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Population-wide distributions of neural activity during perceptual decision-making

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A B S T R A C T

Cortical activity involves large populations of neurons, even when it is limited to functionally coherent areas. Electrophysiological recordings, on the other hand, involve comparatively small neural ensembles, even when modern-day techniques are used. Here we review results which have started to fill the gap between these two scales of inquiry, by shedding light on the statistical distributions of activity in large populations of cells. We put our main focus on data recorded in awake animals that perform simple decision-making tasks and consider statistical distributions of activity throughout cortex, across sensory, associative, and motor areas. We transversally review the complexity of these distributions, from distributions of firing rates and metrics of spike-train structure, through distributions of tuning to stimuli or actions and of choice signals, and finally the dynamical evolution of neural population activity and the distributions of (pairwise) neural interactions. This approach reveals shared patterns of statistical organization across cortex, including: (i) long-tailed distributions of activity, where quasi-silence seems to be the rule for a majority of neurons; that are barely distinguishable between spontaneous and active states; (ii) distributions of tuning parameters for sensory (and motor) variables, which show an extensive extrapolation and fragmentation of their representations in the periphery; and (iii) population-wide dynamics that reveal rotations of internal representations over time, whose traces can be found both in stimulus-driven and internally generated activity. We discuss how these insights are leading us away from the notion of discrete classes of cells, and are acting as powerful constraints on theories and models of cortical organization and population coding.

Contents

Abbreviations: A1, primary auditory cortex; LIP, lateral intraparietal cortex; IT, inferotemporal cortex; M1, primary motor cortex; M2, secondary motor cortex; MT, mediotemporal cortex; OFC, orbitofrontal cortex; PFC, prefrontal cortex; S1, primary somatosensory cortex; S2, secondary somatosensory cortex; V1, primary visual cortex; V2, secondary visual cortex.

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1. Introduction

Over the course of the last century, studies based on lesions, electrophysiology, fMRI, and other methods have quite successfully mapped out where different types of information are represented in the brain (Kandel et al., 2000). During the same period, our understanding of the single neuron and its role in the brain has increased substantially (Koch, 1999). While both research directions have created a wealth of knowledge about the organization of the brain, a large gap remains between them. At the center of this gap lie neural networks—thousands or millions of interconnected neurons, responding in myriad ways to whatever task an organism is engaged in. The number of degrees of freedom in these neural populations explodes, a phenomenon known as the "curse of dimensionality". This dimensionality explosion creates a tremendous challenge to unravel how information in populations of neurons is processed and represented. One challenge is to understand the structure and plasticity of these networks, one to link this structure and plasticity to the generated activity, and one challenge is to describe and interpret this activity. This latter problem will be the focus of our review.

What defines a neural population and how should we represent its activity? A neural population is a collection of single cells in a given region or area of the brain. Accordingly, the population activity is just the collection of the respective single cell activities. A common view is that if a large class of cells is activated by the same type of information, e.g., a feature of a visual stimulus, then any differences in their responses are noise that must be averaged over. At the other extreme, the details of every single neuron matter, and the activation of each neuron has to be considered separately. In this review, we will attempt to strike a balance between these extremes, and center on the statistical approach to characterizing population activity. The statistical approach aims to quantify the probability with which a set of features is represented in a population of neurons.

Such a quantitative, probabilistic description of the population activity will be useful on three fronts. First, it shows how information is embedded in population activity and may thereby expose widespread organizational principles or statistical patterns that are shared across brain areas. Second, such an understanding may help to study the computations carried out in a given circuit. Third, a statistical description of population activity imparts