



## Bumblebees spontaneously map location of conspecific using geometry and features



Sang Ah Lee, Giorgio Vallortigara\*

Center for Mind/Brain Sciences, University of Trento, Corso Bettini 31, Rovereto, Italy

### ARTICLE INFO

#### Article history:

Available online 14 February 2015

#### Keywords:

Spatial memory  
Navigation  
Reorientation  
Geometry  
Features

### ABSTRACT

Researchers of vertebrate navigation have investigated and debated intensely the existence of independent processes underlying spatial representation of environmental geometry and featural cues (e.g., landmarks). One of the most well-known behavioural instantiations of this dissociation originates from the differences in the way animals map locations in the surrounding environment with respect to the external cues such as boundaries or landmarks. Invertebrate researchers have joined this debate in the past few years, showing that insects can be trained to encode spatial locations using a variety of cues within small enclosures. In the present paper, we test insects in a non-rewarded, spontaneous navigation task. We observed bumblebees' spatial navigation in response to the observed location of a conspecific, over manipulations of cue type and arena size. The results indicate that bumblebees spontaneously use both boundaries and features to guide their spatial behaviour. We discuss the similarities and differences in their behaviours to those of vertebrates and speculate on the implications of these findings.

© 2015 Elsevier Inc. All rights reserved.

Spatial navigation is one of the most widely studied topics across many disciplines of cognitive science. The nature of the cognitive and neural processes underlying spatial behaviour, and the degree to which they may be shared across distantly related species, is a key issue underlying this area of research. In vertebrates, there is converging evidence from studies of spatial behaviour and neural representations for the existence of independent processing of environmental boundaries and landmark features (see Lee & Spelke, 2010). Over the past few years, researchers of insect navigation have challenged the field of vertebrate navigation regarding the necessity to evoke complex cognitive dissociations of features and boundaries, when insects may achieve the same behavioural feat using view-matching processes (Cheng, 2008; Wystrach & Graham, 2012). While we find the engagement of researchers of vertebrates and invertebrate navigation in this discussion of spatial representations to be very important and fruitful, there are some crucial methodological differences that make it difficult to compare across experiments. One of these challenges is that despite the fact that the clearest behavioural evidence for dissociable mechanisms of boundary geometry and features are seen in tests of spontaneous, short-term spatial memory (e.g., Cheng, 1986; Lee, Vallortigara, Ruga, & Sovrano, 2012; Wang, Hermer, & Spelke, 1999), no such study exists for an insect species. Because repeated reinforcement training may involve general mechanisms of response learning not only in mammals (see McDonald & White, 1994; Packard & McGaugh, 1996) but also in other animals, we addressed this problem in the present study using a new spontaneous goal-finding paradigm to test untrained spatial memory in bumblebees.

\* Corresponding author at: Center for Mind/Brain Sciences, University of Trento, Corso Bettini 31, I-38068 Rovereto, Italy.  
E-mail address: [giorgio.vallortigara@unitn.it](mailto:giorgio.vallortigara@unitn.it) (G. Vallortigara).

The formulation of the hypothesis that processing of environmental geometry and non-geometric features is dissociable is credited to Cheng and Gallistel (Cheng, 1986; Cheng & Gallistel, 1984; Gallistel, 1990), who showed in a working-memory task that rats reorient in a rectangular environment in accord with its metrical and sense relations, while often ignoring other cues such as visual contrast patterns and distinctive odours. With reinforcement training in a reference-memory task, rats quickly learn to use those other featural cues to distinguish the target location from its geometric twin; nevertheless, the features were used as local markers, and the rats did not learn relative positions or sense relations between them (Cheng, 1986). These behavioural findings were replicated and expanded upon in various other vertebrate species, ranging from fish, to chicks, to humans (see Cheng & Newcombe, 2005; Tommasi et al., 2012; Vallortigara, 2009 for reviews). All experiments reported a successful use of environmental surface layout geometry, but the findings on features and landmarks were mixed. One important factor was that some experiments, especially those on humans, used untrained, short-term memory tasks (see Lee & Spelke, 2010), while most experiments with animals used reference-memory tasks that involved intensive training and rewarding animals at the goal location, and then transforming the environment and measuring the subjects' responses at test. Because the clearest dissociations between geometry and featural cues were reported in spontaneous tasks, more recent studies have addressed this problem, in order to improve the validity of comparisons across studies and species (Lee, Spelke, & Vallortigara, 2012; Lee, Vallortigara, et al., 2012; Lee, Vallortigara, Flore, Spelke, & Sovrano, 2013).

