Grand Unified Theories of the brain need better understanding of behavior: the two-tiered emergence of function.

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Abstract

Over the last few decades, neuroscience, and various associated disciples, has expanded enormously in terms of output, tools, methods, concepts, and large-scale projects. In spite of these developments, the principles underlying brain function and behavior are yet only partially understood. We claim that brain functioning requires the elucidation of the rules associated with all possible task realizations, rather than targeting the activity underlying a specific realization. A first step into that direction was taken by approaches focusing on dynamical structures underlying task performances, as exemplified by Coordination Dynamics. The latter was originally based on experimental demonstrations of functional synergies/coordinative structures in complex movements like speech and interlimb coordination. Its theoretical foundation owes much to Hermann Haken's Synergetics, which provides a formalism, through which the degrees of freedom associated with high-dimensional systems may be effectively reduced to one or a few functional variables. Synergetics' dimension reduction, however, is generally valid in the vicinity of phase transitions, a limiting factor in the framework's domain of explanation. The recent development of Structured Flows on Manifolds (SFM) is less generic than Synergetics, but allows the employment to a potentially broader range of applications. Following novel theoretical work on the onset, propagation, and offset of epileptic seizures, we expand the SFM framework, and propose that the emergent two-tiered fast-slow dynamics may be a basic mathematical organization underlying the architecture of brain and behavior dynamics. Finally, along a few examples, we illustrate how this framework allows for the incorporation of notions cardinal to ecological psychology.

1. On the current situation in neuroscience

Woese argued eloquently that science is driven by both technological advances and a guiding vision (Woese, 2004). The key is to balance their contributions, “without the proper technological advances the road ahead is blocked. Without a guiding vision, there is no road ahead” (Woese, 2004, p. 173). The latter, one could argue, seems to be the case in the modern neurosciences. At the same time, the last decade has seen the development of large-scale neuroscience projects to explore brain function and dysfunction with the goal to understand the mechanisms underlying the emergence of cognition and behavior. The hope is that such large-scale initiatives may help to overcome a certain fragmentation of research, and enable, through such joints efforts, new breakthroughs. Often parallels are drawn from domains outside of neuroscience such as High Energy Physics (e.g., the CERN in Geneva). The US Brain Initiative, the European flagship the Human Brain Project, the China Brain Project, and the Japanese Brain/Minds project are examples of such large-scale endeavors. One could consider this evolution to be an indicator of the increasing maturity of neurosciences, but this is not true *per se*. Some these projects seem to be predominantly driven by technological advances in imaging and data sciences (e.g., US Brain Initiative) rather than a guiding (theoretical) vision. This is perhaps not surprising, considering the extreme complexity to face. The closest to a guiding vision may be currently offered by the Human Brain Project, as expressed by its theoretical objective to understand the human brain using an integrated multi-scale approach, taking this with respect to theory and modeling as well as empirical neuroscience, and supported by recent advance in ICT. Admittedly, this formulation presents more a roadmap than a vision; indeed a Grand Unified Theory (GUT), as we know it from High Energy Physics, remains yet to be delivered.

In this manuscript we argue that a GUT of brain function needs to be anchored in an appropriate representation of behavior. Such a claim is not new to students that have followed a dynamical perspective; for a similar call regarding the importance of incorporating behavior in neuroscience, see Krakauer, Ghazanfar, Gomez-Marin, MacIver, & Poeppel, 2017). Arguing for this perspective, we will propose a framework that links complex brain dynamics with similarly complex emergent behavior. The present framework is rooted in dynamical brain networks that can be decomposed into probabilistic functional modes that are operational for a limited duration and can be conceived of as brain analogues of synergies that are well known in the movement sciences. In this sense, the present approach may be viewed as a natural but necessary extension of Coordination Dynamics. Here, modes are mathematically operationalized as manifolds, along which trajectories on the manifold evolve as the dynamics unfold embedded in a low-dimensional space - hence *structured flows on manifolds* [SFM]. The collection of functional modes available in a neural network constitutes its functional repertoire, which accounts for a complete set of cognitive functions and overt behaviors that a person has at her disposal. We will elaborate on these elements below, but wish to insist that, independent of our particular formulation in terms of SFMs, the argument holds that the lack of a mathematical representation of (real world) behavior is one of the major roadblocks to overcome when developing a GUT of brain function.

