

CONTRIBUTED PAPER

# Multiscale Modeling in Neuroethology: The Significance of the Mesoscale

Julia R. S. Bursten<sup>1</sup>  and Kelle Dhein<sup>2</sup> 

<sup>1</sup>University of Kentucky, Lexington, KY, USA and <sup>2</sup>Santa Fe Institute, Santa Fe, NM, USA

**Corresponding author:** Kelle Dhein; Email: [kelle@santafe.edu](mailto:kelle@santafe.edu)

(Received 13 January 2023; accepted 18 January 2023)

## Abstract

Recent accounts of multiscale modeling investigate ontic and epistemic constraints imposed by relations between component models at varying relative scales (macro, meso, micro). These accounts often focus especially on the role of the meso, or intermediate, relative scale in a multiscale model. We aid this effort by highlighting a novel role for mesoscale models: functioning as a focal point, and explanation, for disagreement between researchers who otherwise share theoretical commitments. We present a case study in multiscale modeling of insect behavior to illustrate, arguing that the cognitive map debate in neuroethology research is best understood as a mesoscale disagreement.

## 1. Introduction

Understanding animal behavior is a complex and multidisciplinary scientific undertaking that requires coordination of multiple research methodologies and conceptual frameworks, as well as the sourcing and analysis of information from multiple types of theoretical models and experimental schemata. Neuroethology is a disciplinary framework in animal behavior research that studies the neurophysiological basis of behavior in animals. In this article, we apply results from recent philosophical accounts of multiscale modeling to the task of analyzing a central debate in neuroethology: Do insects use a cognitive map to navigate? This debate stands in for a larger conceptual disagreement in neuroethology about the relative contributions of instinct and learning in shaping animal behavior.

A new generation of philosophical accounts of multiscale modeling from authors including Bursten (2018), Batterman and Green (2021), Jhun (2021), Batterman (2021), Rice (2021), and Shech and McGivern (2021) have drawn attention to the complex landscape of ontic and epistemic constraints imposed by the relations between the component models at varying relative scales (macro, meso, micro). In particular, Batterman and Green (2021) and Batterman (2021) have argued that concepts arising

at the mesoscale, as opposed to micro- or macroscales, can serve as a locus of scientific knowledge that earlier accounts of scientific modeling overlooked.

Here we show that the cognitive map debate in neuroethology is best understood as a disagreement about what mesoscale model is appropriate to model a multiscale phenomenon. Interpreting the disagreement as a mesoscale disagreement provides two distinct benefits. First, it advances philosophical and historical understanding of animal behavior research by providing an explanation of how the disagreement arises and why it involves such distinct research programs among groups of researchers who agree on so much. Second, it contributes to the literature on multiscale modeling by investigating a novel way in which attention to mesoscale models can contribute to philosophical understanding of scientific knowledge production.

We proceed as follows. In section 2, we introduce the cognitive map debate. Section 3 characterizes this debate as a mesoscale disagreement between research communities who agree on ontology, mechanisms, and methodology at the macro- and microscales. Section 4 lays out the implications of this characterization for understanding the cognitive map debate, while section 5 discusses implications for philosophical accounts of multiscale modeling. Section 6 concludes.

## 2. The cognitive map debate in neuroethology

Neuroethologists seek causal explanations of how neurosensory mechanisms generate and control naturally occurring behavior in naturally occurring contexts (Dhein 2022). As the name suggests, it combines elements of ethology and neurophysiology. Like neurophysiologists, neuroethologists use laboratory experiments to investigate the relationship between phenomena at the neuronal level and phenomena at higher levels of analysis like the muscular and behavioral levels. Like ethologists, neuroethologists also perform field experiments that allow freely moving animals to express behavioral traits in naturally occurring contexts. The discipline emerged in Europe in the 1960s and 1970s.

