Original Research

Nested dynamical modeling of neural systems: A strategy and some consequences

Luis H. Favela [1, 2] *

[1] Department of Philosophy, University of Central Florida, Orlando, FL 32816, USA
[2] Cognitive Sciences Program, University of Central Florida, Orlando, FL 32816, USA

*Correspondence: luis.favela@ucf.edu (Luis H. Favela)

Abstract

Neuroscience has become a big data enterprise. This is due in large part to the rapidly growing quantity and quality of data and increased appreciation of non-neuronal physiology and environments in explaining behavior, cognition, and consciousness. One way neuroscience is dealing with this embarrassment of riches is by appealing to investigative frameworks that put the multiscale nature of neural systems at the forefront. The current work offers one such approach: Nested dynamical modeling, a strategy for creating models of phenomena comprised of multiple spatial and/or temporal scales for purposes of exploration, explanation, and understanding. Building from dynamical systems theory and synergetics, nested dynamical modeling applies a methodological approach aimed at nesting models at one scale of inquiry within models at other scales without compromising biological realism. This strategy is demonstrated via a proof of concept. Some consequences this approach has for the epistemological and theoretical commitments of neuroscience are discussed.

Keywords: Big data, dynamical systems theory, nested dynamical modeling, multiscale, synergetics.

1. Introduction

Neuroscience has become a big data enterprise (e.g., Frégnac, 2017). In the current work, "big data" refers to two characteristics of contemporary neuroscience: one is the quality and quantity of data and the other is the relevant sources of data. Regarding the first, with the advent of ever more sophisticated recording methods, there has been an explosion of data obtained about neural systems and related behaviors. Examples of such research abounds in the neural decoding literature. Here, recorded brain activity are used to make predictions about features in the world and have increasingly been integrated with machine learning tools, like support vector machines (Glaser et al., 2020). Illustrative cases of decoding from large data sets of neural recordings include such machine learning-based analyses of electroencephalography (EEG) data as those that differentiate phonetic prototypes from ambiguous speech sounds (Mahmud et al., 2021), decoding visual percepts during binocular rivalry experiments (Krisst & Luck, 2022), and reconstructing musical stimuli (Ramirez-Aristizabal & Kello, 2022).

Challenges arising from increased data are further compounded when scaling to even finer features of neurophysiology, such as research aimed at integrating dendritic and synaptic activity in neural models (e.g., Poznanski, 2002a, 2002b).

This embarrassment of riches has resulted in calls for prioritizing neuroinformatics databases combined with computational models and analytical tools for analysis, integration, and sharing of experimental neuroscience data (Akil et al., 2011)—and refocusing ongoing projects from experimental research to the development of infrastructure, such as the Blue Brain Project (Markram, 2006) and the Human Brain Project (Human Brain Project, 2022).

Regarding the second, the above-mentioned explosion of data has been in part due to the increasing acknowledgment of the contributions of nonneuronal causally and constitutively relevant factors to phenomena once thought explanatorily and ontologically reducible to the brain. The idea that not only brains, but also the body and environments they are situated in, play significant roles in both constituting and causing behavior, cognition,

and consciousness has resulted in researchers broadening the investigative purview of what is considered relevant to explaining said phenomena (e.g., Amazeen, 2018; Anderson, 2014; Raja, 2018; Spivey, 2007, 2020; Sporns, 2003). What can have interested parties do to reckon with this data deluge?

Logistically speaking, one way researchers have attempted to handle the flood of data is to develop infrastructure for the organization and sharing of information. In terms of investigative practices, researchers have made more central the multiscale nature of neural systems. Here, "multiscale" refers to the tools and strategies used to investigate neural systems. Such treatments in neuroscience include researchers explicitly appealing to brain models that *integrate* data at different spatial and temporal scales. For instance, strategies that combine models developed from principles of neuronal biophysics (i.e., bottom-up) with models developed from recorded neuronal activity (i.e., top-down; D'Angelo & Jirsa, 2022). Other strategies center on *exploring* ill-understood phenomena at multiple scales to obtain understanding (Haueis, 2022). Here, neuroscience practice is understood as having important roles for models that are not aimed at explanation per se, but at probing features of the target system and testing our conceptual understanding of them. Another example are those strategies that attempt *unification* across scales via the application of experimental paradigms previously successful at single scales. An illustrative case in this regard is research that expanded and incorporated a model originally developed to explain one phenomenon, that is, bimanual coordination (Haken et al., 1985), to explain relatively smaller scales (i.e., neuronal oscillations) and larger scales (e.g., human-machine dyads; Tognoli et al., 2020). In that way, phenomena at a range of spatial and temporal scales are unified by appeal to a core structuring principle, namely, coordination dynamics.

