

Multiscale Modeling in Neuroethology: The Significance of the Mesoscale

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, which 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 (2020), 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 (2020) and Batterman (2021) have argued that concepts arising at the mesoscale, as opposed to micro or macro scales, 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 disagreement at the mesoscale 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 has engendered 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 in neuroethology. Section 3 characterizes this debate as a mesoscale disagreement between research communities who agree on ontology, mechanisms, and methods of investigation at the macro and micro scales. Section 4 lays out the implications of this characterization for understanding the cognitive map debate within neuroethology, 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 and drew heavily on European traditions in ethology and neurophysiology.

Insects have been important experimental subjects for neuroethologists since the field's inception (Hoyle 1970; Ronacher 2019; Dhein 2022), and a long-standing debate within insect neuroethology concerns modeling and explaining insect navigation (Menzel et al. 2000; Menzel and Giurfa 2006; Cheesemen et al. 2014a; Cheesemen et al. 2014b; Cheung et al. 2014; Menzel 2019; Wehner et al. 2006; Cruse and Wehner 2011; Hoinville et al. 2012; Hoinville and Wehner 2018; Wehner 2020). 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, 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 ant and honeybee navigation broke with that trend. 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 neuroethological studies into ant and honeybee navigation progressed, it became clear that these insects learn and form memories about their environment to perform 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.

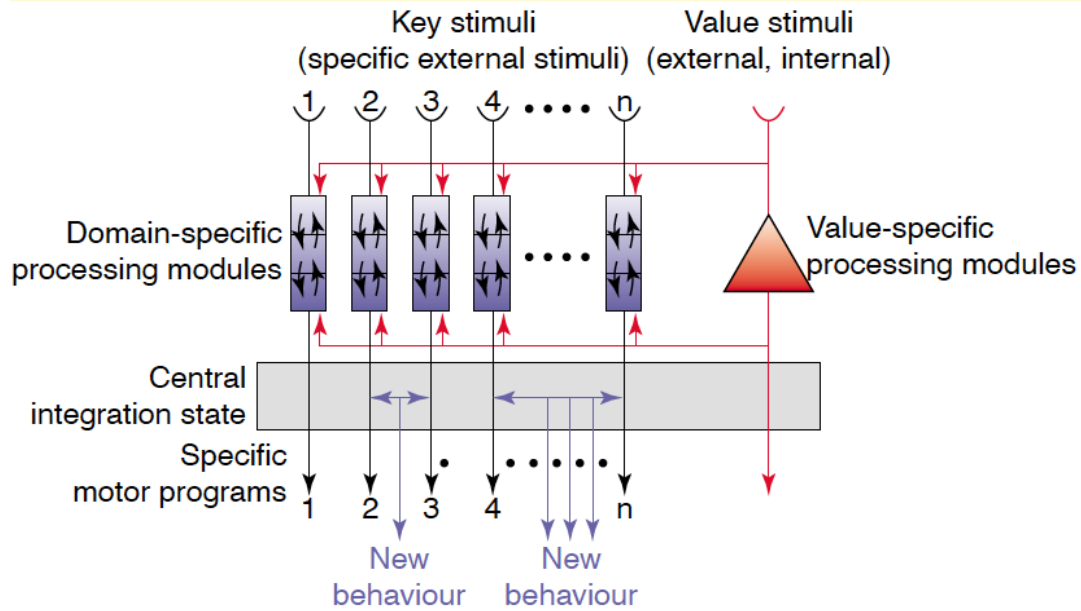


Figure 1: Example of a cognitive-map model of an insect brain (Menzel and Giurfa 2001)

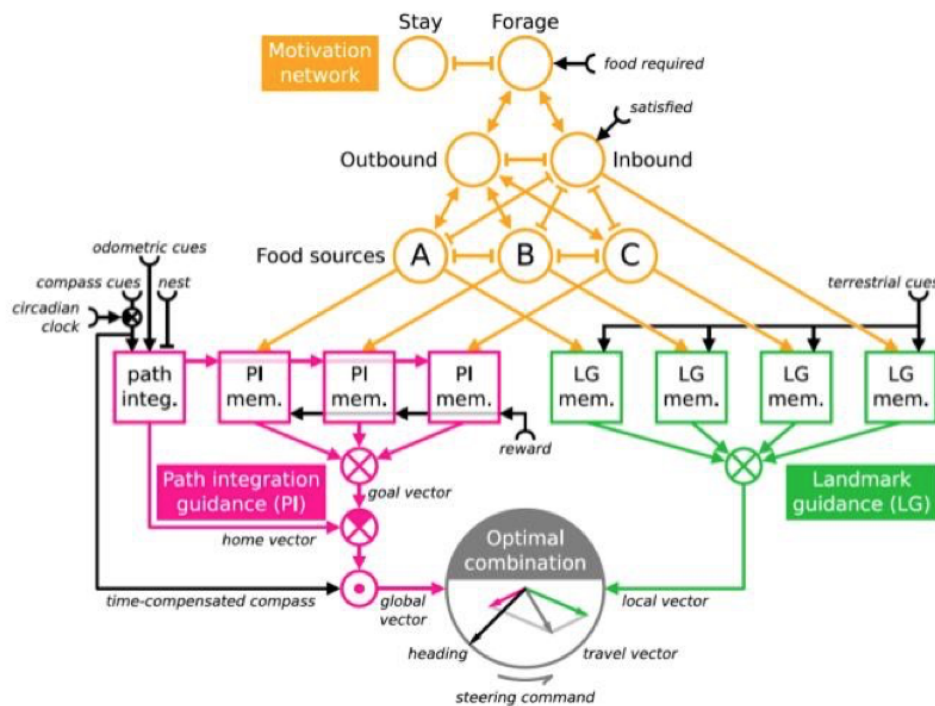


Figure 2: Example of a toolkit model of the cognitive processes underlying Cataglyphis navigation (Hoinville and Wehner 2018, 2825).