Insects have been important experimental subjects for neuroethologists since the field's inception (Dhein 2022; Hoyle 1970; Ronacher 2019), and a long-standing debate within insect neuroethology concerns modeling and explaining insect navigation (Dhein 2023). Historically, neuroethologists focused on behavioral traits that were relatively stereotyped and reproducible in laboratory settings (e.g., a toad shooting its tongue at prey, a fish's rhythmic fin movement, or a cricket singing). This focus on seemingly innate patterns of behavior provided pragmatic advantages to neuroethologists and reflected ethology's traditional emphasis on instinctive behavior over learned behavior. Neuroethological studies on eusocial insect navigation broke with that trend by reemphasizing learning.

As central place foragers, ants and honeybees exhibit remarkably flexible navigation behavior that allows them to travel vast distances in search of resources before returning to their nest. As studies into ant and honeybee navigation progressed, scientists realized how integral learning and memory are to successful foraging. What remains unclear, however, is how exactly learning and memory figure into navigation. That question has become the crux of a decades-long debate over whether insects like ants and honeybees possess a cognitive map.

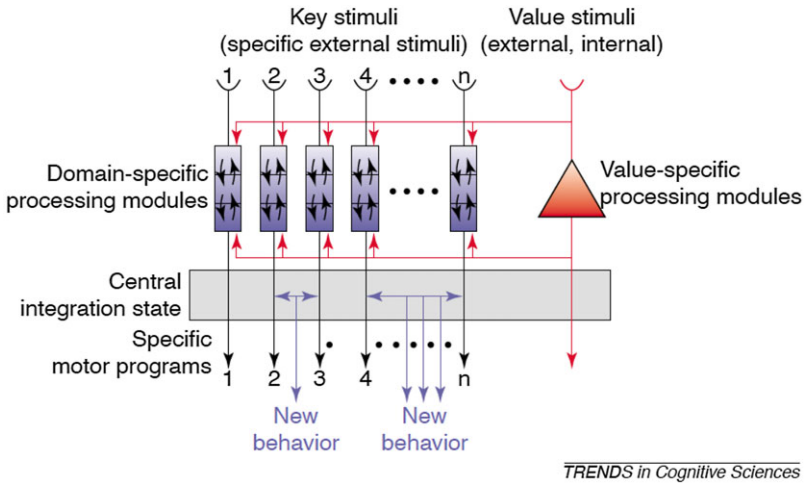


Figure 1. Example of a cognitive-map model of an insect brain (Menzel and Giurfa 2001).

The cognitive map model of insect navigation (see figure 1) holds that insects integrate memories of their environment into a sophisticated, maplike representation using some central processing mechanism in the brain. The representation is maplike because it uses an allocentric frame of reference. That is, it represents objects relative to an environment that is independent of the navigator. The mechanism underlying the cognitive map is supposed to be “central” in the sense that it collects and integrates input from disparate sensory modalities and cognitive subroutines. According to the cognitive map model, insects use their cognitive map to deliberate about where they are and where to go next. An important consequence of this model is the supposition that successful navigation cannot occur without an ability to answer the question, “Where am I?”

The main competitor to the cognitive map model is the toolkit model (see figure 2). The toolkit model maintains that ants and honeybees process neurosensory representations of their environment using multiple task-specific brain mechanisms that run in parallel. The outputs of these mechanisms are then weighted and pooled downstream to determine where the navigator will go next. Unlike the cognitive map model, the toolkit model does not require an answer to “Where am I?” Instead, it supposes that neurosensory representations remain distributed across various nonintegrated processing mechanisms, and only the outputs of those mechanisms are integrated into behavioral commands. In other words, navigators only need answer the question, “Where to go next?”