An interesting aspect of the dissociation between geometric and featural cues is that all vertebrate species (e.g., fish: Sovrano, Bisazza, & Vallortigara, 2007; chicks: Chiandetti, Regolin, Sovrano, & Vallortigara, 2007; Vallortigara, Feruglio, & Sovrano, 2005; monkeys: Gouteux, Thinus-Blanc, & Vauclair, 2001; humans: Learmonth, Nadel, & Newcombe, 2002; Learmonth, Newcombe, Sheridan, & Jones, 2008) tested so far exhibit a tendency to rely heavily on distal features (e.g., in a large testing space) and on proximal boundary geometry (e.g., in a smaller testing space). There are several proposed explanations of such an effect that focus on visual encoding of cues (e.g., Sovrano & Vallortigara, 2006). However, neural evidence from rodents shows that while only distal landmarks are effective in influencing the firing of place cells and head-direction cells (Cressant, Muller, & Poucet, 1997; Zugaro, Berthoz, & Wiener, 2001), proximal environmental boundaries are more effective in determining the firing of boundary cells in the hippocampal formation of rats (Lever, Burton, Jeewajee, O'Keefe, & Burgess, 2009; Solstad, Boccara, Kropff, Moser, & Moser, 2008), suggestive of a more detailed account at the level of representations. While there is not yet a definitive explanation for the room size effect in reorientation behaviour, its prevalence across vertebrates may offer important insights as to the nature of the dissociation between boundary geometry and features.

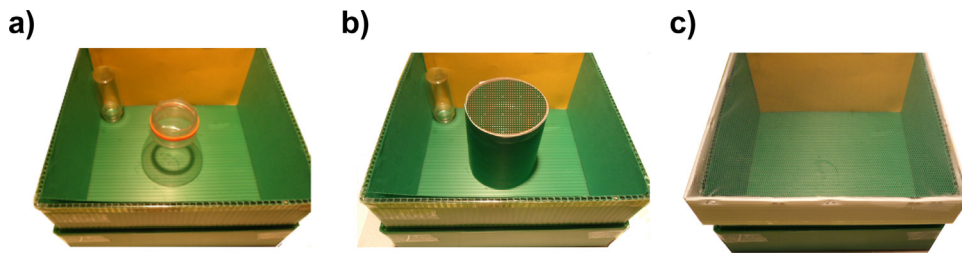
Insect navigation research has a long history that parallels work on rodents, dating back to Tinbergen's documentation of the homing behaviour and landmark use of digger wasps (Tinbergen, 1932). Around the same time as Cheng and Gallistel's (1984) formulation of their modular theory of vertebrate navigation, Collett and Cartwright (1983) offered a theory of a view-based image-matching process in insects. While there have been significant findings and alternate claims regarding insect navigation mechanisms over the years (e.g., Menzel et al., 2005), only in the last few years has the field of insect navigation truly made contact with studies of geometry and landmarks in vertebrates. For instance, experiments carried out with ants showed that they, like vertebrates, learn to use rectangular arena shape, making rotational errors between the two geometrically identical corners (Wystrach & Beugnon, 2009; Wystrach, Cheng, Sosa, & Beugnon, 2011). When provided with featural landmarks, ants are able to use this information to correct their rotational errors. While various versions of view-matching theory now exist (Baddeley, Graham, Philippides, & Husbands, 2012; Collett, Chittka, & Collett, 2013; Wystrach, Mangan, Philippides, & Graham, 2013), insect researchers have proposed that such processes are simpler and may be able to replace more complex theories of spatial cognition that make categorical distinctions between environmental cues (Cheng, 2008; Wystrach & Graham, 2012).