It is in the spirit of contributing to "big data neuroscience" that the current work is situated. This paper aims to offer a strategy for the fruitful investigation of the multiscale nature of neural systems by way of a strategy called *nested dynamical modeling*. In order to better understand nested dynamical modeling, the next section begins with overviews of foundational concepts, methods, and theories from dynamical systems theory and synergetics. Then, nested dynamical modeling is described and a proof of concept of its application is presented. After, some epistemological and theoretical consequences this strategy has for neuroscience are discussed.

Before explaining the investigative strategy currently on offer (i.e., nested dynamical modeling), it is necessary to first obtain a grasp of concepts, methods, and theories from dynamical systems theory and synergetics, which provide its foundations (for detailed explanations and references see Favela, 2020a, 2020b).

2. The strategy: Nested dynamical modeling

2.1. Dynamical systems theory

Dynamical systems theory (DST) utilizes mathematical tools to evaluate changes and patterns of linear dynamic systems. Most systems are "dynamic" in that their activity changes over time. The way DST is usually applied is by way of a quantitative part that accounts for and calculates variables via difference or differential equations and a qualitative part that visually depicts the range of possible states over time via a state space plot. Nonlinear dynamical systems theory (NDST) applies this approach to nonlinear phenomena, which, in the most basic sense, are those phenomena that exhibit outputs that are not proportional to its inputs (e.g., exponential and multiplicative).

When considering their contributions to a research strategy, DST and NDST typically aim at discovering rules that govern a system's temporal evolution. These rules are depicted by difference or differential equations, which are the system's governing equations. Still, equations alone do not necessarily provide understanding of the target of investigation. The reason is that differential equations, especially of nonlinear phenomena, can resist being solved analytically, where "analytic" means gaining knowledge of the behavior of the system by actually solving the equations. Consequently, to obtain a better grasp on system dynamics, state space plots are generated. Here again the strategy is clearly depicted as having a quantitative part (e.g., differential equations) and a qualitative part (e.g., state space plots) to help researchers comprehend in ways each part alone does not.

To illustrate this strategy when applied to neuroscience, consider the FitzHugh-Nagumo model (Izhikevich & FitzHugh, 2006). The aim of this model of single-neuron activity was to make a simpler version of Hodgkin and Huxley's conductance-based model of neuron ion

channels (Skinner, 2006). To do this, the FitzHugh-Nagumo model isolates the necessary mathematical properties needed to only generate the physiologically-relevant activity so as to depict the full range of neuronal excitation and propagation. This was accomplished with the following model of differential equations (Equations 1 and 2):

$$\dot{V} = V - \frac{V^3}{3} - W + I \qquad (1)$$

$$\dot{W} = 0.08(V + 0.7 - 0.8W) \qquad (2)$$

The three variables are the cell membrane potential (V), recovery (W), and stimulus current magnitude (I). Plotting the trajectories generated by the equations in a state space across two dimensions depicts the full range of biologically real behavior (**Figure 1**).

