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Cortical computations via metastable activity

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Metastable brain dynamics are characterized by abrupt, jump-like modulations so that the neural activity in single trials appears to unfold as a sequence of discrete, quasi-stationary 'states'. Evidence that cortical neural activity unfolds as a sequence of metastable states is accumulating at fast pace. Metastable activity occurs both in response to an external stimulus and during ongoing, self-generated activity. These spontaneous metastable states are increasingly found to subserve internal representations that are not locked to external triggers, including states of deliberations, attention and expectation. Moreover, decoding stimuli or decisions via metastable states can be carried out trial-by-trial. Focusing on metastability will allow us to shift our perspective on neural coding from traditional concepts based on trial-averaging to models based on dynamic ensemble representations.

Recent theoretical work has started to characterize the mechanistic origin and potential roles of metastable representations. In this article we review recent findings on metastable activity, how it may arise in biologically realistic models, and its potential role for representing internal states as well as relevant task variables.

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Introduction

Brain circuits consist of large neural networks, where populations of neurons are recurrently coupled via synaptic connections. These circuits can be interpreted as dynamical systems with many coupled degrees of freedom and therefore capable of generating a wealth of dynamical behaviors on very diverse timescales [1]. Those include transient relaxations towards a point or line attractor, oscillatory patterns, chaotic dynamics or metastable activity [2,3]. These dynamical behaviors have been implicated in important brain functions. Transient relaxation to stable neural activity (such as a point or line attractor) may subserve memory [4,5] and perceptual decisions [6,7]. Oscillatory dynamics may subserve respiration, locomotion, and other rhythmic forms of behavior [8,9]. Chaotic dynamics amplify random perturbations and, when successfully tamed by learning, can generate complex computations [10,11]. Metastable dynamics, initially characterized in the presence of a sensory stimulus [12,13], might underlie a range of internal computations during cognitive tasks [14••,15,16••,17••].

Relaxations to an attractor, oscillations and chaotic dynamics typically describe neural activity as smoothly varying over time [18,19]. In contrast, metastable dynamics are characterized by abrupt, jump-like modulations so that neural activity appears to unfold as a sequence of discrete, quasi-stationary 'states'. Metastable activity is being found in an increasing number of brain structures of different species engaged in a variety of tasks, and is the focus of this opinion. The intuitive appeal of metastable activity is that it resonates with our intuition that our thoughts and actions proceed along a sequence of distinct episodes, as we scan alternatives and ponder potential options during everyday tasks. It is natural to think that such episodes are being represented in transient but well-defined neural patterns in our brains. Recent models have started to clarify how metastable activity could emerge spontaneously as a collective phenomenon via attractor dynamics in spiking networks [20••,21,22••,23••]. These models have proved powerful tools to investigate the circuit origin of metastable states and their potential role in sensory and cognitive processes.

In this article we review recent progress in the analysis of metastable state sequences, focusing on issues of detection, modeling and interpretation.

Observing metastable activity

Metastable states were first characterized in electrophysiological recordings from the prefrontal cortex of monkeys performing a delayed localization task [12,24,25]. Spike counts from simultaneously recorded neurons were