2. A roadblock to understand brain and behavior

It has been acknowledged by many neuroscience researchers that the brain is dynamic, but how that translates to their approach to gain understanding of how the brain functions varies widely. At one end, some approach the brain as an input-output system where a signal comes in, a cascade is triggered as the signal propagates, and the system produces an output appropriate to the input (Agus, Thorpe, & Pressnitzer, 2010; Storace & Cohen, 2017). Other theoretical approaches focus on defining mathematical functions for behavioral time series (Abbott *et al*., 2016; Maass, Natschläger, & Markam, 2002), while empirical studies use machine learning algorithms to classify the time series according to the behavior they are thought to support (e.g., perceptual categorization). In neuroimaging, for example, brain regions are typically characterized with respect to specific cognitive and behavioral functions (vision, audition, language, memory) under which they are active, and inferences are drawn about the unobservable processes that were needed to instantiate such functions. We are now in the era of brain networks, where the coherent interactions between regions are believed to represent the substrate for function (default network, salience network, dorsal attention network; see Fransson, 2005). A great deal of research these days emphasizes the system characteristics that support these networks by graph metrics (e.g., node centrality, small world properties, etc.; cf. Achard, Salvador, Whitcher, Suckling, & Bullmore, 2006; Joyce, Laurienti, Burdette, & Hayasaka, 2010; Sporns & Honey, 2006) and by characterizing features of the dynamics, such as scale-free behavior and criticality (Boonstra, He, & Daffertshofer, 2013; Chialvo, 2004). On the microscopic level of brain organization, typically associated with the spatiotemporal organization of action potentials, given the discrete nature of these events, information theory and information routing play an important role in quantifying the capacity of the brain network to transmit and receive signals. Here the concept of information is deeply rooted in Shannon's interpretation of information as a measurable quantity (Shannon & Weaver 1949), comparable to mass or energy. This mathematical theory of communication classifies information as a measurable quantity and, when applied to neural connections, information theory defines upper limits — the channel capacity — on precisely how much information can be communicated between two components of a network given any degree of noise contamination.

If we pause and examine this variety of perspectives and mathematical constructs, it appears that the neuroscience community has indeed done a good job of characterizing *what* the system does, but not *how* it does it. Our insights on brain function are far from what one may expect from invariant principles generalizing to human behaviors. This becomes evident when attempting to use the existing brain models for the simulation of behavior in real world situations. For example, quite some progress has been made in the domain of speech recognition and speech generation, but this progress is largely due to technological advances in artificial intelligence rather than brain-inspired computation. Computer programs are capable of interacting naturally with humans in well-defined environments in which the modes of behavior are limited, such as a phone call to reserve a table in a restaurant. When translating the behavioral repertoire into a different context, which is the essence of "invariant" principles, these applications fail. We need to conceive representations of behavior that not only can be supported and created by brain networks, but are also sufficiently general and robust to be applicable in a range of different contexts.