Although participants do not explicitly frame the cognitive map debate in terms of instinct versus learning, there are historical ties and conceptual affinities linking the cognitive map debate to twentieth-century debates about the relative contributions of instinct versus learning to animal behavior (Dhein 2023). The cognitive map model aligns with American psychology’s learning-heavy approach to theorizing about animal behavior, while the toolkit model aligns with German ethology’s instinct-heavy approach. These influences are evident in the way competing models depict the

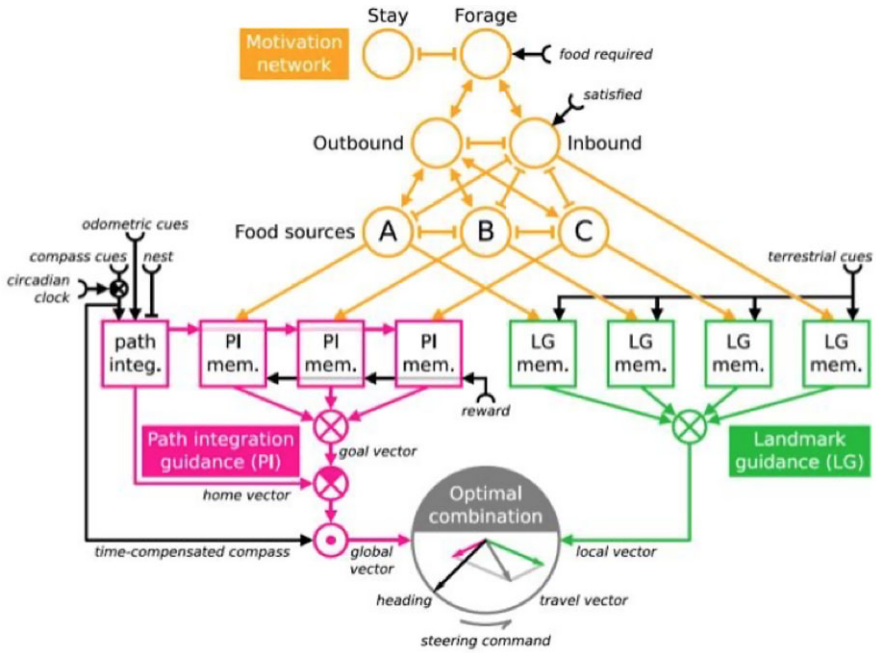


Figure 2. Example of a toolkit model of the cognitive processes underlying *Cataglyphis* navigation (Hoinville and Wehner 2018, 2825).

relationship between (1) motivation and memory and (2) different task-specific navigational subroutines:

- *Motivation and Memory*: One navigational strategy used by ants involves memorizing visual landmarks. In the toolkit model, motivations determine which memories influence behavior: An ant’s memory of a visual landmark is associated with a particular motivational state (e.g., inbound foraging from a food source). Once a landmark memory has been activated by the appropriate motivational state, the ant compares a remembered view with her current view. The landmark guidance mechanism then estimates the similarity between the remembered and current view to output a command to navigate in the most visually familiar direction. In this example, internal states interact with stimuli to selectively trigger procedural memories in a way that is reminiscent of classical ethological theories of instinct. Contrariwise, in the cognitive map model, motivation and memory are less connected. An ant’s cognitive map contains the same learned information regardless of the motivational state that drove her to consult the map. The forager brings her motivations to a maplike buffet of memories and deliberates about how to achieve her goal using those memories.
- *Task-Specific Subroutines*: Both models recognize that insects possess multiple navigational strategies, like landmark guidance and path integration, and that

these strategies work in tandem. However, in the toolkit model, the cognitive subroutines responsible for implementing these strategies are siloed off from one another. For example, the landmark guidance subroutine does not interact with any other subroutine until it has output a command for where to go next. This command is then sent to a hypothesized “optimal combination” mechanism that integrates the command with commands produced by other subroutines implementing different navigational strategies. Alternatively, in the cognitive map model, it is not commands for action that get integrated; it is memories about environmental features that get integrated to form the cognitive map. This sort of integration presupposes sophisticated learning and memory manipulation: the navigator is constantly maintaining and updating a comprehensive representation of their environment. It also presupposes a more centralized cognitive architecture. States of affairs are less directly connected to actions in the sense that a navigator must first locate themselves on the cognitive map and then deliberate about where to go before deciding on an action command.

It remains an open question in neuroethology whether insects navigate using a cognitive map. Underlying this question is a longer-standing disagreement about the extent to which instinct and learning shape behavior. In the following text we frame the cognitive map question, and the larger disagreement, as a disagreement about how to explain behavior at the mesoscale.

