# DURING THE TRAVEL SEASON, THE LOCALS CHANGE OVER TIME

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**Abstract**

Studies of sensory-evoked neuronal responses often focus on the average spike rate, with fluctuations evaluated as internally generated noise. However, fluctuations in spontaneous activity, often organized in the form of moving waves, forming stimulus reactions and sensory sensitivity. The mechanisms underlying these waves are unknown. Moreover, it is not clear that there is no waves correspond to low speed and weakly correlated "asynchronous-disorder"

dynamics observed in cortical recordings.

**Keywords:** spatiotemporal dynamics***, neuroscience, postsynaptic***

***Membrane, approximate balance, high-density, modulation, coding perspective.***

Introduction

A well accepted hypothesis in computational neuroscience is that cognition emerges from the collective interaction of many neurons networked together in the brain. Considering the neuron as the atomic unit of cognition, the brain may then be thought of as a high-dimensional dynamical system in which the membrane potential of each neuron comprises a separate dimension. The dynamics of neural activity in such a network are called spatiotemporal dynamics, reflecting that the neural activity varies in both space and time. It is thus cardinal to understand both the origins and mechanisms of spatiotemporal dynamics in the brain to arrive at a systematic understanding of cognition.

The origins of dynamics in neural networks are intricate (Destexhe et al., 2003). At any given moment in time, a neuron's membrane potential depends on all the synaptic inputs it receives from other neurons. The magnitude of these synaptic inputs is proportional to the number of action potentials fired by the presynaptic neuron. Thus, the postsynaptic membrane potential may be weakly or strongly modulated. Synaptic inputs may be excitatory or inhibitory, meaning they stereotypically increase or decrease the postsynaptic membrane potential, respectively. Furthermore, the overall conductance and current of the postsynaptic neuron depends on the synaptic input, thereby adding another source of variability. All together, the postsynaptic neuron then "spikes" (fires an action potential) if its membrane potential exceeds a threshold. These outgoing spikes are responsible for synaptic inputs to other neurons. At the network level, the complex dynamics of individual neurons combine via immense recurrent connectivity to give rise to especially nontrivial and complex spatiotemporal dynamics.

The activity of cortical neurons is highly variable with respect to spontaneous activity as well as responses to the exact same stimulus. The sources of this variability have been the subject of study for the past several decades. One potential source is the spike-generating mechanism, but Mainen and Sejnowski showed that spike timing is highly reliable in vitro, given realistic input current (Mainen and Sejnowski, 1995). Rather, neural variability is generally considered to arise in neural circuits predominantly from the dense synaptic input to individual neurons, which fluctuate from moment to moment. These fluctuations are well explained by two related sources. First, there is an approximate balance between excitatory and inhibitory synaptic inputs (Brunel, 2000). Second, the large barrage of spikes impinging on postsynaptic neurons in neocortex renders conductances to generally remain high, making membrane potential fluctuations mostly just below threshold (the so-called high-conductance state, Destexhe et al., 2003), and excursions in this balance toward threshold lead to spiking. Hence, transient disruptions of the balanced state from changes in the relative proportion of excitatory and inhibitory input (E-I balance) can modulate spiking activity. For example, such dynamics of E-I balance have been found to influence network oscillations (Brunel and Wang, 2003; Atallah and Scanziani, 2009), and E-I shifts can act as a precise mechanism for modulating the membrane potential of individual neurons, possibly subserving neural coding (Denève and Machens, 2016). The mechanisms underlying these shifts in E-I balance are still unresolved, however. Broadly, excursions from the balanced high-conductance state have been postulated to be driven by stochasticity (Shadlen and Newsome, 1998) or by deterministic yet complex dynamics (Van Vreeswijk and Sompolinsky, 1996; Vogels and Abbott, 2005). In the former case of stochastic neural variability, neural coding has been hypothesized to follow a rate code, where local populations of tightly coupled neurons (such as cortical columns) average their spiking activity into stable and reproducible instantaneous firing rates (Shadlen and Newsome, 1998).

Recent technologies like high-density electrode arrays (Jun et al., 2017) and optical imaging (Demas et al., 2021) can directly record neural activity from hundreds to thousands of points simultaneously in the brains of awake, behaving mammals, and these numbers are quickly increasing. These recordings reveal dynamics possessing salient spatiotemporal structure across neural populations, and on the single-trial level. Perhaps the most intriguing and curious example is waves of neural activity that travel across entire regions of cortex at the level of individual trials in awake, behaving mammals. These traveling waves have recently been observed as part of spontaneous cortical activity that impacts evoked activity and perception (Davis et al., 2020). Since spontaneous traveling waves are a phenomenon apparent at the spatial scale of the entire network, their effect on perception challenges existing theories about neural processing at the level of individual neurons, in which different neurons are posited to possess different specialties with respect to the kind of stimulus (Hubel and Wiesel, 1959). Furthermore, the mechanisms behind and roles of spontaneous traveling waves are active areas of research. Similarly, traveling waves have also recently been observed in the activity of evoked responses (Muller et al., 2014), and their origin and computational role also remain unclear.

This thesis reports on three contributions to the understanding of traveling waves in the visual cortex of the brain.