This challenge is being taken on by approaches in Ecological Psychology and Coordination Dynamics, at least as regards the search for invariant principles on the behavioral level (but see also Kelso, et al., 2012) It is widely acknowledged that (overt) human behavior comes in various forms, or patterns. Indeed, behavioral patterns, and in particular, switches between them, are central to Coordination Dynamics (see Kelso 1995 for a review). As the corresponding main experimental phenomena are well known to the readers of Ecological Psychology, they will not be summarized here. Research conducted from this perspective has convincingly shown that, while similar from one performance to the next, the solutions (i.e., the system's realizations) to sensorimotor problems are never exactly the same ("repetition without repetition"). This feature can be readily accounted for by positing that in its functioning, the nervous system's activity generates a low-dimensional dynamics appropriate to the task constraints. Thus, the ensemble of neuro-muscular degrees of freedom associated with the sensorimotor system is effectively reduced to a smaller number. On the one hand, this guarantees the behavior's lawfulness. On the other hand, it explains why performances, under variations in initial conditions and stochastic fluctuations, are never exactly the same, their lawfulness notwithstanding. The dynamical approach is known for its focus on stability and loss thereof. Indeed, it has been shown that under the impact of certain task parameters, in particular, movement frequency, switches between coordinative states (i.e., phase transitions) may occur. Conceptually, such transitions play a cardinal role as, according to Synergetics, the notion of circular causality (i.e., the emergence of order parameters from nonlinear interactions of microscopic variables prescribing [aka enslaving] the behavior of the microscopic variables), and the associated dimension reduction is only theoretically guaranteed in their vicinity through the local center manifold theorem (see also Huys, Perdikis, & Jirsa, 2014, for a more in-depth discussion Consequently, though phase transitions provide a useful way to empirically identify collective variables in complex systems (Kelso, 2012), theoretically speaking, Synergetics does *not* generally allow for the conceptualization of a high-dimensional (sensorimotor) system collapsing onto a lower dimension in regimes away from phase transitions. This, admittedly narrow, view is valid only in the strict sense, in which bifurcations and phase transitions are local phenomena in the sense of proximity to an instability (as captured by Lyapunov exponents for instance). Other efforts extending this view exist, in which the mathematical basis of the dimension reduction is rooted in theorems such as the inertial manifold theorem, in which the proximity to instability is replaced by a gap condition within the characteristic time scales (Temam, 1990). It is furthermore debatable whether the majority of our behaviors are in the vicinity of phase transitions. If they were, our behaviors would be marginally stable at best, and we would typically have difficulties dealing with the smallest of perturbations, which is not the case. In practice, synergetics' concepts have been primarily developed using local center manifold theorems, which are tightly linked to phase transitions. The latter certainly capture an important component of real-world behaviors, but are insufficient to provide a full representation thereof. In other words, although the synergetic notions of circular causality and enslaving may generalize and be valid as a concept, the mathematical formalization of the concept itself is not evident and the corresponding dimension reduction may not hold in the parameter regimes, in which many real-world behaviors unfold.

How can we move forward? One way is to move beyond the constraints implicit in synergetic phase transitions and their subsequent local validity, while preserving the rule-based architecture of Coordination Dynamics. The locality constraint is absent in the framework of SFM, which moves away from specific instantiations (such as the HKB model) and rather focuses on mechanisms of generating individual realizations of behavior. The price to pay is the loss of the generic nature of the slaving principle formalism. To provide intuition, we understand games such as soccer by understanding the rules of play and understand it deeply by using these rules to build coordination motifs. This is the option that motivates the description of SFM's and is our proposal to move forward: *the goal for understanding brain and behavior is to determine the rules that govern the coordination of behavior*.

3. What are Structured Flows on Manifolds?

Structured Flows on Manifolds (SFMs) are the mathematical objects that capture the dynamic properties that a system requires for it to be capable of the behavior we discussed above. The system under consideration is high dimensional with *N* degrees of freedom and highly nonlinear. In the space spanned by these degrees of freedom, each point is a state vector and represents a potential state of the system. As time evolves, the state of the system changes and thus traces out a trajectory in state space. The rules that the system follows can be understood as forces that cause the changes of the state vector and define a *flow*. In order to allow this system to generate low-dimensional behavior, that is, *M* dimensions with *M<<N*, there must be a mechanism in place that is capable of directing the trajectories in the high-dimensional space towards the lower *M*-dimensional sub-space. Mathematically, this translates into two flow components that are associated with different time scales: first, the low-dimensional attractor space contains a manifold *f(.)*, which attracts all trajectories on a *fast* time scale; second, on the manifold a structured flow *g(.)* prescribes the dynamics on a *slow* time scale, where here slow is relative to the collapse of the fast dynamics towards and onto the attracting manifold. For compactness and clarity, imagine that the state of the system is described by the *N*-dimensional state vector *q(t)* at any given moment in time *t.* Then we split the full set of state variables into the components *u* and *s*, where the state variables in *u* define the *M* task-specific variables linked to emergent behavior in a low-dimensional subspace (the functional network) and the *N-M* variables in *s* define the remaining recruited degrees of freedom. Naturally, *N* is much greater than *M* and the manifold in the subspace of the variables *u* has to satisfy certain constraints to be locally stable, in which case all the dynamics is attracted thereto. Formally,

$$
\begin{aligned}
&\dot{u}_j = -f(u_j, s_i)u_j + \mu g(u_j, s_i) \\
&\dot{s}_i = -s_i + N(s_i, u_j) \\
&u \in \Re^M, s \in \Re^{N-M}, N >> M
\end{aligned}
$$