While it is a bold yet attractive idea that vertebrate navigation may be explained by processes available to insects, a major limitation is that while the strongest behavioural evidence for separate boundary and feature coding in vertebrates comes from spontaneous reorientation tasks requiring more flexible spatial representations, reorientation tests in insects thus far have all implemented a reinforcement learning paradigm.

In the present study we tested a species within the family *Apidae*, whose cognitive and orientation capacity have been widely studied (e.g., Menzel & Giurfa, 2001; Srinivasan, 2010). Recent experiments have shown that disoriented bumblebees (*Bombus terrestris*) can learn to find a goal in small enclosed spaces using both geometrical and featural cues (Sovrano, Potrich, & Vallortigara, 2013; Sovrano, Rigosi & Vallortigara, 2012). The goal of the present experiments is twofold: The first is to provide the first test of spontaneous, unreinforced spatial reorientation by geometry and features in insects, by harnessing the tendency of bumblebees in small, enclosed arenas to approach the last seen location of a conspecific (see Kawaguchi, Ohashi, & Toquenaga, 2006). The second is to provide insight into the underlying mechanisms of spatial memory in bumblebees by manipulating the size of the arenas.

## Material and methods

In this study, we tested bumblebees' spontaneous exploration of the last observed location of a conspecific, following a brief delay during which they were disoriented by covered rotation. Experiment 1 tested spatial memory using environmental geometry in rectangular arenas of two different sizes. Experiment 2 tested feature use in square arenas of two different sizes with one wall differing in colour.



**Fig. 1.** Depiction of testing setup and procedures. (a) Bumblebees were first allowed to observe the arena from a central transparent cylinder, with a conspecific in a small glass vial in one corner of the arena. (b) They were then covered with an opaque cup and rotated for disorientation. (c) Subjects were released into an empty arena with a netted cover, and their approaches to the four corners of the arena were observed for 30 s.

### Subjects

Colonies of bumblebees (*Bombus terrestris*) were supplied by Bioplanet s.c.a. (Cesena, Italy). The nest was kept within a small tent in an isolated laboratory, kept constant at 25 °C and exposed to natural daylight. Animals were provided with pollen and honey-water solution ad libitum. Eighty female worker bees were tested in total, forty in each experiment. An equal number of bees were tested at each of the corners (ten subjects per corner); each bee was tested only once.

### Apparatus

All experimental arenas were made of green plastic sheets and were 8 cm in height; each arena also had a fitted cover, consisting of netting on top. The two rectangular arenas tested in Experiment 1 had the same aspect ratio (0.6 between short and long side) but differed in size (base areas differing by a ratio of 4). The small arena was 7 cm × 11.5 cm at the base; the larger arena was 14 cm × 23 cm. Experiment 2 also tested two arenas; the small square arena had base dimensions 8 cm × 8 cm, and the larger, 16 cm × 16 cm. One entire wall of each arena was yellow-orange (featural cue), distinct against the otherwise green arena. This colour was chosen because preliminary tests found that bees have a strong attraction to other salient colours (e.g., white, purple) or visual patterns (e.g., stripes, checkerboard) as the featural cue. Each testing arena was enclosed within an insect rearing tent made of polyester and vinyl (60 cm in width, 60 cm high), with netted holes through which the experimenter could insert her arms. A camera was positioned over the tent in order to record the tests, and a single, incandescent light bulb above the tent was used to illuminate the environment. Inside the tent, artificial flowers, food and pollen were scattered about randomly on the ground. The experimental room that housed the tent and the testing apparatus was otherwise dark and unoccupied.