Although the applications of DST and NDST can be observed at various periods throughout the history of neuroscience (Favela, 2022), there is no doubt that they are becoming increasingly applied in recent years (Favela, 2021). While not as broadly applied in neuroscience, another powerful approach that nested dynamical modeling draws from is synergetics.
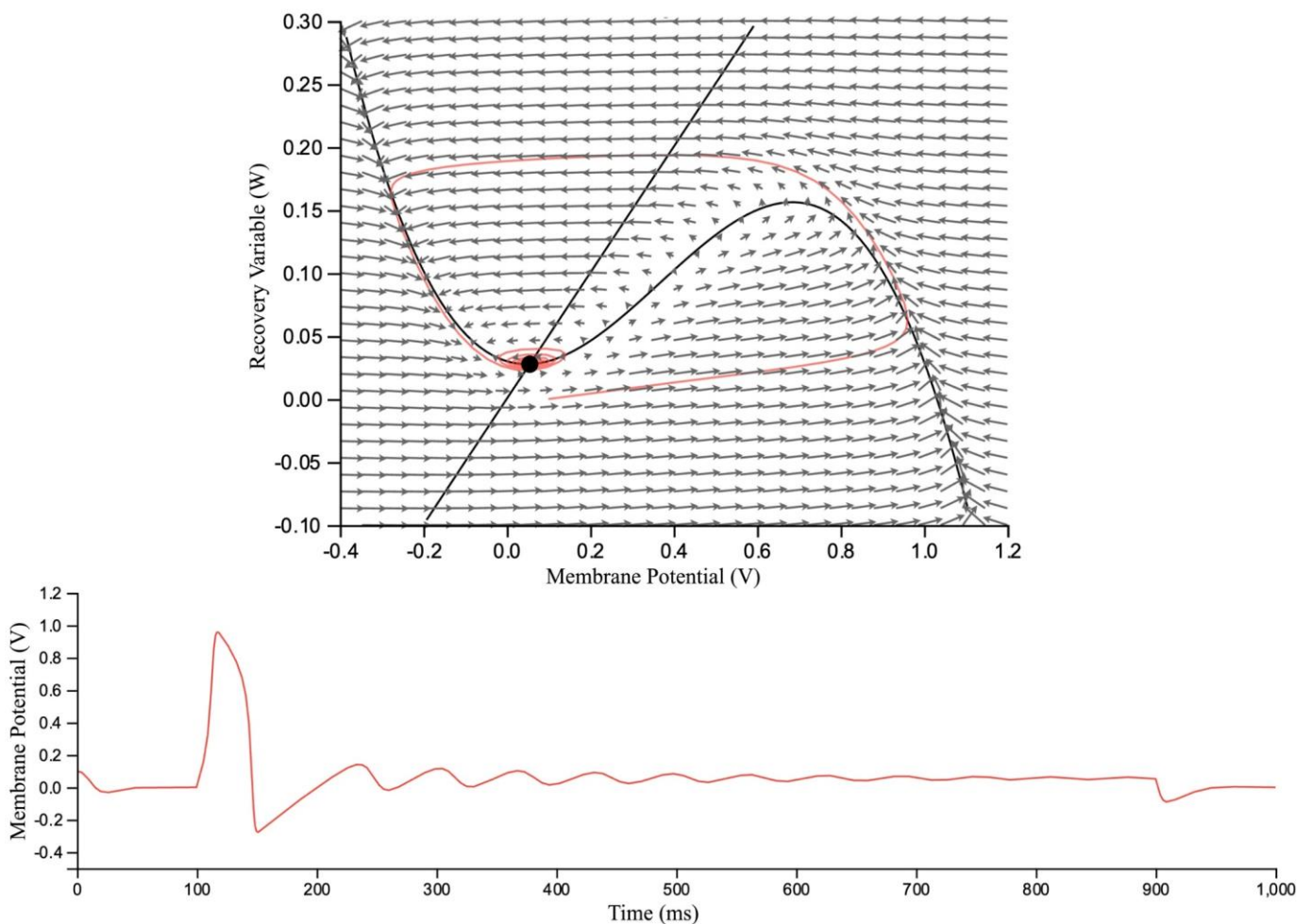

Figure 1. FitzHugh-Nagumo model. State space plot (top) and time series (bottom) of FitzHugh-Nagumo model. As in the differential equations model (Equations 1 and 2). The three variables are the cell membrane potential (V), recovery (W), and stimulus current magnitude (I). (Modified and reproduced with permission from J. Terwilliger, http://jackterwilliger.com/biological-neural-networks-part-i-spiking-neurons/)

2.2. Synergetics

Synergetics is a framework for studying systems with numerous components interacting across a range of spatial and temporal scales. What is more, it emphasizes the investigation of qualitative changes at the relative macroscopic scale of a phenomenon where new functions or structures occur (Haken, 1988; 2006). Synergetics is distinguished from other frameworks that study more macroscale system features in at least four ways. First, it centers on spontaneous processes and structures like self-organization. Second, it aims to discover general principles (or rules; see previous section on DST) that underlie self-organization notwithstanding the composition or material of the system's individual parts (Haken, 2016). Third, as alluded to above, synergetics understands the macroscopic and microscopic spatial and temporal scales of a system in a contextual way. That is to say, defining "macroscopic" and "microscopic" is dependent upon particular targets of investigation, for example, a neuron is "macroscopic" to a synapse but is "microscopic" to a neural network. Fourth, investigations are guided by the definition and application of order and control parameters, two concepts defined below.