The flow of the nonlinear dynamic system is given by the right-hand side of the differential equations and establishes the vector field that drives the state of the system along a trajectory. Each trajectory represents one single specific realization of behavior, whereas the ensemble of all possible trajectories captures, by definition, all possible behaviors. A more compact, but fully equivalent representation of all possible behaviors is to identify the set of the rules underlying the generation of all possible behaviors (i.e., realizations), that is, the flow. The above mathematical representation via a time-scale decomposition is not unique and there may be other equivalent representations capable of capturing the same flow in state space. However, the current representation is attractive for two reasons: First, it provides a clear separation of the time scale via the smallness parameter μ, where the slow time scale is μ <<1 and the fast time scale is on the order of 1. Second, the current form has been successfully linked to networks composed of neural masses, coupled via multiplicative coupling functions, which are fundamental for the emergence of SFMs (Pillai & Jirsa, 2016). Neural masses comprise populations of neurons, which are nonlinear dynamic units coupled via synapses. The multiplicative properties are at the heart of synaptic coupling, as well as conductance-based modeling, which is currently our understanding of neuronal functioning via the Hodgkin-Huxley equations that describe the initiation and propagation of actions potentials in neurons. Mathematically, the multiplicative coupling enables the manifold to be described globally rather than just locally, as is the case of previous formal theories of self-organization. The formulation of SFMs is thus a general framework and the link to neuroscience is accomplished, for instance, when SFMs are derived from neural network equations. In these situations, the state vector *q(t)* is the vector of all activation variables across all brain regions and the SFM is the mathematical representation of the dynamics of the brain network.

4. What is the slow variable?

Given the above discussion of the "set of all behaviors" as a capture of the lawfulness of human behavior, does this mean that once we know these rules for one SFM, our understanding of behavior and its emergence from brain network dynamics is complete in this regard? Certainly not: it would be naive to assume that all behavioral rules can be captured within one flow. But those for a given task and context could. The consequence is that SFMs would need to be created and annihilated through a process evolving on a slower time scale. Switching between tasks will be linked, hypothetically speaking, to switching between modes of operation in the brain. To gain insight into how a slow process may drive the switching process, we turn towards pathologies in the brain, adding a critical element to our reflections on SFMs and model emergence.

Fundamental modeling of epilepsy has led to the postulate of the existence of a slow variable that dictates the expression of the faster seizure activity (Jirsa *et al.*, 2014). During epileptic seizures, the firing activity of billions of neurons becomes organized so that oscillatory activity emerges that can be observed in electrographic recordings. This organization greatly reduces the degrees of freedom necessary to describe the observed activity, from billions of single neurons firing to a few oscillatory collective variables. At the same time, these oscillations trigger a series of processes at the microscopic level that slowly leads towards the end of the seizure. These slow processes can also be described by a collective variable, the so-called permittivity variable, which is involved in the balance between the slowly varying pro- and anti- seizure mechanisms (Jirsa *et al.*, 2014). The permittivity variable is multifactorial and linked to various biophysical parameters that slowly change in the period preceding a seizure and during the ictal state, for example, extracellular levels of ions (Heinemann *et al*., 1986), oxygen (Suh *et al*., 2006), and metabolism (Zhao *et al*., 2011). These parameters have been related to the onset, propagation, and subsequent ending of seizures. *The slow variable drives the brain system through the creation and annihilation of the SFM, which is spanned by the fast variables*. The mathematical model that contains these fast and slow variables and that describes epileptic seizures from onset to offset is called the Epileptor. We can thus describe the evolution of a seizure with a few collective variables acting on different timescales: fast variables that, depending on the value of their parameter, can produce either resting or oscillatory activity, with bifurcations separating these different regimes; and slow variables describing the processes that brings the fast variables across the onset and offset bifurcations.