The cognitive map model of insect navigation (see Fig. 1) holds that insects integrate memories of their environment into a sophisticated, map-like representation via some central processing mechanism in the brain. The representation is map-like because it uses an allocentric frame of

reference, i.e. it represents objects relative to an environment that is independent of the navigator. The proposed 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, a navigating insect uses their cognitive map of the environment to deliberate about where they are and where to go next.

The main competitor to the cognitive map model is the toolkit model (see Fig. 2). The toolkit model maintains that ants and honeybees process neurosensory representations of their environment via 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. Whereas the cognitive map supposes that navigation requires a central pooling of neurosensory representations into a single stable representation of the environment (“Where am I?”), the toolkit model supposes that neurosensory representations remain distributed across various non-integrated processing mechanisms, and it is only the outputs of those mechanisms that are integrated into behavioral commands that answer the question, “Where to go next?”.

Although participants do not explicitly frame the cognitive map debate in terms of instinct vs. learning, there are historical ties and conceptual affinities linking the cognitive map debate to 20th-century debates about the relative contributions of instinct vs. learning to animal behavior. 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 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 map-like buffet of memories and deliberates about how to achieve their 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 the 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 next before deciding on an action command.

It remains an open question in neuroethology whether insects navigate via a cognitive map. Underlying this question is a longer-standing disagreement about the extent to which instinct and learning shape behavior. Below we frame the cognitive-map question, and the larger disagreement, as a disagreement about how to explain behavior at that 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 the insect’s 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 relevant phenomena at the micro and macro scales.

At the microscale, both cognitive-mappers and toolkit-modelers agree about how to model cellular components of the insect nervous system, as well as agreeing 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 also 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. That is, 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, p. 250–251). There is also broad consensus that a neural structure called the central complex is responsible for integrating information relevant to navigation and forming motor commands (Wehner 2020, p. 139–147; Hensgen et al. 2021, p. 160). 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, p. 465; Wehner 2020, p. 140). As a result, neuroethologists working on ant and honeybee navigation 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.¹ 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 had to record how long it took honeybees to fly between observation points and rely on vanishing bearings (the direction a honeybee was flying before an observer lost sight of the bee) to infer the 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 actual flight paths of honeybees. However, the two sides use these new macroscale models differently. Cognitive mappers designed harmonic-radar tracking experiments meant 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; Menzel 2011; Cheesemen et al. 2014a/b).

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. Toolkit modelers were able to perform such demonstrations because they had built 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 that the cognitive map side had subjected honeybees to, the simulated navigator moved along the same paths as the honeybees.

This review of neuroethological strategies for modeling honeybee actual flightpaths illustrates 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; that is, what networks of neurons are the causes of navigation behaviors.

Both cognitive mappers and toolkit modelers posit sensory processing mechanisms that consist of networks of neurons. These are more commonly functional models, as opposed to structural models aiming to veridically represent actual networks of neurons in the brains of ants and

¹ For a rare exception, see responses to Gould (1986): Cartwright and Collett 1987; Dyer and Seeley 1989; Wehner and Menzel 1990

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 that 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 notable preliminary upshot of this new perspective is that recognizing the debate as a mesoscale disagreement can serve to 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 mesoscale of neuroethology. 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 that larger mammalian brains implement. Should the cognitive map be definitively established as real, this will imply that a single mesoscale model of brain processes is applicable across a very broad scope of kinds of animals, and it will in turn impel researchers to further study the connections between this particular mesoscale model and the 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, p. 528–529; Wehner et al. 2016). This decentralization is often recognized as characteristic of the limited scale of the neuronal network employed by insects in cognition; in other words, the toolkit implies a picture of nature where insect brains are relatively unlike more complicated brains, and where this mesoscale model of insect cognition should not be used as a template for models of, e.g., mammalian brains.

Second, these different pictures of nature suggest different research strategies and potential experiments, as well as different relative significance of associated macro vs. micro scale

models. For instance, toolkit modelers perform experiments involving 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), 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 generated characterization of how the outputs of different navigational subroutines are integrated. This characterization is 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 at the microscale learning and memory mechanisms posited by cognitive maps. Mappers adapted an experimental paradigm from American experimental psychology to investigate classical conditioning in honeybees (Bitterman et al. 1983; Menzel 2020). 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 little 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 vs. micromodels imply distinct conceptual strategies² at play in connecting the differing mesoscale models to the agreed-upon macro and micro models. The different mesoscale models likewise generate distinct systems of classification of processes involved in insect navigation, and a different in top-down (cognitive mappers) vs. 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

Section 4's distinctions 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, it cannot be the case the disagreement between the camps is explicable in terms of, or

² To borrow vocabulary from (Bursten, 2018).

reducible to, disagreement about microstructures or microprocesses. Complementarily, the convergence of researchers on macrostructures and macroprocesses complicates emergentist emphases on higher-level novelty out of lower-level commonalities. Below 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 common result among many accounts in the new generation of philosophers of multiscale modeling, namely that classification systems are scale-dependent, or scale-sensitive; that is, 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 process, 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 via other sorts of case studies. It also introduces a new result: that it is possible for multiscale models to diverge at the mesoscale while converging at macro and microscales. It is previously established that the need to conceptually and/or mathematically component models in a multiscale model imposes constraints on modeling strategies, just as empirical data and technological constraints do, and the micro and macro convergence in this example functions as an additional type of 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 the 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 rationalizes a variety of further differences in the aims, strategies, and ontologies of each side of the debate, as well as suggesting reasons for apparent differences in conceptual and classificatory schemes.

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.

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