Like DST and NDST approaches, investigators applying a synergetics framework typically aim to identify the rule(s) that govern a system's temporal state evolution, with those rules depicted as differential equations. In addition, synergetics researchers aim at discovering general principles of self-organization, which are stated as differential equations that depict a system's macroscopic state. Macroscopic states are defined as order parameters in synergetics, which are the collective variable that expresses the phenomenon being studied. Investigating a phenomenon by way of order parameters requires control parameters as well, which are variables that guide the system's evolution. It is worth noting that in terms of control and order parameters, the former does not cause the latter. The causal relationship of control and order parameters is incorrectly understood via linear causation. Instead, the proper form of causation is circular causality (Haken, 2016). In such systems with circular causality, while the order parameter determines (to some degree) the activity of the system's components, so too do the control parameters determine the activity of the macroscale system activity. To illustrate this, consider the now-classic Haken-Kelso-Bunz model of bimanual coordination (HKB; Haken et al., 1985). The HKB model explains the dynamics and transitions of the states of two limbs moving at different frequencies. Specifically, the limbs are the index fingers and the movements begin with each being anti-phase or in-phase positions. Variables for the coordinative states of the two fingers is the order parameter and what guides coordination are the control parameters (Equation 3):

$$\dot{\phi} = -a \sin \phi - 2b \sin 2\phi \qquad (3)$$

The order parameter captures the overall dynamics of the system, which in this model is $\dot{\phi}$. The control parameters are finger one frequency a and finger two frequency b. Regarding circular causation, a "starting point" in a linear causal chain to explain the macroscale dynamics cannot be identified among the variables. This is because while a and b contribute to and constrain the dynamics exhibited by $\dot{\phi}$, it is also the case that $\dot{\phi}$ contributes to and constrains the dynamics exhibited by a and b. With the concepts and methods of DST/NDST and synergetics at hand, the discussion can move to the main strategy of the current work: nested dynamical modeling.

2.3. Nested dynamical modeling

Multiscale modeling strategies in neuroscience are not new (for a small sample see Breakspear & Stam, 2005; Poznanski & Riera, 2006; Siettos & Starke, 2016; Zhang et al., 2020). It is arguable that the received view of the architecture of the brain would inevitably lead to multiscale models. Specifically, understanding the brain as having a hierarchical organization entails multiple scales, for example, neurons at one scale, cortical columns at another, functional brain regions at another, and so on. *Nested dynamical modeling* is a strategy for creating models of phenomena comprised of multiple spatial and/or temporal scales for purposes of exploration, explanation, and understanding (cf. Favela, 2014, 2015, 2018). The methodological approach is to integrate (i.e., "nest") dynamical models at one scale of inquiry within dynamical models at other scales. "Scales" are understood in terms of relatively defined order and control parameters. That is to say, depending on the research target, what is a control parameter at one scale and for one target of investigation could be an order parameter at another scale and for another target of investigation.

The epistemic motivation of this strategy is to facilitate comprehensibility of large and complicated data sets

obtained from multiple scales by focusing on the necessary mathematical properties needed to only generate the physiologically-relevant activity. Such "dimension reduction" is commonly required due to complex systems phenomena—like neural systems—readily becoming incomprehensible due to big data issues of the sort discussed in the introduction above. Granting that nested dynamical modeling requires appeals to idealization (Batterman, 2009; Frigg & Hartmann, 2020; Potochnik, 2017), the goal is to ground the methodology in empirically-verifiable data so as to maintain scientific explanatory virtues like control and manipulation, prediction, and simplicity without compromising realism. In the following subsection, a proof of concept of nested dynamical modeling in neuroscience research is presented. The proof of concept will demonstrate how dynamical models at the scale of single synapses can be nested in increasingly macroscales up to networks of neurons.