Evidence for the existence of fast and slow variables in epileptic seizures was reported recently by Saggio and colleagues (Saggio *et al*., in preparation). These authors found that, across multiple patients, most had seizures characterized by different bifurcations revealing themselves at different moments, which implies that different classes of seizure types coexist (and can described with the same model), so that ultra-slow changes in the parameters of the fast variables can bring the patient closer to one or the other seizure type. From the perspective of dynamical system modeling, this states that there must exist some slow variable dynamics (under the assumption of autonomous systems). Key to our present elaboration is the idea that the two-tiered architecture underlying brain dynamics is not only a signature of seizures, but constitutes a fundamental ingredient of brain function present in both pathological and healthy physiology.

We here propose that the slow variable dynamics plays an equally important role in healthy conditions and co-evolves together with the fast variable dynamics as the actual emergent subsystem, or in Haken's words, its “order parameters” (see figure below).

Synergetics is agnostic with regard to the number of time scales in the emergent order parameters. In our framework, however, the emergent order parameters of brain and behavior must have an intrinsic time scale separation and comprise co-evolving fast and slow variables. The fast variables act upon the slow variables and vice versa. The mutual presence of multiple time scales in the emergent order parameter system, the SFM, is reflective of the adaptive nature of the brain.

5. A Gibsonian neuroscience?

As the present paper is intended for a special issue of *Ecological Psychology*, it is pertinent to ask if, and if so, how notions cardinal to the Gibsonian paradigm can be incorporated in the dynamical two-tiered conception of the functioning of the nervous system discussed above. While not exclusive, we here briefly discuss how the proposed framework aligns with several notions pertinent to ecological psychology, or is at least readily amendable thereto (see also Kelso, 2008).

A main tenet of the ecological approach is that action is, first and foremost, guided by information. The parameters associated with the fast dynamics, that is, those governing the flow $g(.)$ may be, if not unequivocally will be, a function of the context within which an actor behaves. Effectively, due to its general formulation, under certain constraints, such as the boundedness of the flow (Jirsa & Kelso, 2005), many examples figuring in the literature on how information shapes behavioral dynamics can be fitted into our framework (Huys *et al*., 2014; Warren, 2006). To make a point in case, we here briefly discuss goal-directed aiming. As repeatedly shown, and formalized in a two-dimensional dynamical model (Mottet & Bootsma, 1999), the relation between target size and the distance between targets determines the ensuing movement kinematics observed in rhythmical goal-directed aiming (Bootsma, Boulard, Fernandez, & Mottet, 2002; Huys, Fernandez, Bootsma, & Jirsa, 2010; Lazzari, Mottet, & Vercher, 2009). That is, visual information modifies the flow governing the behavior. Pillai and Jirsa recently showed how this two-dimensional flow arises from a generic (high-dimensional) network model under appropriate connectivity among network nodes (Pillai & Jirsa, 2017). Let us further point out that a given flow *g*(.) may arise in different workspaces, that is, manifolds *f*(.) that differ in terms of their geometry. For instance, the flow governing a given sensorimotor coordination is topologically equivalent under most stimulus frequencies irrespective of whether an actor coordinates her behavior relative to a visually specified or auditory-specified event (cf. Varlet, Marin, Issartel, Schmidt, & Bardy, 2012 and references therein). That is, the relation between actor and environment is invariant if the temporal structure is identical in distinct energy arrays. Having said this, visual-motor, auditory-motor, and multimodal-motor coordination typically differ slightly in terms of established relative phases and their stability (Elliott, Wing, & Welchman, 2010; Repp & Penel, 2004; Varlet *et al*., 2012). We conjecture that, under identical (temporal) stimulus properties, such differences can, in principle, be traced back to the connectivity patterns of the sensorimotor networks implicated in these coordination patterns.

