significantly higher in the symmetric arenas than in the asymmetric one, and the latency of finding the center was significantly longer in the latter. This effect was indicated by a higher intercept estimate in the regression model. Nevertheless, in subsequent trials (in all arenas), the time spent in the center increased and the latency decreased, albeit to a highly varying degree. The data obtained from the control condition performed in the "cold" (non-heated) arena emphasizes the learning aspect of the observed behavior as the crickets, aside from learning to find the center, had to suppress their initial thigmotaxis reflex (see Kastberger, 1982). Overall, our hypotheses seem to be

corroborated, allowing us to infer that layout symmetry facilitates spatial learning and can be considered a robust cue for successful place finding.

Moreover, the obtained results converge with the previous findings of Wessnitzer, Mangan, and Webb (2008), who employed the TW model with the non-visual experimental setup serving as a control (the tested crickets were unable to learn to locate the cool spot). Although these authors used the circular arena, similar to one of the conditions of our study, the cool spot was positioned asymmetrically. We suggest that the asymmetric arena (our study) and asymmetrically located spot (Wessnitzer et al., 2008) could be considered functionally equivalent. The inability of the crickets to learn to find the asymmetrically localized target in the study by Wessnitzer et al. (2008) closely matches our results obtained from the asymmetric quadrilateral arena.

A significant reduction in observed latency indicates that the capacity of the cricket to find the center could not be explained in terms of learning to interrupt the random search (or scanning) when the cool spot is reached. If this were so, the time spent on the cool spot would increase, but the latency would have remained constant (Foucaud, Burns, & Mery, 2010). Furthermore, another study performed using the MWM test revealed that the execution of non-spatial search routines, such as scanning or chaining, could lead to comparable latencies as direct search and related strategies (Garthe, Behr, & Kempermann, 2009; Wolfer & Lipp, 2000). Thus, if crickets relied on these strategies, it would be expected that time spent in the center of the asymmetric quadrilateral arena would be comparable to symmetric ones, since those strategies are independent of either enclosure shape or clues. Therefore, the acquired data provide robust evidence for the reliance of the crickets on memorizing the layout symmetry of the arena during navigation.

Hence, we suggest that in order to successfully learn to find the target in our experimental setup, the insect has to either employ a non-spatial search strategy (similar to chaining, scanning or random search, or some other movement heuristic; Foucaud et al., 2010) or perform internal reconstruction of the arena shape from previously memorized cues. Even so, if some non-spatial search strategy was employed by crickets in the presented study, such a strategy would have to work well exclusively in symmetric arenas, which seems unlikely considering our current knowledge of non-spatial search routines. For example, the insect could walk in a spiraling

path, further and further from the perimeter of the arena, finally reaching the central point. However, such a strategy would work equally well in all the tested arenas. Such behavior was not observed. Instead, insects tended to briefly visit the perimeter and venture to the center in all the symmetrical arenas. Therefore, our results may be considered supporting evidence for the presence of an internalized representation of space in insects (Giurfa & Capaldi, 1999; Gould, 1986; Menzel et al., 2005; Webb, 2019; Wray, Klein, Mattila, & Seeley, 2008), especially taking into account that neural circuits for the processing of direction were recently discovered (Fisher, Lu, Alessandro, & Wilson, 2019; Kim, Hermundstad, Romani, Abbott, & Jayaraman, 2019).

Supporting, though indirect, evidence for the internalized representation of space could be formulated on the basis of research on the memory capacity of insects (Collett et al., 2013; Mizunami, Weibrecht, & Strausfeld, 1998; Santos-Pata, Escuredo, Mathews, & Verschure, 2018). Tested symmetric arenas are computationally easier to encode (e.g., all walls and angles of a square arena are equal) in comparison to asymmetric quadrilateral arenas (in which all walls and angles differ). Hence, it is possible that a description of the asymmetric quadrilateral arena could exceed the memory capacity of the crickets. Therefore, the observed ability to navigate proficiently in symmetric spatial layouts could be explained as a derivative effect of a limited memory of the internalized representation of space. This potential explanation requires further study.

In order to test the memory-based explanation of the observed effect, it would be reasonable to test the navigational capacity of crickets in arenas of a less complicated shape than the asymmetric quadrilateral one used in the presented study (e.g., rectangular, with two pairs of equally long walls). Moreover, further validation of the proposed navigation models would require additional testing of the ability of crickets to transfer the pre-learned center-finding skill to novel arenas of different, but geometrically regular, shapes. Such a study could reveal another interesting convergence of vertebrate and invertebrate behavior, since Tomassi, Vallortigara and Zanforlin (1997) and Tomassi and Thinus-Blanc (2004) found knowledge transfer in birds and rodents, respectively.

In the context of the debate on navigation models, our results obtained by applying a non-visual paradigm provide data that challenge the visiocentrism predominant in spatial navigation

studies. Both competing theoretical frameworks, namely, GM and VM, are overly focused on visually guided navigation (Hohol et al., 2017). The presented study provides direct evidence for non-visual apprehension of layout symmetry and its utilization in place finding by insects. Furthermore, vision provides access to distal cues, while tactile perception is predominately limited to proximal and momentary (during locomotion) cues (see, however, Yamamoto, Moizumi, & Kitazawa, 2005). Such specificity of tactile perception starkly contrasts with vision and thus VM- and GM-based explanations. Views encompass a large portion of the surroundings of insects at once, providing more comprehensive information about their location. Hence, views do not necessarily require further transformations in order to create a complete representation, but could be processed immediately. Conversely, the GM approach assumes that there is a high-level cognitive mechanism specialized in directly encoding layout geometry solely from visual input, which cannot be penetrated by non-visual information (Cheng, 1986; Gallistel, 1990).

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