

On the brain's dynamical complexity: coupling and causal influences across spatiotemporal scales

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Summary

The goal of this paper is to reflect on how neural ensembles affect one another, that is, to characterize their causal influences. The work is based on the tenets that function emerges at several levels of organization between micro- and macro-scale and unfolds on multiple time scales. Such dynamical context creates the condition for complexity and blurs the classical Shannonian definition of transmission upon which causality can be unambiguously established. Our arguments are supported by analysis of models of and empirical support for spatiotemporally metastable brain dynamics: a scale-independent self-sustained regime in which integration (tendencies for the parts to act in a coordinated manner) and segregation (tendencies for independent behavior) are simultaneously realized in space and time.

1 Introduction

Function is a fundamental concept for biological systems. It rests on two foundations. The first one is *coordination* between parts of the system. As a matter of fact, it is difficult to imagine any function produced by just one biological entity: a single thing “is” but does not “do”. In effect, exchange of information, energy or matter between parts creates functional coupling or synergies, from which function emerges [1]. The second foundation is *dynamics*: for the system to adapt to ever changing external and internal milieu, it is proscribed that interactions between its parts would be fixed. This is most evident when studying the cognitive brain. If spatiotemporal patterns of brain activity ever freeze rather than perpetually change, thinking, memory, perception, emotion, action and consciousness vanish hopelessly. Within the framework of Brain Coordination Dynamics, and its key concept, metastability [1-3], here we explore how functionally meaningful neural ensembles influence each other. After a theoretical discussion of concepts (section 2), we will consider two types of informational paths, that of synaptic coupling of neurons (sections 3-4), and that of extracellular neuromodulation of neural ensembles by global neural fields (section 5).

2 Functional coupling: irregular contours in space~time

The brain exhibits organized activity at many spatial and temporal scales, in which neural ensembles couple and uncouple dynamically. This complex spatiotemporal patterning has been demonstrated empirically, both at rest and during interaction with the environment. The fact that change in spatiotemporal organization arises spontaneously (and with it, associated itinerancy of the mind) imposes specific constraints on our theories of the brain: a plausible theory should explain changing spatiotemporal patterns from within, without resort to inexplicit control mechanisms, the brain's *deus-ex-machina*. Theories have proposed that the brain's dynamically coordinated behavior is accomplished under the rule of attractors [1,4-5] or more flexible attractor remnants [1,3,6] or both [2]; in the presence of attractors, spontaneous changes in brain coordination dynamics are obtained from multistability on one end, and noise (rest) or incoming energy (stimulation) on the other; in the absence of attractors, spontaneous changes naturally occur as attractor remnants are successively visited and escaped from. A model of coupled oscillators

Brain dynamics across spatiotemporal scales

that exhibit simultaneous phase-locking (attractors) and metastability (attractor remnants) is that of Kuramoto and Battogtokh [7]. In this model, oscillators that do escape phase-locking were initially described as following an “incoherent” behavior [7]. We have demonstrated that their dynamics exhibited dwell–escape patterns of relative phase behavior that is characteristic of metastability [8]. Study of this model revealed that integrative tendencies exist within irregular space–time contours (fig.1). Over time, larger or smaller ensembles integrate their activity, and from the complementary spatial standpoint, oscillators join collective behavior for longer or shorter periods of time. The resulting space-time portrait of this behavior (in the Minkowski sense) reveals irregular contours: a challenge for separate spatial or temporal approaches (see boxes, fig.1) that if not addressed, limits our understanding of brain complexity.

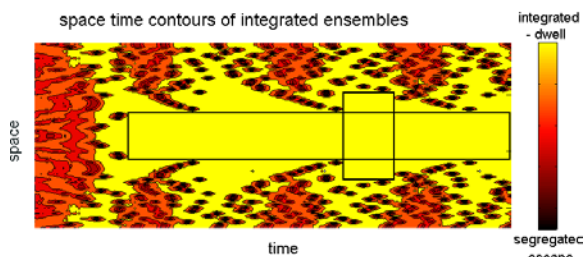


Fig.1: From Kuramoto and Battogtokh’s chimera model [7], a space~time portrait of integration is shown. Oscillators are represented on the vertical axis and their partaking in collective behavior over time (horizontal axis) is encoded following the color scale on the right (integrative tendencies in yellow; segregative in dark red). Integrative behavior emerges in a space~time domain that has irregular contours (yellow surface) which are not properly captured by techniques that follow only a spatial or temporal approach: as black rectangles suggest, only a fraction of the integrative behavior is expressed in such partial approaches, namely those with less complex and dynamical coordination behavior.

By relaxing the constraints on spatial and temporal order simultaneously (fig.2), spatiotemporal metastability also presents the joint possibility for integrative behavior and information flows. It offers a

compromise between two radical views in which the brain is deemed to function in terms of information propagation (in the strict Shannonian sense) or coupled oscillations [e.g. 1,4-5,9]. Yet, metastability creates difficulties with the interpretation of the direction of information flow which emerge at multiple levels of description and become dependent on spatial and temporal scales, as we further discuss in section 3.

