Traveling Electrical Waves in Cortex: Measurements with Optical Imaging Techniques and Insights from Phase Dynamics

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The theory of coupled phase oscillators [1] provides a framework to understand the emergent properties of networks of neuronal oscillators [2]. Such oscillators are a common feature in many brain areas [3]. When the architecture of the network is dominated by short-range synaptic connections, the pattern of electrical output is predicted to correspond to traveling plane and rotating waves of electrical activity, in addition to synchronized output. Here we discuss the experimental evidence for such patterns, and argue that the theory of coupled phase oscillators provides the foundation for understanding the traveling electrical waves that are observed in a variety of species.

We present the results of experiments on three preparations in which the issue of large-scale electrical activity was addressed, all of which involved the response to natural stimuli in the intact brain of awake animals. These include: (i) the central olfactory organ of the mollusk *Limax maximus* [4;5]; (ii) the primary visual cortex of turtle, *Pseudemys scripta* [6;7]; and (iii) the visuomotor cortices of cat [8]. The data collection involved the use of multiple-site electrical techniques, both with standard electrodes and with optical imaging technology in conjunction with voltage sensitive dyes [9].

The data reveal that waves are typically present during periods outside of stimulation, while synchronous or near-synchronous activity typically dominates in the presence of a strong stimulus [2]. We suggest that the continuum of phase-shifts during periods with traveling waves provide a means to scan and categorize the incoming sensory stream for novel features. Experiments to test the validity of the phase oscillator approach, as well as computational aspects of wave motion, are presented [2]. We further discuss possible mechanisms for the switch from patterned electrical activity to synchrony [10].

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