2.3.1. Proof of concept of nested dynamical modeling

The first scale in the proof of concept of nested dynamical modeling is model of individual synaptic activity (Equation 4 [A in Figure 2]):

$$I_{\text{synaptic}}(t) = \sum_i g_i(t)(E_i - v) \qquad (4)$$

In this model of synaptic activity, the order parameter is I, which denotes the sum of all input currents that includes experimentally-validated biological features like time-varying conductance ($g_i(t)$) and molecular chemical activity (i = AMPA, GABA$_A$, GABA$_B$, and NMDA), or the control parameters. Other variables are defined as v = voltage and E = reverse potential of the molecular chemical activity. The model of synaptic activity (Equation 4) can be nested within a model of single-neuron activity (Izhikevich, 2010; Equations 5 and 6):

$$C\dot{v} = k(v - v_{\text{rest}})(v - v_{\text{thresh}}) - u + I \quad (5)$$
$$\dot{u} = a[b(v - v_{\text{rest}}) - u] \qquad (6)$$

This model of spiking neurons and recovery variable ($C\dot{v}$ and $\dot{u}$) demonstrates features like threshold (v_{thresh}) and voltage resting (v_{rest}) states. In order to nest the model of synaptic activity (Equation 4) within a model of spiking neurons, that model (Equations 5 and 6) must

first be simplified into an equivalent but more general form (Izhikevich, 2010; Equation 7 [B in **Figure 2**]):

$$\dot{v} = f(v,u) + g(t)[E(t) - v] + I \qquad (7)$$

In this simpler form, the spiking neuron model (Equation 7) nests the synaptic term (I; Equation 4). Thus, the order parameter is single-neuron activity ($\dot{v}$) with various control parameters, especially synaptic activity (I), which was the order parameter at a different scale.

It is worth pausing here to stress that biological realism is maintained during the nesting step from Equation 4, to 5 and 6, and then to 7. Note that all activity of the individual synaptic activity model is nested within the model of single-neuron activity. Consider that if all of the molecular chemical (e.g., AMPA, GABA$_A$, GABA$_B$, and NMDA) activity exhibited during synaptic activity were yet to be identified, it would still be possible to develop a model of single neuron activity that is biologically realistic (Equations 5 and 6). This is because it would be based on empirically-verified data. Still, with the current situation that the molecular chemical properties of synapses being known, more detailed information can be obtained from the model by "zooming" in on the values constituting the I term. If such details were not known, the general model of single-neuron activity (Equation 7) would still be considered a justifiable explanation. The same, as will be shown, holds true as the nesting moves to increased macroscales.

The next step is the nesting of single-neuron activity (Equation 7) within a neuronal network model. Izhikevich and Edelman (2008), neuronal network model of the mammalian thalamocortical system is defined in terms of total synaptic connections, where each neuron is defined as a "compartment" connected to other "compartments." The model for total synaptic activity at each compartment of the neuronal networks is as follows (Equation 8 [C in **Figure 2**]):

$$
\begin{aligned}
I_{\text{syn}} &\qquad\qquad\qquad (8)\\
&= g_{\text{AMPA}}(v - 0)\\
&+ g_{\text{NMDA}}\frac{[(v + 80)/60]^2}{1 + [(v + 80)60]^2}(v - 0)\\
&\quad + g_{\text{GABA}_A}(v + 70) + g_{\text{GABA}_B}(v + 90)\\
&\qquad\qquad + I_{\text{gap}}
\end{aligned}
$$

Note that I_{gap} defines the gap-junction current with decaying conductance based on distance between

neighboring neuronal soma. This model nests the $\dot{v}$ term from Equation 7, thereby shifting it from an order parameter at the previous scale to a control parameter in the current scale. In order to nest the neuronal network compartment model (Equation 8) within the next scale, it must first be simplified into an equivalent but more general form (Izhikevich & Edelman, 2008). Here, the activity of Equation 8 is defined by the single term $\dot{y}$, which serves as the order parameter, and gives the following (Equation 9 [D in Figure 2]):

$$\dot{y} = \left(I_{\text{syn}}(z)\right) - y/500 \qquad (9)$$

This model (Equation 9) can be nested within a model of more macroscale activity, namely, from a compartment of neuronal network activity to a larger neuronal network across a brain region (Rubinov et al., 2011). The model of brain region neuronal activity is as follows (Equation 10 [E in Figure 2]):