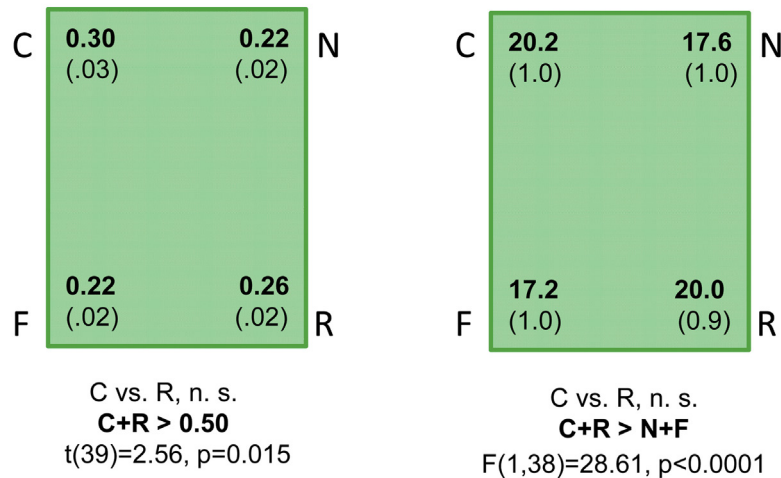
### Procedures

Each subject was released in the tent to habituate for about 10 min before starting the test. The bumblebee was then tested for ten trials with a 2-min inter-trial-interval. For both Experiments 1 and 2, each trial required the same procedure. First, the bumblebee was caught and placed at the centre of the test arena in a small transparent cylinder (6 cm wide, 6.5 cm high) from which it could visually explore the arena. A transparent glass tube housing another bumblebee was positioned at one corner of the arena. After a period of 1 min during which the subject was allowed to observe the environment and the conspecific, the cylinder was covered with an opaque cover so that the subject could no longer see, and the tube containing the conspecific was removed from the corner. The subject was disoriented by inserting a thin sheet of paper under the covered cylinder, then rotating the paper (along with the cylinder and the bee) both clockwise and counterclockwise for about 10 s. On each trial, the box was rotated 90° clockwise from its previous orientation, to counteract the use of any extra-arena cues. After disorientation, the cylinder was lifted from the subject and removed from the arena, and the subject was trapped in the empty arena by quickly placing the netted cover over it. The approaches to the corners made by the subject in the arena were recorded by the video camera for 30 s. The target corner (position of the conspecific) was varied across subjects but held constant during all trials within a subject, although without any reinforcement (no conspecific visible during the 30-s approach phase) (Fig. 1).

### Coding

Offline coding was performed by one experimenter; a second encoding was performed by a second experimenter on a random sample of the video recordings. Inter-coder reliability was above 90%. For trials in which there was a discrepancy, the two coders watched the video clip together and reached an agreement. An approach to a corner was defined as entering an area of 2 cm × 2 cm in each corner of the small enclosures, and 4.5 cm × 4.5 cm for the large enclosures.

a) First Choice Proportions      b) Total Approaches in 30s



**Fig. 2.** Results of geometry test in Experiment 1. (a) Proportions of first approaches to each corner (SEM in parentheses) of the rectangular arenas are shown above, along with a test of correct geometry use, comparing the proportions of first approaches to the two geometrically correct corners to a chance level of 0.50. (b) Total approaches to each corner of the rectangular arenas in the 30-s period thereafter are provided (SEM in parentheses), along with a test comparing number of approaches to the two geometrically correct corners vs. incorrect corners. Because the goal corner was varied, the data have been rotated to represent the correct corner (C), its rotationally symmetric corner (R), the near geometrically incorrect corner (N), and the far incorrect corner (F). Comparisons between C vs. R show that bumblebees did not discriminate between the correct corner and the rotationally symmetric corner, indicating successful disorientation and the absence of uncontrolled external cues.

### Experiment 1

Experiment 1 tested bumblebees' spontaneous use of boundary geometry – the long and short walls of the arena – in rectangular arenas of two different sizes.