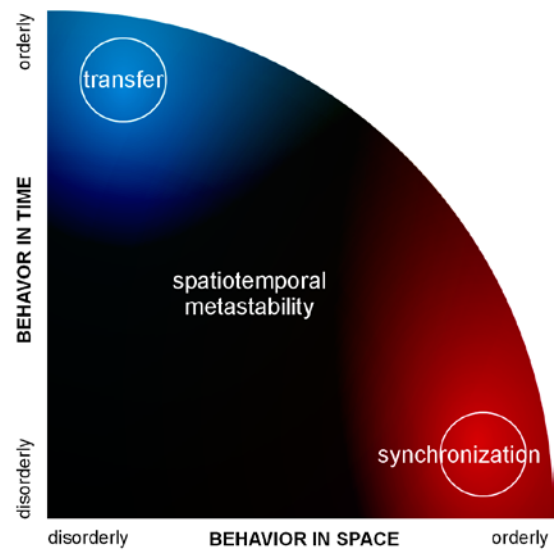


Fig.2: A conceptual view of the spatial and temporal order in the behavior of neural ensembles. Concepts of order in time (blue, “transfer”) and space (red, “synchronization”) have been most studied. In their pure form, each hampers the meaningful expression of the other. Complexity lives in the dark areas of this diagram (spatiotemporal metastability) -with its mixture of integrative and segregative tendencies in space~time.

3 Causality in simple and complex systems

Coupling is a concept more akin to spatial order (section 2), whereas causality relates more closely (albeit not exclusively) to temporal order. In this latter respect, a substantial part of today’s neuroscience paradigm draws from Shannon’s “Mathematical Theory of Communication” (1948) [10]. This seminal paper describes transfer of information between emitter and receiver in

Brain dynamics across spatiotemporal scales

telecommunication networks, and implies two fundamental boundaries: discrete communication acts, and well-defined direction for the transfer of information in unique channels. In a single channel of communication with emitter and receiver as defined by Shannon [10], to define causality, it suffices to track the temporal ordering of information to determine the system's causal flows. The paradigm's success in Neuroscience owes much to the fact that it works sufficiently well insofar as only two brain components are isolated: with their directional interactions, a pair of neurons immediately comes to mind as an ideal substratum for Shannonian transmission. Even in a more complicated system composed of multiple components and reciprocal connectivity, if the system is initially silent and then subjected to external stimulation, its transmission path(s) can readily be identified. But the brain as a whole is operating in a self-sustained nonequilibrium regime [1,6,11-13], and is not amenable to such formalism: if observed for sufficient time especially at meso- and macro-levels, it is clear that parts of the brain "talk" continuously and simultaneously to each other: they are self-organized. When there is energy input coming in (for instance, a stimulus entering the system through sensory receptors), what happens is not the recruitment of mute regions that suddenly enter into action -each at their turn- and return to rest. What happens instead is that the ongoing coordination is "perturbed" and ripples across the many spatial and temporal scales at which brain self-organization lives. The "event" is woven into the brain's ongoing activity. In this (general) case, causal influences between brain parts are much less straightforward to define. Since information flows cannot be described as departure from equilibrium states, well-defined causality is restricted to narrow spatiotemporal windows in the vicinity of a particular "input" or "event" (see also fig.5 from Izhikevich and Edelman [14] for related account). And because observation windows are finite, empirical quantifications of information flows are restricted: lack of information about the system's past prevents accurate characterization of ongoing dynamics and its coupling with incoming information (see section 4).

4 Entangled precedence

We have argued that spatiotemporal metastability prevents stagnation of information flow, while simultaneously allowing for collective (coordinated) behavior (fig.2). The challenge becomes to determine which brain parts influence which others, through space and time, and across their respective scales of observation (fig.3). When emitter and receiver are not *a priori* defined, a useful concept is that of precedence (section 3). However, even in the simpler case of the resting brain transiently removed from external input, its intrinsic dynamics includes continuous exchange of information between the parts (A-causes-B-causes-A...), and salient "causes" to any neural event exist at multiple times in the history of the system's self-organized dynamics: causes are entangled over continuous and reciprocal information exchange. To understand spatiotemporal influences between brain parts requires one to confront this "entangled precedence": that is, to incorporate precedence and causality from Shannonian systems (section 3) with ongoing coupling expressed at multiple time scales (section 2), which, under metastable regimes of coordination, fluctuates over time.

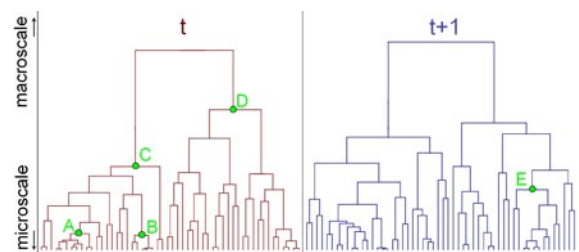


Fig.3: Functional nodes across spatial scales shown at two successive time points t and $t+1$: the dendrograms link microscopic parts (bottom) according to their momentary coupling. Every node influences every other at all times, with a finite strength $k(i_i, j_{ij})$. A few nodes are marked to exemplify upward and downward causation (e.g. influence of B on C, and vice-versa), instantaneous (e.g. A on B) and delayed (D on E) causality. An important challenge is to discover key causal nodes in this system: which set of relationship is strongest across spatial scales, within and across time [15].