$$C\frac{dV}{dt} = C\frac{dy_1}{dt} = -gy_1 + y_2 - y_3 \qquad (10)$$

The order parameter $\dot{y}$ from Equation 9 is now a control parameter nested within Equation 10, which models an increased macroscale of activity. This model depicts the integration of synaptic currents across all neuronal activity in a brain region. Here, y_1 is equivalent to $\dot{y}$ in model of more microscale activity (Equation 9), with the other variables serving control parameters capturing experimentally-verified biological features like membrane conductance (g). Variables are defined as $C =$ membrane conductance, $g =$ leakage conductance and $y =$ synaptic currents, where y_1 is the current across one dimension and y_2 and y_3 expand model to capture currents across three dimensions (Rubinov et al., 2011, supporting information 1). A visual depiction of the nesting relationships among this models is presented in **Figure 2**. There, it is clearly presented how variables that serve as an order parameter at one scale becomes a control parameter at a more macroscale. With a better sense of what nested dynamical modeling is and this proof of concept at hand, potential epistemological and theoretical consequences for neuroscience are discussed in the next section
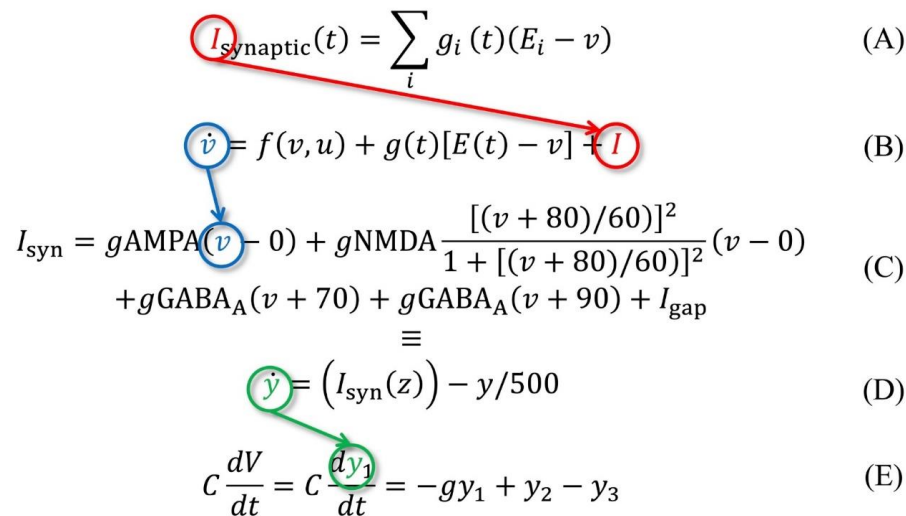

$$I_{\text{synaptic}}(t) = \sum_i g_i(t)(E_i - v) \qquad \text{(A)}$$

$$\dot{v} = f(v, u) + g(t)[E(t) - v] + I \qquad \text{(B)}$$

$$I_{\text{syn}} = g\text{AMPA}(v - 0) + g\text{NMDA}\frac{[(v + 80)/60]^2}{1 + [(v + 80)/60]^2}(v - 0) + g\text{GABA}_A(v + 70) + g\text{GABA}_A(v + 90) + I_{\text{gap}} \qquad \text{(C)}$$

$$\equiv$$

$$\dot{y} = \left(I_{\text{syn}}(z)\right) - y/500 \qquad \text{(D)}$$

$$C\frac{dV}{dt} = C\frac{dy_1}{dt} = -gy_1 + y_2 - y_3 \qquad \text{(E)}$$

Figure 2. Proof of concept of nested dynamical modeling. (A [in text Equation 4]) Individual synapse activity model with product I (red). (B [in text Equation 7]) Model of single-neuron activity with product $\dot{v}$ (blue). Here, the red arrow indicates the nesting of a variable that was an order parameter from one model into another model, and now playing the role of a control parameter. (C [in text Equation 8]) Model of compartment of neuronal network synapse activity. Here, the blue arrow indicates the nesting of order parameter variable $\dot{v}$ into another model as a control variable. (D [in text Equation 9]) Equivalent simplified model of compartment of neuronal network synapse activity with product $\dot{y}$ (green). The equivalency of (C) and (D) is identifiable via the "$\equiv$" notation. (E [in text Equation 10]) Model of networks of neurons. Here, the green arrow indicates the nesting of order parameter $\dot{y}$ into a model at an increased macroscale to serve as a control parameter.