#### Results and discussion

A univariate ANOVA was conducted with proportions of geometric first choices (to the correct + rotationally symmetric corners) as the dependent variable and size of the arena (small vs. large) as the between-subjects variable. There was no effect of arena size ( $F < 1$ , n.s.). When the proportion of geometrically correct first choices was compared against the chance level of 0.50, we found that bumblebees significantly preferred the corners with the same geometric properties as the last-seen location of a conspecific ( $t(39) = 2.56, p = 0.015$ ) (see Fig. 2). The bumblebees did not discriminate between the correct corner and its geometric equivalent ( $t(39) = 1.05, p = 0.3$ ), ensuring that the disorientation procedure was effective and that the bumblebees could not use any uncontrolled cues to break the environmental symmetry.

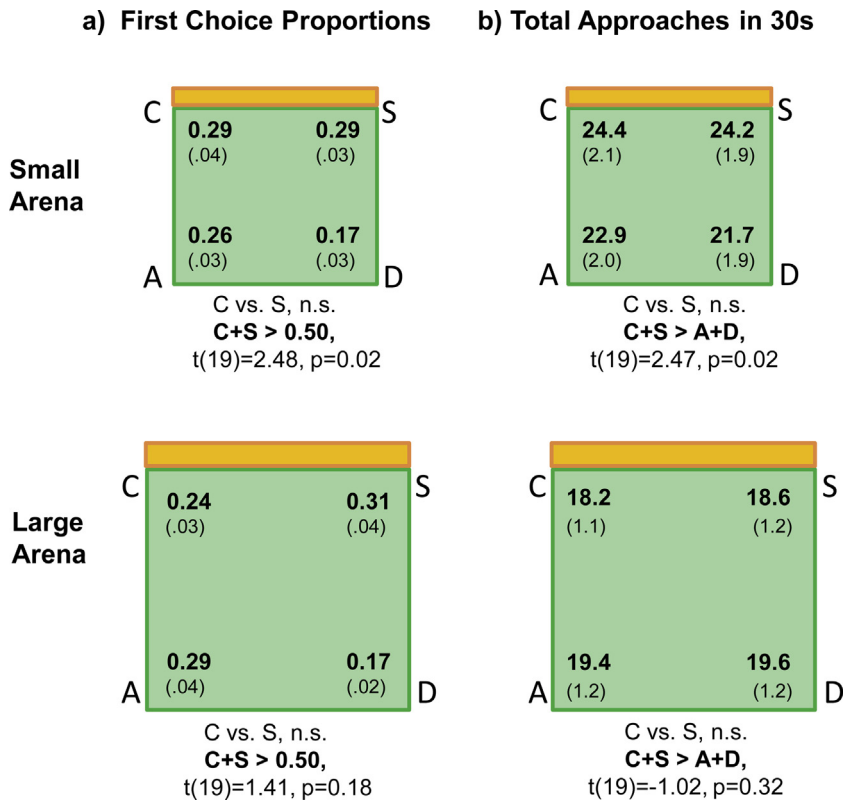
For the total number of approaches within the 30-s period, a repeated measures ANOVA was conducted with geometry as the within-subject variable (geometrically correct vs. incorrect) and arena size (small vs. large) as the between-subjects variable. A significant effect of geometry was found  $F(1,38) = 28.61, p < 0.0001$ , with the geometrically correct corners preferred over the incorrect corners. There was no interaction of geometry use with arena size ( $F < 1$ , n.s.). No significant difference was found between the correct corner and its geometric equivalent, providing further evidence for disorientation ( $t < 1$ , n.s.).

### Experiment 2

Experiment 2 tested bumblebees using the same procedures as Experiment 1 but in square arenas of two different sizes consisting of one distinctively coloured wall as the feature cue.