A further idea advanced by ecological psychologists is that the perception of possibilities for action, i.e., affordances, are modulated by an observer's bodily dimensions. In task contexts as different as judging the "graspability" of objects (Kim & Frank, 2016), "walk-throughability" of apertures (Warren & Whang, 1987), and "climbability" of stairs, the information used by individuals is scaled relative to their body dimensions. Such individual scaling may be conceived of as instantiations of how structure impacts function. Above, we discussed SFMs and hypothesize that their appearance and disappearance is governed by a slow variable. Previous neural modelling by one of the current authors has shown that (i) the strength of the connections across neurons or populations of neurons, captured by a connectivity matrix in modelling studies and by the connectome in brain data, may alter qualitative and quantitative aspects of the flow (Pillai & Jirsa 2017; Woodman & Jirsa, 2013), and that (ii) the multiplicative form of the coupling, in modeling captured by a neuromodulator factor, determines the emergence of the manifold (Pillai & Jirsa 2017). It is noteworthy that both studies also showed that no unique one-to-one mapping exists between network structure and ensuing dynamics; any given network may embed different flows, and, inversely, different networks may realize the same flow. That is, the networks show redundancy and degeneracy (Edelman, 1987). Regardless, both factors (connectivity, neuromodulation) vary to some degree across individuals, and thus provide a window into individual differences. (As an aside, individual differences in brain connectivity are nowadays fed into mathematical brain models to study epileptic seizure propagation as a clinical aid underlying chirurgical intervention (Jirsa *et al*., 2017; Proix, Bartolomei, Guye, & Jirsa, 2017)). That is, individual differences in brain wiring impact individual brain functioning, and may potentially (help to) account for individual differences in perceptual-cognitive-behavioral functioning, especially in cases where differences in individuals' bodily dimensions are unlikely to account for individual (perceptual) differences. A case in point, by hypothesis, are transition frequencies in the perception of ambiguous features (Ditzinger & Haken, 1989). While brain connectivity can hardly be said to have featured prominently on the Gibsonian agenda, under the proposed framework it appears, to the present authors, continuous with its previous attempts to try to understand how structure affects function, and vice versa.

Of further relevance to the discussion of the perception of affordances is the repeated finding of negative hysteresis. In this phenomenon the transition between modes occurs under a smaller magnitude of the control parameter in the descending sequence of the parameter than under its sequential increase, rather than the more established inverse, positive hysteresis (see Frank, 2015; Frank, Profeta, & Harrison, 2015; Kim & Frank, 2016; Lopresti-Goodman, Turvey, & Frank, 2013, and references in these papers). To model this phenomenon, Frank and colleagues used an approach that has important similarities with the one here advocated. Recall, the main gist of the two-tiered approach is a time-scale separation between the slow order parameter dynamics that governs the emergence and disappearance SFMs and the latter's task-specific fast dynamics underlying perceptual-cognitive-behavioral functioning. In the onset and offset of epileptic seizures, the slow dynamics arises 'from within' and a number of biophysical parameters have been identified that may be linked to the slow variable. In previous work, Perdikis and colleagues (Perdikis, Huys, & Jirsa, 2011a, 2011b) portrayed the slow variable in terms of a competition dynamics ξ 'selecting' a behavioral mode (i.e., flow) from a repertoire of modes for a given behaviorally-relevant duration. While those authors have not aimed to link the competition dynamics to task-relevant information and affordances, in later work they conjectured that the competition in many cases is likely to be information-driven (Huys *et al.*, 2014). Unbeknownst to those authors at that time, the establishment and formalization of that link has been pursued by Frank and colleagues in a number of studies (Frank, 2015; Frank *et al.*, 2015; Kim & Frank, 2016; Lopresti-Goodman *et al.*, 2013) in which they addressed affordance perception. In brief, Frank *et al*. account for switches between competing mutually exclusive perceptual-cognitive-behavioral modes via a competition dynamics ξ_i, identical to the approach pursued by Perdikis *et al*. (2011a, 2011b), following Ditzinger and Haken (1989) and Haken (1991). (In contrast to Perdikis *et al*., the modes in the studies of Frank and colleagues embodied no dynamics but were assumed to correspond to given perceptual-cognitive-behavioral states.) In Frank and colleagues' work, two parameters are associated with the competition dynamics; "availability" parameters λ_i — those defining the possibilities for a mode *i* to be realized, and between-mode interaction parameters g_i (for i = 1 to the numbers of modes available). A control parameter α, in the original synergetic sense, is incorporated by assuming the availability parameters λ_i to be a function of control parameter α and a system parameter *L* (Saltzman & Munhall, 1992). System parameters are assumed to be constant on the time scale of a perceptual-cognitive-behavioral act. Crucially, however, they may become dynamic during adaptation, learning, and development, that is, when considering time scales longer than those pertaining to a single act. In that case, and by assuming that system parameter *L* evolves in a manner that depends on which behavioral mode is active, or "on", the system parameter *L* acts as a control parameter, but one that is auto-regulated (rather than manipulated by an experimenter). The similarities between the approach developed by Frank and colleagues and the one here presented indicates that the two-tiered framework may readily incorporate ecological notions as affordance, and direct perception (for further discussion, see Frank *et al*., 2015; Lopresti-Goodman *et al*., 2013).