Rather than attempting to identify causality in a time-independent manner, a solution consists of quantifying its manifold expression across temporal and spatial scales (which are interrelated: see e.g. fig.1). Fig.3 shows a dendrogram that clusters phase similarity of neural ensembles over spatial scales at different times. Each node of the dendrogram speaks of a transient neural ensemble, which exerts a finite influence k on each of the other nodes. The strongest directional couplings between pairs of nodes in the system reveal key causal relationships.

5 Beyond synapses: dendritic sensing of the extracellular field

So far, we have only explored (slow) information exchange via synaptic coupling. This scheme of information exchange suffers delays of several tens of milliseconds for the communication of information between most distant neural groups. Dendritic trees however are exposed to two types of information: that delivered through their synaptic contacts and that due to local fluctuations in the ionic composition of extracellular space. This raises the theoretical possibility that neurons attune themselves to specific aspects of extracellular fields, using their spatially extended dendritic branches to appreciate extracellular gradients and to sense the global patterning of the brain near-instantaneously. According to this suggested mechanism, the brain would be endowed with two ways to exchange information, one global and fast, the other local or selective and slow. Such a mechanism could have a profound impact on the definition and quantification of coupling and causality in the brain.

5 Conclusion

Identifying information flows in the brain constitutes an important challenge with significant consequences: for instance, with such knowledge, ideal functional nodes for therapeutic intervention could be discovered and operationalized. We have stressed that brain complexity constitutes an obstacle to the unambiguous and unique definition of causal paths in the brain. We discussed whether causality : 1) is uniquely defined by the structural network; 2) is context-dependent; 3) flows in an identical manner

across spatial scales of description; and 4) is expressed in a similar manner across different temporal scales. These considerations point toward the importance of spatiotemporally metastable dynamics for understanding the workings of the brain.

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References

- [1] Kelso, J.A.S. (1995). *Dynamic Patterns: the Self-organization of Brain and Behavior*. Cambridge, MIT Press.
- [2] Kelso, J.A.S., Tognoli, E. (2007). *Toward a Complementary Neuroscience: Metastable Coordination Dynamics of the Brain*. In R. Kozma & L. Perlovsky (Eds.) *Neurodynamics of Higher-level Cognition and Consciousness*. Springer, Heidelberg.
- [3] Tognoli E., Kelso J.A.S. (2009). *Brain Coordination Dynamics: True and False Faces of Phase Synchrony and Metastability*. *Prog. Neurobiol.*, 87(1): 31-40.
- [4] Freeman, W.J. (1975). *Mass Action in the Nervous System*. New York: Academic Press.
- [5] Bressler, S.L., Tognoli, E. (2006). *Operational Principles in Neurocognitive Networks*. *Int. J. Psychophysiol.*, 60: 139-148.
- [6] Tsuda, I. (1992), *Dynamic Link of Memory--Chaotic Memory Map in Nonequilibrium Neural Networks*. *Neural Networks*, 5: 313-326.
- [7] Kuramoto, Y., Battogtokh, D. (2002). *Coexistence of Coherence and Incoherence in Nonlocally Coupled Phase Oscillators: a Soluble Case*. *Nonlin. Phenom. Complex Syst.* 5: 380-385.
- [8] Kelso, J.A.S., Tognoli, E. (*in prep*). *The Metastable Brain*.
- [9] Hebb, D.O. (1949). *The Organization of Behavior*. New York: John Wiley.
- [10] Shannon, C.E. (1948). *A Mathematical Theory of Communication*, *Bell System Technical Journal*, 27, 379–423, 623–656.

Brain dynamics across spatiotemporal scales

- [11] Fuchs, A., Kelso, J.A.S., Haken, H. (1992). Phase transitions in the human brain: spatial mode dynamics. *International Journal of Bifurcation and Chaos*, 2(4): 917-939.
- [12] Kelso, J.A.S., Bressler, S.L., Buchanan, S., De Guzman, G.C., Ding, M., Fuchs, A., Holroyd, T. (1992). A phase transition in human brain and behavior. *Phys Lett A*, 169:134–144.
- [13] Chialvo, D. (2010). Emergent Complex Neural Dynamics. *Nature Phys.* 6: 744-750.
- [14] Izhikevich, E.M., Edelman, G.M. (2008). Large-scale Model of Mammalian Thalamocortical Systems. *Proc Natl Acad Sci USA*, 105: 3593-3598.
- [15] Sporns, O. (2011). *Networks of the Brain*. Cambridge: MIT Press.