### 3. The cognitive map debate as mesoscale disagreement

Neuroethologists aim to explain behavior in terms of neurophysiological mechanisms that exist at various spatial scales, from the microscale of neurons to the macroscale of organismal movement. As a result, multiscale modeling in neuroethology is widespread. Strikingly, in the cognitive map debate, there is a high degree of agreement about how to model phenomena at the micro- and macroscales.

At the microscale, both cognitive-mappers and toolkit-modelers agree about how to model cellular components of the insect nervous system. They also agree about the structural organization of the insect nervous system. That is, they agree on, and share, models of the neuron and of insect brains. This agreement leaks into each side’s account of the causal mechanisms responsible for microscale processes: Both sides generally agree about what brain structures are most likely responsible for performing the cognitive functions posited in the cognitive map and toolkit models. Both sides believe that two prominent neuropils (called the mushroom bodies) play a major role in forming memories and integrating sensory input from different modalities (Menzel 2014; Wehner 2020, 250–51).

Further, there is broad consensus that a neural structure called the central complex is responsible for integrating information relevant to navigation and forming motor commands (Hensgen et al. 2021, 160; Wehner 2020, 139–147). Intracellular electrophysiological recordings are a well-established method for localizing cognitive functions to neural structures. However, the small brains of ants and honeybees make them poorly suited to this method (Menzel 2004, 465; Wehner

2020, 140). As a result, researchers have often used findings from intracellular recordings on bigger-brained insects, like locusts, to inform their models of ant and honeybee brains.

There is also significant agreement between camps at the macroscale. There, scientists rarely challenge the veridicality of models representing the movements of insects in each other's navigation experiments.<sup>1</sup> Scientists also generally agree about how to model the routes of foraging ants and honeybees, though conventions for modeling insect movement have changed with improved tracking technologies. For instance, prior to the 2000s, researchers could not directly track the flight paths of bees. To model long-distance flight paths, neuroethologists recorded how long it took honeybees to fly between observation points and relied on vanishing bearings (the direction a honeybee was flying before the observer lost sight of the bee) to infer actual flight paths. Vanishing bearings were modeled with a single point in the center of a circle. The point represented the observer, and the arrows disseminating out from the point represented the direction of departing bees. Then, scientists devised a way to track honeybee flight paths with harmonic radar (see Osborne et al. 1997 for the introduction of the method; see Menzel et al. 2005 for its use in the cognitive map debate). This led to models that represented honeybee flight paths as multicolored clouds overlaid on satellite maps. Different colors within the cloud represent different probabilities of a bee being at that location.

Both cognitive mappers and toolkit modelers currently employ this strategy for modeling the flight paths of honeybees. However, the two sides use these new macroscale models differently. Cognitive mappers designed harmonic-radar tracking experiments to provide decisive evidence for (or against) the cognitive map hypothesis. They argued that models representing the flight paths of honeybees in their experiments affirmed that honeybees use a cognitive map to plan novel shortcuts and make decisions about what navigational goals to pursue (Menzel et al. 2005).

To undercut those arguments, toolkit modelers performed proof-of-concept demonstrations that showed their toolkit model could account for the flight paths of honeybees in the cognitive map side's experiments. These demonstrations consisted of an artificial neural network that simulated an agent's navigation behavior according to the principles of the toolkit hypothesis. When toolkit modelers subjected their simulated navigator to the same navigation problem to which the cognitive map side had subjected honeybees, the simulated navigator moved along the same paths as the honeybees.

This research strategy indicates that while both sides of the debate share a common pool of macroscale models representing the navigation routes of insects under various experimental circumstances, they still interpret those models differently. While both sides agree on the relevant structures and causal processes at the micro- and macroscale, they disagree on *how* structures and processes at the microlevel interact to determine macrolevel phenomena. More specifically, they disagree about how cellular components of the nervous system interact to determine navigation behavior.