6. Final thoughts

We have posited that one of the major roadblocks towards a grand unified theory (GUT) of brain function is the need for an adequate representation and formalization of behavioral dynamics. This lacuna incapacitates us in two ways: first, we need a formal, theoretically grounded framework of behavior; second, we need a well-defined explanatory target for brain theories.

For the former, the task of formalizing behavior is harder than one may think initially and behavioral biologists themselves do not agree on what constitutes behavior (Levitis, Lidicker, & Freund, 2009). After systematic analysis of surveys, Levitis, Lidicker and Freund propose that behavior constitutes the set of internally coordinated actions (or inactions) of an organism in the presence of internal and/or external stimuli. The mention of coordination is noteworthy, as it underwrites the emergence of low-dimensional patterns from numerous processes and constraints (internal and external to the actor, Huys *et al*., 2014) and requires forces, aka flows, to guide the coordination. Coordination Dynamics has served this role to a large degree, but at least when restricted to phase transitions, has limited capacity to generate new insights and translate across tasks and contexts (but see, e.g. Dumas et al 2014 and Kostrubiec, et al., 2012 where this restriction does not apply). Having allowed ourselves this critical note, we see SFM as a crucial extension of Coordination Dynamics in building a new field of behavioral neuroscience focusing on the dynamic mechanisms underlying behavior, as opposed to the physiological or mechanical mechanisms (in multi-limb movements tasks for instance).

For the latter as regardsbrain theory, the consequences are more severe. For decades, the scientific community has developed the idea that behavior is adequately described by a set of quantifiers such as reaction times, movement speed, detection sensitivity, standard deviations and errors around task-specific targets (cognitive, sensory, motor), and many more. As these parameters are useful in describing behavior and performance, it is a common fallacy to equate them with parameter targets, towards which the brain should be tuned to create function. On the brain level, this form of searching optimality finds its equivalent in teleonomic attempts of optimizing information transmission (Plenz & Beggs, 2004), maximizing information (Deco & Jirsa, 2011), and minimizing Free Energy (Friston, 2010). These quantities certainly make a meaningful link to conditions underlying adequate functioning, but we should refrain from linking them to the emergent function itself, and thus will not serve satisfactorily as an emerging target of brain dynamics. As such, they do not have the capacity to guide the development of a unified theory of brain function. We hope that our proposal brings us closer to this. We here propose a two-tiered organization of brain coordination dynamics, fast dynamics linked to activation pattern dynamics in the brain and actions evolving on a time scale of hundreds of milliseconds, and slow dynamics linked to the changes of tasks, evolving on a time scale of seconds. The formalisms underlying the SFM framework are sufficiently specific to be applied to a given instantiation of a behavior, but also generalizable to capture the richness of brain dynamics that governs the corresponding richness of our thoughts and actions.

