

# Cortical signal propagation - Balance, amplify, transmit

Jake P. Stroud<sup>1</sup> and Tim P. Vogels<sup>1</sup>

<sup>1</sup>*Centre for Neural Circuits and Behaviour, Department of Physiology, Anatomy and Genetics, University of Oxford, Oxford, UK, OX1 3SR*

Corresponding author TPV: email: [tim.vogels@cncb.ox.ac.uk](mailto:tim.vogels@cncb.ox.ac.uk); phone: + 44 (0) 1865 612712

## Abstract

The neural code of cortical processing remains uncracked, however, it must necessarily rely on faithful signal propagation between cortical areas. In this issue of *Neuron*, Joglekar et al. (2018) show that strong inter-areal excitation balanced by local inhibition can enable reliable signal propagation in data-constrained network models of macaque cortex.

## Main text

Sensory stimuli are typically processed in local specialised circuits (Jiang et al., 2015) and relevant information is then transmitted to other (sometimes distant) brain areas. In modelling studies, simple propagation of specific signals has been used successfully as a proxy of such processing, demonstrating that synchronous and asynchronous action potentials (spikes) can be transmitted along layered networks of neurons (Kumar et al., 2010). These models are typically not constrained by biologically plausible architectures, lacking lateral or feedback connectivity, and they often contain purely excitatory connections. Although such models capture some fundamental neuroanatomy of cortex (particularly for sensory systems), signals can become corrupted along their path of propagation and they are limited in their transmission capacity of spatiotemporally complex signals. How signal propagation is affected by biologically realistic, heterogeneous inter- and intra-areal connectivity (Markov et al., 2014) and more diverse neuron types remains unclear.

In this issue of *Neuron*, Joglekar et al. (2018) show that reliable signal transmission can occur in large-scale recurrent network models of macaque cortex. The authors use recently available connectivity data (Markov et al., 2014) in which interestingly, approximately half of the total number of inter-areal cortical connections are feedback. To prevent runaway excitatory activity in this strongly recurrent network, the authors introduce inhibitory neurons in each cortical area that specifically stabilise neuronal activity by ‘tightly’ balancing excitatory inputs (see Figure 2, Hennequin et al., 2017). Such balanced networks are stable during spontaneous activity but they react quickly and with large firing rates to particular momentary perturbations. This phenomenon, called *balanced amplification* (Murphy and Miller, 2009), occurs when an external input suddenly disrupts inhibitory tracking of excitatory activity. The thus liberated excitatory feedback loops then produce fast transients before inhibition eventually quenches the network activity. In their large-scale cortical model, Joglekar et al. (2018) find that such an amplification mechanism enables signals to propagate between cortical areas for a wide range of (inhibition-balanced) inter-areal coupling strengths, and network inputs do not cause unstable activity -- as would be the case without any inhibition. Moreover, the mechanism allows stable (yet more attenuated) propagation when the network does not feature the experimentally observed feedback connections.

In line with experimental and theoretical studies, Joglekar et al. (2018) find that a sudden and temporary increase in firing rate introduced to an area at the bottom of the cortical hierarchy (such as V1) can trigger different levels of activity across cortex -- reminiscent of different stages of conscious processing. Such patterned activation across multiple regions, and in particular reaching parieto-frontal areas, is referred to as *global ignition* (Dehaene and Changeux, 2005). In their model, Joglekar et al. (2018) show that low level input into V1 causes increased activity in the occipital lobe compared to other areas -- similar to *subliminal* processing (Dehaene et al., 2006). When increasing the input strength, activity suddenly spreads to the temporal lobe and areas involved in sensory-motor processing -- as suggested to occur during *preconscious* processing (Dehaene et al., 2006). Finally, a sufficiently strong input activates all areas, including prefrontal cortex -- commonly associated with *conscious* processing (Dehaene et al., 2006). Furthermore, randomly permuting the connections between areas or removing feedback connections in the model results in either no activation in some areas (particularly frontal cortex) or a smooth increase in activity in all areas -- both of these controls are at odds with the global ignition hypothesis. These results provide a step towards understanding the mechanisms driving brain activity observed during conscious perception.

To demonstrate the generality of their results, Joglekar et al. (2018) use both rate-based and more biologically plausible spiking models. The authors test two distinct modes of signal propagation in their spiking networks: *asynchronous* and *synchronous*. Asynchronous or 'rate coded' activity commonly refers to a case in which stimuli are encoded using only the firing rates of populations of neurons (Vogels and Abbott 2005). On the other hand, propagation is said to be synchronous when a stimulus is encoded by volleys of near-instantaneous spikes (Kumar et al., 2008). Propagation of either of these two codes is thought to rely on distinct network architectures -- synchronous codes can reliably propagate when connections are dense but weak, whereas asynchronous codes can propagate via sparser but stronger connections (Kumar et al., 2010).

Joglekar et al. (2018) instead show that balanced amplification allows both asynchronous and synchronous activity to propagate across relevant areas of the cortical hierarchy. This rejuvenates the idea that rate-mode and synchronous coding are extremes of the neural code, and that the majority of information is encoded as combinations of fast transients and slower, more subtle population signals. It will be interesting to see a more systematic evaluation of such propagation schemes in amplifying feedforward networks, dissociated from pre-defined connection densities between areas. Importantly, artificially generated connectivity could serve as a theoretical test of the limits of signal transmission through balanced amplification and how it is affected by the density and strength of connections as mentioned above. Additionally, it will be interesting to see how the macro-circuitry of inter-areal connections will combine with the local organization of the micro-circuits (Jiang et al., 2015). For example, distinct targets for feedforward and feedback connections into the same area could give rise to computations through their interacting dynamics. Studying how spatially and temporally rich inputs are differentially amplified in each local circuit throughout the cortical hierarchy will be an exciting direction of future research.

Joglekar et al. (2018) have successfully united central ideas of neural processing in local circuits and large-scale inter-areal cortical networks. Their contribution is to show that a balanced amplification mechanism enables reliable signal propagation in data-constrained

network models of primate cortex, and thus provide a step towards bridging the gap between local circuit dynamics and larger scale cortical activity. Understanding the relationship between synaptic connectivity, local circuit dynamics, and large-scale cortical interactions will edge us closer to answering the ultimate question: How do we compute?

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