#### Results and discussion

A univariate ANOVA was conducted with proportions of first choices to the four corners as the dependent variable and size of the arena (small vs. large) and goal distance from feature (along orange wall vs. along green walls) as the between-subjects variables. There were no significant between-subjects effects. Overall, bumblebees preferred the two corners with the correct features (e.g., the two all-green corners if the target corner was an all-green corner),  $t(39) = 2.72, p = 0.01$  (see Fig. 3). Nevertheless, they did not discriminate between the correct corner and the corner with similar features ( $t < 1$ , n.s.), suggesting that they could neither use the feature as a relative positioning cue nor distinguish between the mirror image



**Fig. 3.** Results of feature test in Experiment 2. (a) Proportions of first approaches to each corner of the square arena (SEM in parentheses) with one orange-coloured wall are shown above, along with a test of using the colour feature as a local marker, comparing the proportions of first approaches to the two featurally similar corners to a chance level of 0.50. (b) Total approaches to each corner in the 30-s period thereafter are provided (SEM in parentheses), along with a test comparing number of approaches to the two featurally similar corners vs. featurally incorrect corners. Because the goal corner was varied, the data have been rotated to represent the correct corner (C), the featurally symmetric corner (S), the adjacent corner with the incorrect feature (A), and the diagonal corner with the incorrect feature (D). Results for the smaller and larger arenas are shown separately (not scaled to size). There were no differences between C and S, indicating a failure to use the featural cue as a directional, relative positioning cue to break the mirror symmetry.

corners with orange-green vs. green-orange features. Moreover, the proportion of their approaches to the correct corner (mean =  $0.26 \pm 0.02$ ) did not exceed a chance level of 0.25 ( $t < 1$ , n.s.).

For total number of approaches within the 30-s period, a repeated measures ANOVA was conducted with the four corners as the within-subject variable and arena size (small vs. large) and goal distance from feature (along orange wall vs. all green walls) as the between-subjects variables. A significant Corner  $\times$  Size interaction was found ( $F(3,108) = 2.77, p = 0.045$ ). A significant between-subjects main effect of size was found ( $F(1,36) = 4.878, p = 0.034$ ), showing that there were more corner approaches in the smaller arena than the larger one in the 30-s period, as would be expected given the difference in navigable space. No other main effects or interactions were found.

When separate ANOVAs were conducted for the large and the small arenas, surprisingly, significant differences among corners only held for the small arena ( $F(3,54) = 2.95, p = 0.041$ ), and not for the larger arena ( $F < 1$ , n.s.). In the small arena, bumblebees discriminated the corners near the orange feature and the all-green corners ( $t(19) = 2.47, p = 0.023$ ), but did not distinguish the correct corner over the featurally similar one ( $t < 1$ , n.s.) (see Fig. 3).

## Conclusions

This study provides the first demonstration that bumblebees successfully use both geometry and features to spontaneously encode and approach the last seen location of a conspecific. These results once again show that insects, despite their small brains, are capable of complex, on-line spatial processing, even without any reinforcement training. Interestingly, there was no effect of arena size on geometry, along with a significant effect of arena size on the use of the wall colour feature *but* in the opposite direction from what has been reported in vertebrates (i.e., stronger reliance on features in larger arenas), providing initial evidence that the underlying mechanisms that guide place finding in bumblebees may be distinct from those of vertebrates. Although the finding on better feature use in the smaller arena (compared to the larger arena) was only significant in the 30-s total approach measure and should be interpreted cautiously, even in the small arena, bumblebees only used the feature to distinguish between the corners near the feature from those distal from the feature, without discriminating the mirror-image corners from one another. This result has an interesting implication for

theories of insect navigation by snapshots. It seems that no simple snapshot representations of corners (orange–green vs. green–orange) guided the bumblebees' place coding; rather, the orange feature seems to have been used more like a beacon or an associative near/far cue to location.

What could be driving this suggestive difference in behaviour between the small and large arenas in the feature condition? While it is not clear, there are a few possibilities that could be discussed. First, it is possible that in the larger arena, the target conspecific was more difficult to see. While in the geometry condition the green background made the conspecific bumblebee easily visible, in the feature condition there was an orange background for half of the subjects, making the target less visible for those subjects. However, this is not a very convincing explanation because if it were the case, there should be a difference in performance in the subjects who had the target at the orange wall vs. those who had the target at the green wall. Another possibility is that for the bumblebees in this enclosure-based spontaneous task, a featural cue is more effectively remembered if immediately available in the vicinity.

