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Review

Functional interactions between intrinsic brain activity and behavior

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ABSTRACT

The brain continuously maintains a remarkably high level of intrinsic activity. This activity is non-stationary and its dynamics reveal highly structured patterns across several spatial scales, from fine-grained functional architecture in sensory cortices to large-scale networks. The mechanistic function of this activity is only poorly understood. The central goal of the current review is to provide an integrated summary of recent studies on structure, dynamics and behavioral consequences of spontaneous brain activity. In light of these empirical observations we propose that the structure of ongoing activity and its itinerant nature can be understood as an indispensible memory system modeling the statistical structure of the world. We review the dynamic properties of ongoing activity, and how they are malleable over short to long temporal scales that permit adapting over a range of short- to long-term cognitive challenges. We conclude by reviewing how the functional significance of ongoing activity manifests in its impact on human action, perception, and higher cognitive function.

Contents

Introduction

The brain is often compared to a computer or related metaphors. But unlike man-made computers that are highly modular the brains themselves that designed such computers have a very different layout. In the brain, the counterparts of a central processor, the software and the data memory seem to be housed in one and the same entity. This entity is the brain's wiring structure or “connectome”, a structure that is continuously modified by memory traces from development and experience. Radically different from computers, operational memory encoded by the connectivity structure is permanently at least partially replayed even in the absence of extrinsically induced processing demands. This process underpins the observation of “spontaneous” or intrinsic activity. Moment-to-moment fluctuations of intrinsic activity hence reflect the past history of the system but they also influence present and future operations. Current operations in turn again leave traces and thereby shape the connectivity pattern. In the following, we elaborate on this condensed sketch in more detail.

First, we discuss this two-way relation between intrinsic brain activity and operations underlying perception and behavior. The material reviewed speaks to this interaction as an essential feature of the brain's processing architecture rather than an epiphenomenon of neurophysiological mechanisms. It further suggests that to adequately understand brain function one needs to deepen the empirical study of intrinsic neural activity and conceptually incorporate these results into functional models.

Throughout this review, we discuss relevant research from the perspective of what it tells us about the functional role of spontaneous brain activity. In the first section, we describe how the structure of ongoing activity reflects a memory system modeling the statistical structure of the world. We then discuss why brain function requires

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such an internal model, and finally propose reasons for why this model operates in an itinerant fashion. The second section characterizes more closely the dynamic structure of ongoing activity. We discuss how this structure is malleable over short to long temporal scales permitting to adapt to cognitive challenges ranging from current perception to gradual learning. The last section describes how, as a consequence, itinerant ongoing activity fluctuations affect human perception and behavior.

Ongoing activity and the brain's internal memory of external causal dynamics

Functional importance of ongoing brain activity is suggested by its continuous presence and its sheer amount on top of which evoked brain responses appear as minor perturbations. Ongoing activity hence accounts for the bulk of brain energy consumption, which in turn constitutes 1/5 of total body energy expenditure (Raichle, 2009). The most striking property of intrinsic activity is that it fluctuates spontaneously. Over several orders of magnitude across both time and space these fluctuations are highly structured (for a discussion on temporal and spatial characteristics see Sadaghiani et al., 2010). We propose that this spatiotemporal structure of ongoing activity is a way of replaying intrinsic, operational network memory. Here, we use the term memory to refer to the sum of the system's evolved connections, recent activity history, and current context that are reflected in dynamic network states. The notion of memory thus encompasses structural network connectivity (Fuster, 1997), functional connectivity continuously expressed on the structural connectivity backbone (Lewis et al., 2009), and context-sensitive dynamics of these ongoing activity patterns (Fontanini and Katz, 2008; Stopfer and Laurent, 1999). We thereby integrate several perspectives on memory. This means that our usage of the term extends beyond the usual cognitive notion of what memory is.

Orientation preference maps of primary visual cortex provide an intuitively accessible illustration of network memory and of its continuous reactivation in a spatio-temporal activity structure. The spatially ordered organization of orientation columns directly reflects observable regularities of the world, specifically continuous edges and contours of particular orientations. This structural organization is expressed in functional connectivity through reactivation of and rapid switching between different iso-orientation domains (~40 ms per state, Kenet et al., 2003; cf. Fig. 1A). Importantly, these functional dynamics are continuous as demonstrated during anesthesia, i.e., mental states arguably lacking consciousness and perception. Although in principle present at birth (Wiesel and Hubel, 1974), this mesoscopic organization of structural (and by consequence functional) connectivity is highly dependent upon and shaped by visual experience over the course of early development. Cats raised in environments that lack certain spatial orientations will develop aberrant orientation preference maps and show deficient perceptual responses to stimuli of the respective orientation (Blakemore and Cooper, 1970; Blasdel et al., 1977). Notably, experience- and activity-dependent changes continue to shape these maps in the adult visual cortex (Dragoi et al., 2000; Godde et al., 2002).