3. Some consequences for neuroscience

The purpose of this section is to explore what, if any, epistemological and/or theoretical consequences the nested dynamical modeling strategy has for neuroscience. First, what consequences might nested dynamical modeling have for the particular theoretical aspects of neuroscience? One potential consequence concerns causation. Like most (if not all) of the other biological and social sciences, neuroscience is arguably understood as assuming a kind of unidirectional and sequential sense causation. That is to say, that neural phenomena have starting points and ending points, with a chain of steps in between. It is true that many neural phenomena exhibit nonlinearities and feedback. However, those are also understood as causal in the unidirectional and sequential sense. Consider, for example, Bayesian approaches to neuroscience like predictive processing (Clark, 2013). An illustrative example of predictive processing is when somebody hears a sound (sensory input), thinks it is a song they know (current prediction based on prior expectation), but then they realize it is not the song they thought (prediction error followed by updated prior). Upon realizing it is not the song they thought it was, the next time they hear it they will not have the same incorrect perceptual expectation. Feedback is displayed here in the form of the sensory input not confirming the prior expectation and then the next time the sensory input is received having a new expectation. While there is feedback, it is unidirectional in that the causal chain is sequential, for example: prior expectation → sensory input → prediction error → etc.

The wealth of research in synergetics has demonstrated that much neural physiology and related behavioral and cognitive capacities operate not in such unidirectional and sequential causal chains; rather, they exhibit circular causation (e.g., Fingelkurts et al., 2013; Haken & Portugali, 2016; Kozma & Freeman, 2016; for additional discussion see Buzsáki, 2006; Favela, 2020a). As discussed above, if the order and control parameters strategy is appropriately applied to modeling a system, then it is likely the case that the phenomenon exhibits circular causation in the form of its macrostates (order parameter) simultaneously constraining and being constrained by its microstates (control parameters). Such relationships are not properly understood via unidirectional and sequential causation. Consequently, nested dynamical modeling, like synergetics, may force

neuroscience to rethink some of its theoretical aspects, such as the kind of causation it is committed to.

Another theoretical consequence, though not as broad as notions of causation, centers on the intersection of nested dynamical modeling and a well-known contemporary theory of consciousness: the integrated information theory (IIT) of consciousness. IIT is a scientific theory of consciousness aimed at describing the essential properties of consciousness (i.e., "axioms") and then inferring the necessary features of the physical systems that can support such properties (i.e., "postulates;" e.g., Tononi, 2015; Tononi & Koch, 2015). Part of IIT's popularity (and controversy; for a review of challenges see Merker et al., 2022) concerns its attempt to define consciousness via a quantifiable value. As indicated by its name, IIT defines the consciousness of a system primarily via the integration and information axioms and postulates, which underlie the amount of integrated information, or Φ ("phi"). Over the course of various iterations of IIT, proponents have supplemented the theory with the claim that each system can only have a single consciousness that is defined as its maximum Φ (Φ^{Max}; Hoel et al., 2016). While arguments have been made to attempt to defend the notion of Φ^{Max} on grounds of parsimony (i.e., "it is simpler for one system to have one consciousness then to have multiple consciousnesses"), critics have not been persuaded. Schwitzgebel (2015), for example, has argued that IIT has no in principle reason for denying that one system can house multiple consciousnesses simultaneously. The line of argument goes that if consciousness just is information integration, then anywhere there is integrated information there will be consciousness. Consequently, even if an intuitively conceived spatially-temporally isolated entity has various coinciding instances of integrated information, then that entity will have multiple consciousnesses simultaneously. Humans, for instance, have multiple coinciding locations where information is integrating, even in the brain alone. Therefore, IIT is committed to stating that humans can have multiple consciousnesses at a time.

It is unclear if nested dynamical modeling or other multiscale modeling strategies can help to arbitrate this issue. As discussed above, nested dynamical modeling, like synergetics, motivates openness to acknowledging different notions of causation than are typical of much standard scientific practice in the biological and social sciences. Recent iterations of IIT have made more

explicit that integrated information has causal powers, such that the Φ^{Max} of a system has specific causal capacities that other Φ values even within the same system would not (e.g., Hoel et al., 2016). Different causal capacities alone do not rule out the kind of multiple consciousnesses that critics like Schwitzgebel claim are allowed by IIT. In addition, if nested dynamical modeling does not privilege any particular scale of investigation, and thus does not hold a priori where causal capacities can be located, it is unclear if its methodology could support an in principle case for single consciousness (i.e., Φ^{Max}) among multiple other possible simultaneous consciousness states (i.e., other Φ values in the same system). In this way, perhaps nested dynamical modeling allows for far too promiscuous of a theoretical basis for neuroscience.