The contrasting effect of arena size in bees and vertebrates seems to suggest that there may indeed be fundamental differences between insect and vertebrate spatial coding that must be taken into account in considering the existence of shared abilities. Future experiments clarifying the exact nature of the neural representations underlying insect navigation will be crucial to this end.

## Acknowledgments

This paper is partly based on experiments which were part of Caterina Magri's undergraduate thesis. We would like to thank Caterina Magri, Sara Forti, and Francesco Cerri for their help in conducting these experiments. This research was funded by a research fellowship to S.A.L. from the University of Trento.

## References

- Baddeley, B., Graham, P., Philippides, A., & Husbands, P. (2012). A model of ant route navigation driven by scene familiarity. *PLOS Computational Biology*, 8, e1002336.
- Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition*, 23, 149–178.
- Cheng, K. (2008). Whither geometry? Troubles of the geometric module. *Trends in Cognitive Sciences*, 12, 355–361.
- Cheng, K., & Gallistel, C. R. (1984). Testing the geometric power of an animal's spatial representation. In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.), *Animal Cognition: Proceedings of the Harry Frank Guggenheim conference* (pp. 409–423). Hillsdale, NJ: Erlbaum.
- Cheng, K., & Newcombe, N. (2005). Is there a geometric module for spatial orientation? Squaring theory and evidence. *Psychonomic Bulletin and Review*, 12, 1–23.
- Chiandetti, C., Regolin, L., Sovrano, V. A., & Vallortigara, G. (2007). Spatial reorientation: The effects of space size on the encoding of landmark and geometry information. *Animal Cognition*, 10, 159–168.
- Collett, T. S., & Cartwright, B. A. (1983). Eidetic images in insects: Their role in navigation. *Trends in Neurosciences*, 6, 101–105.
- Collett, M., Chittka, L., & Collett, T. (2013). Spatial memory in insect navigation. *Current Biology*, 23, R789–R800.
- Cressant, A., Muller, R. U., & Poucet, B. (1997). Failure of centrally placed objects to control the firing fields of hippocampal place cells. *Journal of Neuroscience*, 17, 2531–2542.
- Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.
- Gouteux, S., Thinus-Blanc, C., & Vauclair, J. (2001). Rhesus monkeys use geometric and nongeometric information during a reorientation task. *Journal of Experimental Psychology: General*, 130, 509–519.
- Kawaguchi, L. G., Ohashi, K., & Toquenaga, Y. (2006). Do bumble bees save time when choosing novel flowers by following conspecifics? *Functional Ecology*, 20, 239–244.
- Learmonth, A. E., Nadel, L., & Newcombe, N. (2002). Children's use of landmarks: Implications for modularity theory. *Psychological Science*, 13, 337–341.
- Learmonth, A. E., Newcombe, N. S., Sheridan, N., & Jones, M. (2008). Why size counts: Spatial reorientation in large and small enclosures. *Developmental Science*, 11, 414–426.
- Lee, S. A., & Spelke, E. S. (2010). Two systems of spatial representation underlying navigation. *Experimental Brain Research*, 206, 179–188.
- Lee, S. A., Spelke, E. S., & Vallortigara, G. (2012). Chicks, like children, spontaneously reorient by three-dimensional environmental geometry, not by image matching. *Biology Letters*, 8, 492–494.
- Lee, S. A., Vallortigara, G., Flore, M., Spelke, E. S., & Sovrano, V. A. (2013). Navigation by environmental geometry: The use of zebrafish as a model. *Journal of Experimental Biology*, 216, 3693–3699.
- Lee, S. A., Vallortigara, G., Ruga, V., & Sovrano, V. A. (2012). Independent effects of geometry and landmark in a spontaneous reorientation task: A study of two species of fish. *Animal Cognition*, 12, 661–670.
- Lever, C., Burton, S., Jeewajee, A., O'Keefe, J., & Burgess, N. (2009). Boundary vector cells in the subiculum of the hippocampal formation. *Journal of Neuroscience*, 29, 9771–9777.
- McDonald, R. J., & White, N. M. (1994). Parallel information processing in the water maze: Evidence for independent memory systems involving dorsal striatum and hippocampus. *Behavioral and Neural Biology*, 61, 260–270.
- Menzel, R., & Giurfa, M. (2001). Cognitive architecture of a mini-brain: The honeybee. *Trends in Cognitive Sciences*, 4, 59–65.
- Menzel, R., Greggers, U., Smith, A., Berger, S., Brandt, R., Brunke, S., et al. (2005). Honeybees navigate according to a map-like spatial memory. *Proceedings of the National Academy of Sciences*, 102, 3040–3045.
- Packard, M. G., & McGaugh, J. L. (1996). Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. *Neurobiology of Learning and Memory*, 65, 65–72.
- Solstad, T., Boccara, C. N., Kropff, E., Moser, M., & Moser, E. I. (2008). Representation of geometric borders in the entorhinal cortex. *Science*, 322, 1865–1868.
- Sovrano, V. A., Bisazza, A., & Vallortigara, G. (2007). How fish do geometry in large and in small spaces. *Animal Cognition*, 10, 159–168.
- Sovrano, V. A., Potrich, D., & Vallortigara, G. (2013). Learning of geometry and features in bumblebees (*Bombus terrestris*). *Journal of Comparative Psychology*, 127, 312–318.
- Sovrano, V. A., Rigosi, E., & Vallortigara, G. (2012). Spatial reorientation by geometry in bumblebees. *PLoS ONE*, 7, e37449.
- Sovrano, V. A., & Vallortigara, G. (2006). Reorientation by geometric and landmark information in environments of different size. *Developmental Science*, 8, 393–401.
- Srinivasan, M. V. (2010). Honey bees as a model for vision, perception, and cognition. *Annual Review of Entomology*, 55, 267–284.
- Tinbergen, N. (1932). Über die orientierung des bienenwolfes (*Philanthus triangulum* Fabr.). *Zeitschrift für vergleichende Physiologie*, 16, 305–335.