---

<sup>1</sup> For a rare exception, see responses to Gould 1986; Cartwright and Collett 1987; Dyer and Seeley 1989; Wehner and Menzel 1990.

Both sides posit sensory processing mechanisms that consist of networks of neurons. These are often functional models, as opposed to structural models aiming to veridically represent actual networks of neurons in the brains of ants and honeybees. Nonetheless, both the cognitive map and the toolkit are mesoscale models of insect navigation behavior: They are conceptual, mechanistic models that posit assemblies of processes (such as path integration or motivational state activation) that mediate between the microscale firing of neurons and the macroscale movement of insects through space.

Thus, the disagreement between cognitive mappers and toolkit modelers is a disagreement about what mesoscale model appropriately mediates between neurons and navigation.

#### 4. Implications for cognitive map debate

Recognizing the cognitive map debate as a disagreement at the mesoscale provides a novel perspective on the stakes of the debate both for neuroethologists and for historians and philosophers of science. A preliminary upshot of recognizing the debate as a mesoscale disagreement is that it helps explain why two groups of researchers who agree on so much are in disagreement at all. In the remainder of this section, we articulate further consequences of this perspective for neuroethology.

First, the disagreement generates two distinct pictures of the machinations of nature at the neuroethological mesoscale. Whether there is or is not a cognitive map is an ontological question about the structures and processes of the brain, and it leads to further methodological questions about the proper classification and characterization of structures, systems, and processes in the mesoscale of the brain.

In the picture of nature suggested by proponents of the cognitive map, insect cognition is hierarchical, relies on centralized processing mechanisms, and achieves sophisticated feats of learning and memory manipulation (Menzel 2004; Menzel and Giurfa 2006). This implies that scientists should not assume that small insect brains are incapable of implementing the same strategies as larger mammalian brains. Should the cognitive map be definitively established as real, it would imply that a single mesoscale model of brain processes is applicable across a very broad scope of animal kinds, and it would in turn impel researchers to study further the connections between this particular mesoscale model and better-established microscale and macroscale models.

The picture of nature suggested by toolkit proponents differs. There, insect cognition is heterarchical, relies on decentralized processing mechanisms, and achieves task-specific solutions within a limited range of stimuli and situations (Wehner 1987, 528–29; Wehner et al. 2016). This decentralization is often recognized as characteristic of the limited scale of the neuronal network employed by insects. In other words, the toolkit implies a picture of nature where insect brains are relatively unlike larger, more complicated brains, and where mesoscale models of insect cognition are unlikely to be viable templates for models of mammalian brains.

Second, these different pictures of nature suggest different research strategies and potential experiments, as well as different relative significance of associated macro-versus microscale models. For instance, toolkit modelers perform experiments that involve subjecting a foraging insect to stimuli that indicate conflicting routes a

forager could take (Wehner et al. 2016). By observing where the insect navigates when subjected to conflicting stimuli, scientists produce evidence about how the insect's neurophysiology processes stimuli to govern navigation behavior. In one experiment (Bregy et al. 2008), researchers found ants took a compromise path between the route suggested by one navigational subroutine (path integration) and another (landmark identification). By calculating the relative influence of each stimulus on the compromise route, experimenters made inferences about how the outputs of different navigational subroutines are integrated. This characterization was then used to train a neural-net model of subroutine activity. Note that in this experiment, toolkit modelers use macromodels of ant navigation routes to inform the conceptual and neural-net mesoscale models.

Experimental progress differs for cognitive mappers. Those researchers localize and characterize learning and memory mechanisms at the microscale. Mappers adapted an experimental paradigm from American experimental psychology to investigate classical conditioning in honeybees (Bitterman et al. 1983; Menzel 2021). The paradigm exploits the fact that honeybees have a reflex that causes them to extend their proboscis when they are hungry and their antennae are stimulated with sucrose solution. By restraining individual honeybees in tubes so only their heads protrude, researchers can use the proboscis extension reflex to investigate how honeybees learn to associate stimuli with rewards. Because the bees are immobilized, scientists have also been able to directly manipulate the honeybee nervous system to investigate what role different microlevel structures and processes play in learning and memory (Hammer and Menzel 1995; Menzel 2014). As a result, cognitive mappers can articulate causal physiological models of learning and memory mechanisms at the microscale.