Recurrent co-activation patterns also occur at larger spatio-temporal scales. At these scales they represent more complex levels of regularities in the environment, of our perceptions and actions in it, and of our internal "world". At the mesoscopic level illustrated above, the

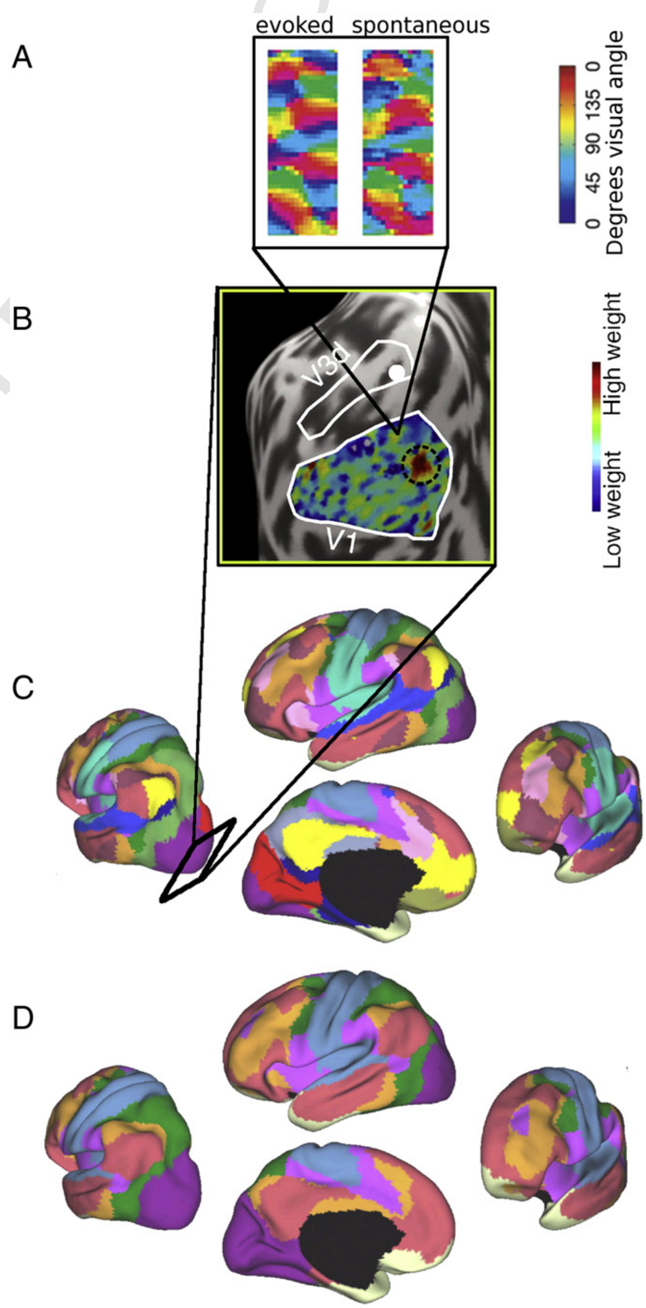

Fig. 1. Hierarchical spatio-temporal structure of ongoing brain activity. A) On a very fine spatial scale spontaneous activity in V1 displays highly structured spatio-temporal patterns that closely resemble those evoked by selective stimulus features, i.e. edges and contours of particular orientations (color coded according to visual angle). Ongoing activity is coherent across neural populations with a similar orientation preference, and switches iteratively between iso-orientation domains of the pinwheel maps. Optical imaging results from few mm^2 of cat V1 under anesthesia (modified from Kenet et al., 2003). B) On a larger spatial scale ongoing activity is spatio-temporally structured in retinotopic maps. The color code illustrates the predictive power of V1 voxels (distribution of weights of the optimal linear combination of signal time courses) to predict spontaneous activity fluctuations of the V3 voxel marked by a white dot. The V1 area of highest predictive power (dashed circle) corresponds to the same position in retinotopic space as the predicted V3 voxel. Functional MRI of human occipital cortex during resting wakefulness. Posterior view of the inflated occipital cortical surface (modified from Heinzle et al., 2011). C) At a yet larger spatial scale spontaneous activity delineates large subdivisions within visual cortices. These are driven by topographic eccentricity, however, on a very coarse scale of a central (purple) and a peripheral sub-system (bright red). Functionally connected regions include local sensory networks such as the visual subdivisions, but also distributed networks of association regions. Here, 17 intrinsic functional connectivity networks (ICNs, represented by different colors) are estimated. D) These local and distributed ICNs can be defined at different levels of the correlation hierarchy. This time, the brain is parceled into 7 ICNs, and several ICNs previously segregated in finer subdivisions in B) are now unified into larger ICNs at this coarser level of spatio-temporal organization. C–D) Human functional MRI during resting wakefulness. Surface-based views of the left hemisphere. Areas that show coherent activity fluctuations (functional connectivity) are marked by the same color (modified from Yeo et al., 2011). This figure illustrates that multiple spatial levels of functional connectivity are hierarchically embedded and concurrently present in the brain. Note that temporal scale might be tightly linked to spatial scale. While spontaneous iso-orientation domains switch in tens of milliseconds (A) large-scale networks observed with fMRI show activity fluctuations on the order of tens of seconds (C–D).

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