In Work 1 (Chapter 2), my coauthors and I employed a high-resolution, conductancebased spiking network model to investigate the spontaneous activity patterns that emerge under biologically constrained circuit motifs (Davis et al., 2021). We found that, with realistic synaptic density, and in networks on the order of millimeters (containing up to one million neurons), the effects of local connectivity and distance-dependent time delays become meaningful, resulting in "sparsely spiking" spontaneous traveling waves that statistically agree with those observed in vivo (Davis et al., 2020) and with the asynchronous-irregular spiking regime that is known to describe spontaneous cortical activity (El Boustani et al., 2007). Lastly, we show how the high-conductance state associated with the wave activity explains a recent experimental result of traveling waves impacting perceptual sensitivity across the entire marmoset area MT (Davis et al., 2020), and propose it as a mechanism of gain modulation (Chance et al., 2002).

Work 2 (Chapter 3) makes an abstraction relative to Work 1 (Chapter 2), using a network of coupled nonlinear oscillators possessing distance-dependent time delays. Such systems are reminiscent of networked neural systems as they exhibit broadband fluctuations, self-organization, and possess heterogeneous time delays. Using a novel complex-valued

formulation of the equation of motion, we obtained a delay operator whose eigenmodes predict the individual traveling waves in the network. Notably, this result allows for such predictions at the level of individual realizations of the network rather than averages of realizations, and was successfully applied to tractography data from the Human Connectome Project.

In Work 3 (Chapter 4), we studied a model of stimulus-evoked traveling waves in a single visual cortical area, and asked how such a system might perform short-term prediction of naturalistic visual inputs (Benigno et al., 2023). We leveraged the analytical insight gained about traveling waves from Work 2, and studied these dynamics under a formulation of a single-layer recurrent neural network. Following training of the network, traveling waves emerge in response to a few input movie frames. These waves facilitate good predictions several frames into the future due only to the intrinsic network state. After shuffling the recurrent connections responsible for the waves and retraining the network, both the traveling waves and prediction performance are lost. These results suggest that traveling waves may be integral in the visual system for processing spatiotemporal inputs represented on dynamic spatial maps.

In the visual cortex, the spontaneous activity of the neurons displays a high degree of variability. This variability is believed to originate from the synaptic inputs in the highly recurrent networks (Destexhe et al., 2003). Although a time series recording at an individual location in the network appears stochastic (Shadlen and Newsome, 1994), simultaneous recordings taken across the network show that the same time series can belong to spatiotemporal dynamics structured as waves traveling across the entire area of the cortex; however, these spontaneous traveling waves were initially only observed while the subject was anesthetized

(Arieli et al., 1996; Kenet et al., 2003; Tsodyks et al., 1999). During wakefulness, neural fluctuations are higher in frequency and lower in amplitude (Destexhe et al., 1999), rendering the experimental detection of spontaneous traveling waves in this state more challenging. Lastly, stimulus onset reduces variability in spatiotemporal dynamics (Churchland et al., 2010), and spontaneous traveling waves had been hypothesized to play a minor part in a network's response to stimulus (Sato et al., 2012).

More recently, spontaneous traveling waves have been shown to be present during wakefulness. Moreover, their presence has been shown to impact both the extent of stimulus-evoked response and the visual perception of the subject (Davis et al., 2020). Yet, their mechanistic origins were uncharacterized, and furthermore, it was unclear how their spatiotemporal structure could be reconciled with the low-correlation asynchronous-irregular spiking regime known to pervade cortex during wakefulness (El Boustani et al., 2007). Since the observed propagation speeds in the spontaneous traveling waves in Davis et al., 2020 agree with the measured axonal conduction speeds of unmyelinated horizontal fibres in layer 2/3 (Bringuier et al., 1999; Girard et al., 2001; González-Burgos et al., 2000), we asked whether the spikes traveling along these fibres are a potential source of these waves. To answer this question, we conducted a study of a large network of spiking neurons representing a patch of neocortex. Specifically, we explored this network model at a myriad of physiologically relevant densities of neurons, connection probabilities that depend on distance, balances of excitation and inhibition, and values of synaptic conductance. Notably, these networks possessed time delays of spike propagation proportional to the distance between the synaptic pair of neurons, representing time delays from unmyelinated horizontal axonal fibers. These delays were found to be responsible for the traveling-wave dynamics observed in the model, which agreed with the traveling waves found in vivo. Furthermore, these spontaneous traveling waves were robustly present across the parameter space in this model, and the spatiotemporal dynamics simultaneously exhibited asynchronous-irregular activity.

A priori, the presence of these traveling waves may seem to give rise to spatial correlations in the network that (1) violate the asynchronous-irregular regime of spontaneous waking cortex and (2) have been shown to be detrimental to perception (Nandy et al., 2019). From a coding perspective, spatial correlations of spiking activity may impair perception by limiting the expressibility of the neural system since correlated variability imposes a redundancy on the network representation (Huang et al., 2022). The present model provides an explanation for why traveling waves need not induce correlations in spiking activity. Consistent with the multi-unit recordings in visual cortex of the marmoset, the results here show that individual neurons possessed low probabilities of spiking, despite the presence of waves in the network. Hence, the waves are referred to as sparse waves. In contrast, smaller-scale network models produce dense waves in which individual neurons have high probability of spiking as the wave goes past. Thus, sparse traveling waves can propagate across whole regions of cortex without appreciably increasing spatial correlations at the individual-neuron scale, thereby respecting the asynchronous-irregular spiking regime in local cortical neighbourhoods.

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