Additional differences cascade from these: The different relative importance of macromodels versus micromodels imply distinct conceptual strategies<sup>2</sup> for connecting the differing mesoscale models to the agreed-upon macro- and micromodels. The different mesoscale models likewise generate distinct systems of classification of processes involved in insect navigation and a difference in top-down (cognitive mappers) versus bottom-up (toolkit) approaches to modeling the trajectories of flight paths. More broadly, the mesoscale disagreement leads to differences in the identified aims of neuroethological research, with cognitive mappers aiming to uncover parallels between insect behavior and mammalian learning, while toolkit modelers aim to improve neural-net models of simulated navigators. These comparisons will develop more in future research.

## 5. Implications for multiscale modeling

The distinctions in section 4 illustrate that mesoscale models play a powerful role in shaping the concepts and models that in turn shape scientific research. This is a significant result for philosophers of multiscale modeling, insofar as it provides a new kind of evidence against reductionist analyses of multiscale modeling: Because neuroethologists agree at the microscale, the disagreement between camps cannot be explicable in terms of, or reducible to, disagreement about microstructures or

---

<sup>2</sup> To borrow vocabulary from Bursten (2018).



microprocesses. Complementarily, the convergence of researchers on macrostructures and macroprocesses complicates emergentist emphases on higher-level novelty out of lower-level commonalities. In the following text we unpack a further implication of this case for multiscale modeling.

Bursten (2016) argues that differences in characteristic dynamics at each scale of a multiscale system generate differences in the classificatory principles relevant to identifying the structures, properties, and processes operating at that scale. This reflects a result common among many accounts in the new generation of philosophers of multiscale modeling, namely that classification systems are scale-dependent, or scale-sensitive. There are different native structures, properties, and processes at each scale of a multiscale system and the structures, properties, and processes at one scale need not reduce to those at a lower scale. For instance, in multiscale models of materials, the properties of a given material can be variously modeled by quantum mechanics (microscale), classical rigid-body mechanics (mesoscale), and continuum mechanics (macroscale). The processes in quantum models, such as the evolutions of wavefunctions, are distinct from the processes in classical models, such as the elastic collision of atoms, and in continuum models, such as the propagation of a shockwave. Similar results have been identified in systems biology (Gross and Green 2017), neuroscience (Haueis 2018), and economics (Jhun 2021).

The cognitive map debate reinforces the need for scale-dependent approaches to classification. The multiscale accounts show that there are differences in the characteristic structures and processes, and therefore in the classification systems, native to each scale in a multiscale system. The cognitive map debate shows that analogous differences can be identified within a scale between the two mesoscale models, while each system is still connectable to the same macroscale and microscale models.

This is additional evidence that the characteristic dynamics at each scale are autonomous from one another, a result previously established through some of the aforementioned case studies and discussed extensively in Batterman (2021). It also introduces a new result: That it is possible for multiscale models to diverge at the mesoscale while converging at macro- and microscales. Philosophers of multiscale modeling previously established that the need to conceptually and/or mathematically integrate component models in a multiscale model imposes constraints on modeling strategies, just as empirical data and technological constraints do, and the micro- and macroconvergence in this example functions as an additional type of conceptual constraint that has not been previously identified in the literature. The situation is analogous to one in which a steel bar is described by a single set of microscale crystal structures and macroscale continuum properties while being describable by two conflicting accounts of mesoscale grain structure. It is notable that such a situation is highly unlikely in materials modeling, where mesoscale models are well-established and it is generally expected that differences in mesoscale structures will correlate with differences in macroscale properties. The cognitive map case provides a novel configuration of multiscale models for analysis.

