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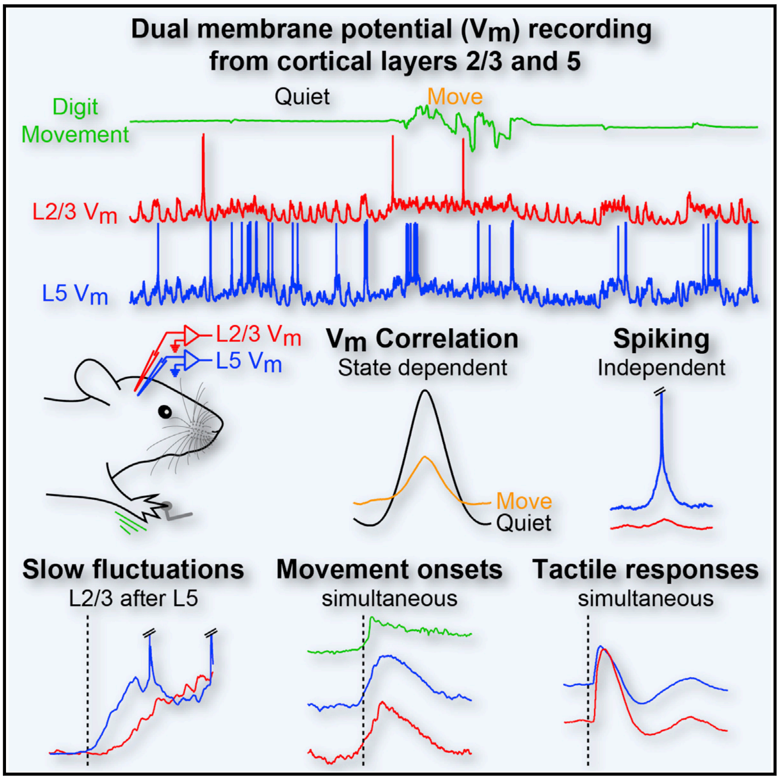
Translaminar Cortical Membrane Potential Synchrony in Behaving Mice

Graphical Abstract



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In Brief

Zhao et al. use dual whole-cell recordings from primary somatosensory cortical excitatory neurons in layers 2/3 and 5 in awake mice to identify layer-specific cellular properties and firing rates, and they show that translaminar membrane potential synchrony is dependent both on behavioral state and the source of the synaptic input.

Highlights

- We made dual whole-cell recordings from L2/3 and L5 cortical neurons in behaving mice
- Layer-specific membrane properties determine higher mean firing rates of L5 neurons
- Synchrony of translaminar synaptic activity is determined by the origin of input
- L5 neurons signal spontaneous and sensory-triggered movements

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Translaminar Cortical Membrane Potential Synchrony in Behaving Mice

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SUMMARY

The synchronized activity of six layers of cortical neurons is critical for sensory perception and the control of voluntary behavior, but little is known about the synaptic mechanisms of cortical synchrony across layers in behaving animals. We made single and dual whole-cell recordings from the primary somatosensory forepaw cortex in awake mice and show that L2/3 and L5 excitatory neurons have layer-specific intrinsic properties and membrane potential dynamics that shape laminar-specific firing rates and subthreshold synchrony. First, while sensory and movement-evoked synaptic input was tightly correlated across layers, spontaneous action potentials and slow spontaneous subthreshold fluctuations had laminar-specific timing; second, longer duration forepaw movement was associated with a decorrelation of subthreshold activity; third, spontaneous and sensory-evoked forepaw movements were signaled more strongly by L5 than L2/3 neurons. Together, our data suggest that the degree of translaminar synchrony is dependent upon the origin (sensory, spontaneous, and movement) of the synaptic input.

INTRODUCTION

Primary sensory cortex is composed of six layers of interconnected microcircuits. Gain- and loss-of-function experiments have shown laminar-specific effects on local cortical processing (Beltramo et al., 2013; Olsen et al., 2012), but how the layers work together remains unclear. The synchrony of action potential (AP) firing across cortical layers is thought to be a fundamental aspect of translaminar processing and is determined by the strength, sign and timing of the underlying synaptic input. Here, we investigate the synaptic mechanisms of cortical synchrony between excitatory neurons in layers 2/3 and 5 in behaving mice.

Measuring translaminar membrane potential (V_m) synchrony and linking it to sensory processing and behavior require simultaneous V_m recordings from different layers in awake animals. However, the vast majority of V_m recordings of cortical neurons in behaving animals have been made from superficial layers (Bennett et al., 2013; Crochet and Petersen, 2006; Gentet et al., 2010; Polack et al., 2013; Poulet and Petersen, 2008; Poulet et al., 2012; Reimer et al., 2014; Zhou et al., 2014). These studies have shown that internally generated, spontaneous network activity dominates the V_m of cortical neurons across cortical regions and is correlated with the behavioral and arousal state. Large-amplitude, slow fluctuations are highly correlated between neighboring layer 2/3 (L2/3) neurons in resting animals but are abolished during movement, resulting in a desynchronized or "active" cortical state (Harris and Thiele, 2011; Poulet and Petersen, 2008). The active state may result from arousal-related effects associated with movement and has been linked to a modulation in sensory responsiveness (Crochet and Petersen, 2006; Otazu et al., 2009; Pinto et al., 2013; Polack et al., 2013; Reimer et al., 2014; Schneider et al., 2014; Vinck et al., 2015; Zhou et al., 2014), adaptation (Castro-Alamancos, 2004), and even perception itself (Bennett et al., 2013; McGinley et al., 2015).

Few studies have examined the V_m activity of deeper layer cortical neurons in behaving animals (McGinley et al., 2015; Schiemann et al., 2015). Extracellular recordings, however, have shown higher spontaneous and sensory-evoked firing rates in deeper layer neurons (de Kock et al., 2007; O'Connor et al., 2010) and, intriguingly, that sensory-evoked and spontaneous spiking have different temporal structures across layers (Sakata and Harris, 2009).

The rodent forepaw somatosensory system is a relevant and accessible model system to investigate cortical sensory processing during behavior. The forepaw has five digits (Figure 1A) that can be used to grasp and manipulate objects as well as discriminate somatosensory stimuli (Milenkovic et al., 2014). We made whole-cell recordings from primary forepaw somatosensory cortex L2/3 and L5 excitatory neurons in awake mice to compare the synchrony and integration of external (sensory) and internal (movement-evoked and spontaneous) synaptic input. Our data highlight layer-specific membrane properties that underlie differences in AP firing and show that translaminar V_m synchrony is dependent both on the behavioral state and the source of synaptic input.