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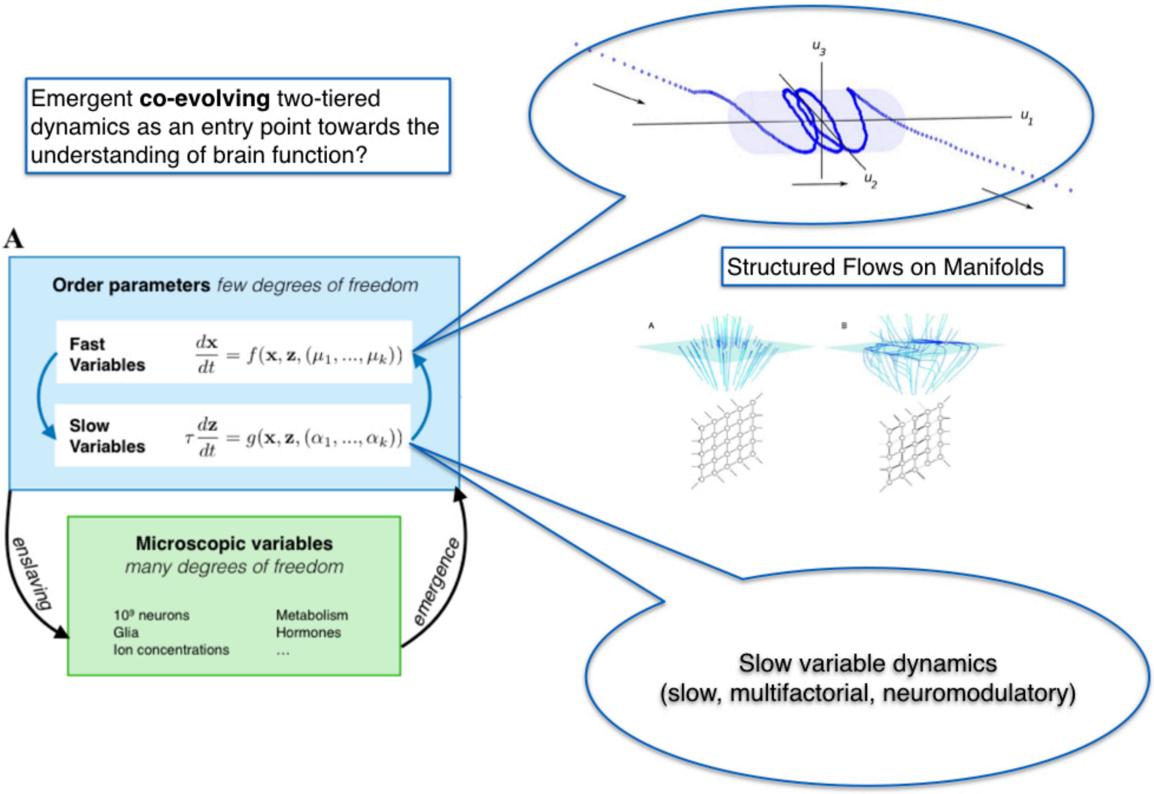
Figure captions

Figure 1: Co-evolving two-tiered dynamics of behavioral and brain organization. On the left, the brain system comprises many microscopic variables, which in self-organized interaction give rise to the emergence of a set of low-low-dimensional variables, the order parameters. These emergent order parameters are composed of at least two separate time scales, where the fast variables are linked to the execution of cognitive and action variables, and the slow variables to the creation of behavioral dynamics and context.



Emergent **co-evolving** two-tiered dynamics as an entry point towards the understanding of brain function?
A
Order parameters *few degrees of freedom*
Fast Variables $\frac{d\mathbf{x}}{dt} = f(\mathbf{x}, \mathbf{z}, (\mu_1, ..., \mu_k))$
Slow Variables $\tau \frac{d\mathbf{z}}{dt} = g(\mathbf{x}, \mathbf{z}, (\alpha_1, ..., \alpha_k))$
enslaving
emergence
Microscopic variables
many degrees of freedom
10^9 neurons
Glia
Ion concentrations
Metabolism
Hormones
...
u_3
u_1
u_2
Structured Flows on Manifolds
A
B
Slow variable dynamics
(slow, multifactorial, neuromodulatory)