## 6. Conclusions

We have established that the cognitive map debate in neuroethology is best understood as a conflict between mesoscale models within a multiscale model of

insect behavior, wherein both sides of the debate agree on the microscale and macroscale models in use. Viewing the cognitive map debate through this perspective recasts its history in a new light that illuminates the philosophical stakes and fault lines at the heart of the debate. It highlights how differences in conceptual and classificatory schemes, experimental practices, theoretical commitments, and epistemic aims lead scientists to promote incompatible mesoscale ontologies.

One direction of future work will continue to develop the portrait of this conflict in neuroethology through additional historical detail, and another will explicate the epistemic impacts of this novel configuration of multiscale models. Particularly, we suspect that the possibility of mesoscale divergence with macroscale and microscale convergence could lend a novel form of support to Batterman's recent (2021) argument that the mesoscale is the most natural and appropriate scale from which to draw one's ontological conclusions: The fact that the macro- and microscales agree seems largely immaterial to the researchers' pictures of nature in this case.

**Acknowledgments.** We would like to thank University of Kentucky's Lyman T. Johnson Postdoctoral Fellowship Program for providing the funding and support that made this collaboration possible. This material is based in part upon work supported by the National Science Foundation under Award #2132038.

**Author contributions.** Both authors contributed equally to this article.

## References

- Batterman, Robert W. 2021. *A Middle Way: A Non-Fundamental Approach to Many-Body Physics*. Oxford: Oxford University Press.
- Batterman, Robert W., and Sara Green. 2021. "Steel and Bone: Mesoscale Modeling and Middle-Out Strategies in Physics and Biology." *Synthese* 199(1):1159–184.
- Bitterman, Morton E., Randolph Menzel, Andrea Fietz, and Sabine Schäfer. 1983. "Classical Conditioning of Proboscis Extension in Honeybees (*Apis mellifera*)." *Journal of Comparative Psychology* 97(2): 107–19.
- Bregy, Patrick, Stefan Sommer, and Rüdiger Wehner. 2008. "Nest-Mark Orientation Versus Vector Navigation in Desert Ants." *Journal of Experimental Biology* 211(12):1868–73.
- Bursten, Julia R. 2016. "Smaller than a Breadbox: Scale and Natural Kinds." *The British Journal for the Philosophy of Science* 69(1):1–23.
- Bursten, Julia R. 2018. "Conceptual Strategies and Inter-Theory Relations: The Case of Nanoscale Cracks." *Studies in the History and Philosophy of Modern Physics* 62:158–65.
- Cartwright, B. A., and Collett, Thomas. 1987. "Landmark Maps for Honeybees." *Biological Cybernetics* 57(1):85–93.
- Dhein, Kelle. 2022. "From Karl von Frisch to Neuroethology: A Methodological Perspective on the Frischiean Tradition's Expansion into Neuroethology." *Berichte zur Wissenschaftsgeschichte* 45:30–54.
- Dhein, Kelle. 2023. "The Cognitive Map Debate in Insects: A Historical Perspective on What Is at Stake." *Studies in the History and Philosophy of Science* 98:62–79.
- Dyer, Fred C., and Thomas D. Seeley. 1989. "Orientation and Foraging in Honeybees." In *Insect Flight*, edited by Graham J. Goldsworthy, 205–30. Boca Raton: CRC Press.
- Gould, James L. 1986. "The Locale Map of Honey Bees: Do Insects Have Cognitive Maps?" *Science* 232(4752):861–63.
- Gross, Fridolin, and Sara Green. 2017. "The Sum of the Parts: Large-Scale Modeling in Systems Biology." *Philosophy, Theory, and Practice in Biology* 9(10):1–26.
- Hammer, Martin, and Randolph Menzel. 1995. "Learning and Memory in the Honeybee." *Journal of Neuroscience* 15(3):1617–630.
- Hauéis, Philipp. 2018. "Beyond Cognitive Myopia: A Patchwork Approach to the Concept of Neural Function." *Synthese* 195(12):5373–402.