Second, what consequences could nested dynamical modeling have for the epistemology of neuroscience? One consequence concerns the goals of neuroscience. Specifically, is the only or primary goal of neuroscience research to provide explanations of targets of investigation? Building on arguments made by Haueis (2022), the big data nature of neuroscience forces neuroscientists to confront themselves about what they are aiming for when they use multiscale modeling approaches. It is arguable that much multiscale modeling work does not appear to provide "explanations" of target phenomena and are thus referred to as merely "descriptive," where that term is used in a derogatory sense. Haueis can be understood as arguing that multiscale modeling work in neuroscience need not be either explanatory or descriptive. Instead, it can be readily understood as "exploratory." Multiscale modeling qua exploratory research may not always provide or be for the purpose of explanation. They can serve other epistemically valid purposes, such as getting a future line of inquiry going, provide proof of principle, be potential explanations, and allow for reassessing how to think about targets of investigation (Haueis, 2022). Nested dynamical modeling is readily understood along these lines. As such, it contributes to examples and arguments in favor of viewing exploratory research in neuroscience as being a respectable way to conduct day-to-day business.

Another epistemic consequence of nested dynamical modeling concerns reasons for excluding or prioritizing certain kinds of explanation over others. For nearly 30 years, a majority of philosophers of science have argued that the search for mechanisms is the most fundamental kind of explanation in the life sciences (e.g., Bechtel & Abrahamsen, 2005; Craver & Darden, 2013), including neuroscience (e.g., Piccinini, 2020). Many criticisms have been made against this position (e.g., Silberstein, 2021) and in defense of the validity of other kinds of explanation. For example, Chemero (2009) argues that dynamical systems theory modeling can provide explanations of phenomenon on their own (e.g., HKB model of bimanual coordination; Haken et al., 1985), without necessitating mechanistic features. Favela (2020a) argues that complexity science provides explanations via an investigative framework consisting of fruitful concepts, methods, and theories, some which adhere to commitments contrary to some mechanistic requirements for purported complete explanations. Lange (2017) defends the viability of non-causal explanations, such as those in pure mathematics, which are explanatory in virtue of proofs and particular formal properties, like Euler's theorem. Ross (2023) also focuses on the notion of causation and argues that mechanisms do not capture the only kind of causation appealed to in the biological sciences; others, like cascades, are causally significant, while not being a distinct form of mechanism.

If nested dynamical modeling is a viable investigative strategy, one that exhibits various epistemic virtues (e.g., prediction, simplicity, etc.), then it—and other multiscale approaches—can help to dissolve the debate about which kind of explanation rules them all. The reason is that such multiscale strategies do not seem readily categorized under one of the common explanatory approaches. Is nested dynamical modeling a mechanistic approach? Yes and no: yes, because it can be appealed to as a way to identify specific causally-relevant features of a system (e.g., quantified synaptic activity in Equations 4, 7, and 9) via localization. But no because certain multiscale models resist common mechanistic methods (e.g., decomposition and localization) and favor interpretations more readily understood in terms of covering-law explanations. For example, Rubinov, et al (2011) expand Equation 10 to incorporate the universality class of self-organized criticality, which can be understood as serving the role of a covering law in this case. It may be the case that nested dynamical modeling and other multiscale modeling approaches make the case not for one particular explanatory kind over others, but for explanatory pluralism (Favela & Chemero, 2021).

4. Conclusion

Contemporary neuroscience faces an embarrassment of riches due to recent methodological and theoretical developments. Methodologically, more areas of neuroscience are obtaining increased quantity and quality of data about their targets of investigation. Theoretically, more areas of neuroscience are acknowledging the roles of nonneuronal physiology in explaining phenomena of interest. One-way neuroscience is reckoning with this state of affairs is by appealing to investigative frameworks that put the multiscale nature of neural systems at the forefront. The current work has described and provided a proof of concept of one such approach: nested dynamical modeling. While it is an open empirical question whether such an approach can be productive, the previous section explored potential consequences it may have for neuroscience. Theoretically, nested dynamical modeling may motivate neuroscience to embrace different forms of causation and to be open to unintuitive ideas like single systems having more than one consciousness. Epistemologically, nested dynamical modeling may bolster the case for doing neuroscience research that is more exploratory in nature and for embracing explanatory pluralism. Notwithstanding such potential epistemological and theoretical consequences nested dynamical modeling may have for neuroscience, it is clear that multiscale approaches will continue to have increasing presence in the study of neural systems and related phenomena.

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