- Tommasi, L., Chiandetti, C., Pecchia, T., Sovrano, V. A., & Vallortigara, G. (2012). From natural geometry to spatial cognition. *Neuroscience and Biobehavioral Reviews*, *36*, 799–824.
- Vallortigara, G. (2009). Animals as natural geometers. In L. Tommasi, L. Nadel, & M. Peterson (Eds.), *Cognitive biology: Evolutionary and developmental perspectives on mind, brain and behavior* (pp. 83–104). Cambridge, MA: MIT Press.
- Vallortigara, G., Feruglio, M., & Sovrano, V. A. (2005). Reorientation by geometric and landmark information in environments of different size. *Developmental Science*, *8*, 393–401.
- Wang, R. F., Hermer, L., & Spelke, E. S. (1999). Mechanisms of reorientation and object localization by children: A comparison with rats. *Behavioral Neuroscience*, *113*, 475–485.
- Wystrach, A., & Beugnon, G. (2009). Ants learn geometry and features. *Current Biology*, *19*, 61–66.
- Wystrach, A., Cheng, K., Sosa, S., & Beugnon, G. (2011). Geometry, features, and panoramic views: Ants in rectangular arenas. *Journal of Experimental Psychology: Animal Behavioral Processes*, *37*, 420–435.
- Wystrach, A., & Graham, P. (2012). What can we learn from studies of insect navigation? *Animal Behaviour*, *84*, 13–20.
- Wystrach, A., Mangan, M., Philippides, A., & Graham, P. (2013). Snapshots in ants? New interpretations of paradigmatic experiments. *Journal of Experimental Biology*, *216*, 1766–1770.
- Zugaro, M. B., Berthoz, A., & Wiener, S. I. (2001). Background, but not foreground, spatial cues are taken as references for head direction responses by rat anterodorsal thalamus neurons. *Journal of Neuroscience*, *21*, RC154.