Neuron
Perspective

The Metastable Brain

Emmanuelle Tognoli[1,*] and J. A. Scott Kelso[1,2,*]
[1]The Human Brain and Behavior Laboratory, Center for Complex Systems and Brain Sciences, Florida Atlantic University, 777 Glades Road, Boca Raton, FL 33431, USA
[2]Intelligent Systems Research Centre, University of Ulster, Magee Campus, Northland Road, Derry BT48 7JL, Northern Ireland, UK
*Correspondence: tognoli@ccs.fau.edu (E.T.), kelso@ccs.fau.edu (J.A.S.K.)
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Neural ensembles oscillate across a broad range of frequencies and are transiently coupled or "bound" together when people attend to a stimulus, perceive, think, and act. This is a dynamic, self-assembling process, with parts of the brain engaging and disengaging in time. But how is it done? The theory of Coordination Dynamics proposes a mechanism called metastability, a subtle blend of integration and segregation. Tendencies for brain regions to express their individual autonomy and specialized functions (segregation, modularity) coexist with tendencies to couple and coordinate globally for multiple functions (integration). Although metastability has garnered increasing attention, it has yet to be demonstrated and treated within a fully spatiotemporal perspective. Here, we illustrate metastability in continuous neural and behavioral recordings, and we discuss theory and experiments at multiple scales, suggesting that metastable dynamics underlie the real-time coordination necessary for the brain's dynamic cognitive, behavioral, and social functions.

Introduction

> Today we know that neurons fire and we know that they are connected. We don't know how they act in concert to govern behavior, the essential question in treating neurological disease and mental-health disorders (Allen and Collins, 2013).

The life of a brain is marked by a vast number of ongoing electrical and chemical processes spanning multiple spatial and temporal scales (Pritchard, 1992; Linkenkaer-Hansen et al., 2001; Kozma et al., 2005; Honey et al., 2007; Plenz and Chialvo, 2009; Werner, 2010; Lowen et al., 1997) that both arise from and modulate interactions with the body and the environment (Edelman, 1999; Thompson and Varela, 2001; Sporns, 2003; Kiebel et al., 2008; see also Longtin et al., 2003). Such processes take place in a network of cells whose organization emerges at multiple levels, as a result of phylogeny and ontogeny (Deacon, 1990; Krubitzer, 2009; Zhang and Poo, 2001; Chklovskii et al., 2004; Casanova et al., 2007; see also Kaiser et al., 2010). In such complex systems, space and time comingle; not much is to be gained by treating them separately or in turn. An obstacle to understanding the brain resides in our difficulty to incorporate both spatial and temporal dimensions in a common theoretical and analytical framework (Elbert and Keil, 2000; Tognoli and Kelso, 2013; Kelso, 1995; Kelso et al., 2013). Resulting from complex interactions in space-time, the coordinative "acting in concert" behavior of neural ensembles lies between the dual poles of segregation (tendencies for neural ensembles to diverge and function independently) and integration (tendencies for neural ensembles to converge and work together) (Tononi et al., 1994; Kelso, 1991, 1992, 1995; Friston, 1997; Sporns et al., 2004; Kelso and Tognoli, 2007; Pitti et al., 2008). Such coordination happens dynamically, with ensembles of various sizes coming together and disbanding incessantly (Eguíluz et al., 2005; Kozma et al., 2005; Plenz and Chialvo, 2009).

The theoretical framework elaborated here is called Coordination Dynamics (Kelso, 1995, 2009; Fuchs and Jirsa, 2007; Tschacher and Dauwalder, 2003; see also Von der Malsburg et al., 2010 for a related "dynamic coordination" view). Originally grounded in the concepts and methods of self-organized pattern formation in physics, chemistry, and biology (Haken, 1983) and the tools of nonlinear dynamical systems, Coordination Dynamics embraces both spontaneous self-organizing tendencies and the need to guide or direct such tendencies in specific ways. In Coordination Dynamics, the system's parts and processes communicate via mutual information exchange, and information is meaningful and specific to the forms coordination takes. Coordination Dynamics seeks to identify and then track the temporal evolution of coordination or collective states, emergent quantities that specify how the linkage between components and processes changes over time. The rationale behind this perspective is that the function of a complex biological system lies in the interaction between (context-sensitive) components (see also Pattee, 1976; Miller and Phelps, 2010). In an open, nonequilibrium system, in which many components have the opportunity to interact, some ordering in space and time emerges spontaneously due to self-organization (Kelso and Haken, 1995; Laughlin and Pines, 2000). As a consequence, pattern formation and change may take the form of lower dimensional dynamics (Haken, 1983; Kelso, 2009; Schöner and Kelso, 1988), a plus in the case of large systems (e.g., $\sim 10^{10}$–10^{11} neurons; Williams and Herrup, 1988; Lent et al., 2012).

In Coordination Dynamics, coordination variables are key quantities that specify functionally meaningful collective behaviors such as pattern generation in neural circuits (Grillner, 1975; Kelso, 1984, 1991; Marder, 2001; Schöner and Kelso, 1988; Yuste et al., 2005). Coordination variables span domains or subdomains (components, processes, and events): they may encompass entities that are often assumed to be incommensurable (Kelso, 2009; Tognoli et al., 2011). In the complex systems of living things, coordination variables are not known in advance but have to be