- Hensgen, Ronja, Laura England, Uwe Homberg, and Keram Pfeiffer. 2021. "Neuroarchitecture of the Central Complex in the Brain of the Honeybee: Neuronal Cell Types." *Journal of Comparative Neurology* 529(1):159–86.
- Hoinville, Thierry, and Rüdiger Wehner. 2018. "Optimal Multiguideance Integration in Insect Navigation." *Proceedings of the National Academy of Sciences* 115(11):2824–29.
- Hoyle, Graham. 1970. "Cellular Mechanisms Underlying Behavior—Neuroethology." In *Advances in Insect Physiology*, vol. 7, edited by J. W. L. Beament, J. E. Treherne, and V. B. Wigglesworth, 349–444. Cambridge: Academic Press.
- Jhun, Jennifer. 2021. "Economics, Equilibrium Methods, and Multi-Scale Modeling." *Erkenntnis* 86(2):457–72.
- Menzel, Randolph. 2004. "Randolf Menzel." In *The History of Neuroscience in Autobiography*, vol. 4, edited by L. R. Squire, 452–84. Cambridge: Academic Press.
- Menzel, Randolph. 2014. "The Insect Mushroom Body, an Experience-Dependent Recoding Device." *Journal of Physiology-Paris* 108:84–95.
- Menzel, Randolph. 2021. "A Short History of Studies on Intelligence and Brain in Honeybees." *Apidologie* 52(1):23–24.
- Menzel, Randolph, and Martin Giurfa. 2001. "Cognitive Architecture of a Mini-Brain: The Honeybee." *Trends in Cognitive Sciences* 5(2):62–71.
- Menzel, Randolph, and Martin Giurfa. 2006. "Dimensions of Cognition in an Insect, the Honeybee." *Behavioral and Cognitive Neuroscience Reviews* 5(1):24–40.
- Menzel, Randolph, Uwe Greggers, Alan Smith, Sandra Berger, Robert Brandt, Sascha Brunke, Gesine Bundrock, Sandra Hülse, Tobias Plümpe, Frank Schaupp, Elke Schüttler, Silke Stach, Jan Stindt, Nicola Stollhoff, and Sebastian Watzl. 2005. "Honey Bees Navigate According to a Map-Like Spatial Memory." *Proceedings of the National Academy of Sciences* 102(8):3040–45.
- Osborne, Juliet L., I. H. Williams, N. L. Carreck, G. M. Poppy, J. R. Riley, A. D. Smith, D. R. Reynolds, and A. S. Edwards. 1997. "Harmonic Radar: A New Technique for Investigating Bumblebee and Honey Bee Foraging Flight." *Acta Horticulturae* 437:159–163.
- Rice, Collin. 2021. *Leveraging Distortions: Explanation, Idealization, and Universality in Science*. Cambridge, MA: MIT Press.
- Ronacher, Bernhard. 2019. "Innate Releasing Mechanisms and Fixed Action Patterns: Basic Ethological Concepts as Drivers for Neuroethological Studies on Acoustic Communication in Orthoptera." *Journal of Comparative Physiology A* 205(1):33–50.
- Shech, Elay, and Patrick McGivern. 2021. "Fundamentality, Scale, and the Fractional Quantum Hall Effect." *Erkenntnis* 86(6):1411–430.
- Wehner, Rüdiger. 1987. "'Matched Filters'—Neural Models of the External World." *Journal of Comparative Physiology A* 161(4): 11–31.
- Wehner, Rüdiger. 2020. *Desert Navigator: The Journey of an Ant*. Cambridge, MA: Harvard University Press.
- Wehner, Rüdiger, and Randolph Menzel. 1990. "Do Insects Have Cognitive Maps?" *Annual Review of Neuroscience* 13(1):403–414.
- Wehner, Rüdiger, Thierry Hoinville, Holk Cruse, and Ken Cheng. 2016. "Steering Intermediate Courses: Desert Ants Combine Information from Various Navigational Routines." *Journal of Comparative Physiology A* 202(7):459–472.

---

**Cite this article:** Bursten, Julia R. S. and Kelle Dhein. 2023. "Multiscale Modeling in Neuroethology: The Significance of the Mesoscale." *Philosophy of Science*. <https://doi.org/10.1017/psa.2023.12>