A ubiquitous spectrolaminar motif of local field potential power across the primate cortex. Mendoza-Halliday D, Major AJ, Lee N, Lichtenfeld MJ, Carlson B, Mitchell B, Meng PD, Xiong YS, Westerberg JA, Jia X, Johnston KD, Selvanayagam J, Everling S, Maier A, Desimone R, Miller EK, Bastos AM (2024) Nat. Neurosci. doi: 10.1038/s41593-023-01554-7. Article

Re-interpretation based on the IPL mechanism

During the development of cerebral cortex, there is a particular pattern in which neuronal cells move and settle in the cortical layers. This has a profound influence on the inter-neuronal inter-spine interactions and hence the waveform of oscillating extracellular potentials. At one stage of development, neuronal cells from the periventricular zone move up along the vertically oriented processes of the radial glia towards the pial surface (Marín-Padilla, 1998). The neurons that reach the subpial region anchor their processes to the marginal zone close to the pia and then descend towards the direction of the ventricular zone area (**Fig.1**). As the new neurons arrive at their destination, they continue to settle one above the other. Thus, the first set of neurons becomes the sixth neuronal layer of the cortex. This is followed by the fifth neuronal layer and so on. Layer 1 cortical neurons that are mostly GABAergic send horizontal processes interconnecting several postsynaptic terminals of apical tufts. Because of the subpial anchoring of the apical dendritic tufts for all the neurons of all the layers, dendritic arbors of all cortical pyramidal neurons overlap each other more densely in cortical layer 2. The overlap will be less in layer 3; further reduced in layer 4 and so on (**Fig.2**). Maximum number of synapses and hence inter-neuronal inter-spine interactions are expected to occur in layer 2 providing large number of components of oscillating extracellular potentials in layer 2. Furthermore, large number of thalamocortical inputs also contribute large number of components for these oscillations. Hence, the net effect is expected to increase the frequency of oscillating extracellular potentials in layer 2 when two differential electrodes (extracellular) are placed at two locations in the cortex. This provides an explanation for the observation of high frequency gamma waveforms of oscillating extracellular potentials in layers 2 & 3, and comparatively low frequency alpha and beta waves in deeper layers in the work of Mendoza-Halliday et al.,. This also acts as an indirect retrodictive finding that matches with the semblance hypothesis.

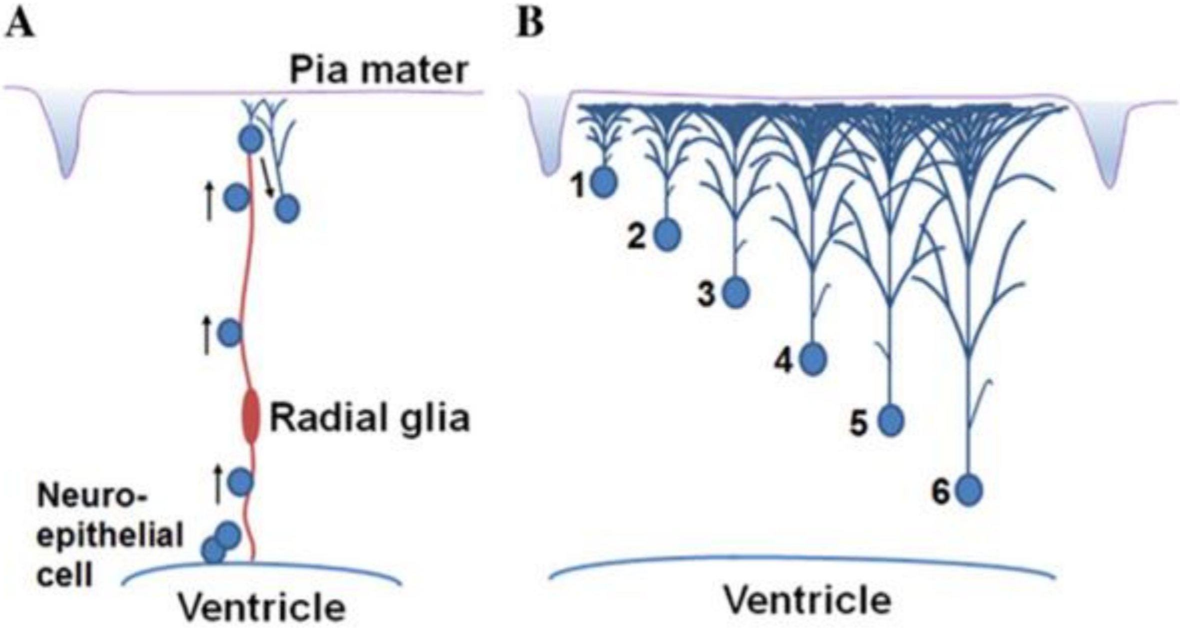

Figure 1. Stages of neuronal migration and arrangement of neurons in different neocortical neuronal orders. Both figure panels are views of the vertical section through the cortex. **A:** Progenitor neuroepithelial cells in the fetal ventricular zone proliferate, and the newly formed daughter cells migrate along the processes of the radial glia towards the superficial layer of the cortical plate. The new cells develop processes, and the dendrites are anchored to the extracellular matrix structural proteins at this region. As new cells arrive at the superficial layer, the older ones get pushed towards the direction of the ventricular zone. However, their apical dendrites remain anchored to the superficial layer. Since the dendrites are already anchored to the superficial layer, the main dendritic stem elongates. This continuous process results in the displacement of the oldest cell layer, namely layer 6 located close to the ventricular zone and the last arrived cells to remain at the most superficial layer as neuronal order 1. **B:** Figure showing the dendritic trees of neurons that belong to different neuronal orders (numbered 1 to 6). Note that the dendrites of neurons of almost all the neuronal orders anchor at the subpial region, making this region rich in dendritic spines. As the dendritic spine density is very

high at the cortical layers 1 and 2, the role of this arrangement contributing to the interspine interactions and oscillatory waveform of the cortical surface-recorded potentials are explained in the following sections (figure modified from Vadakkan, 2015).

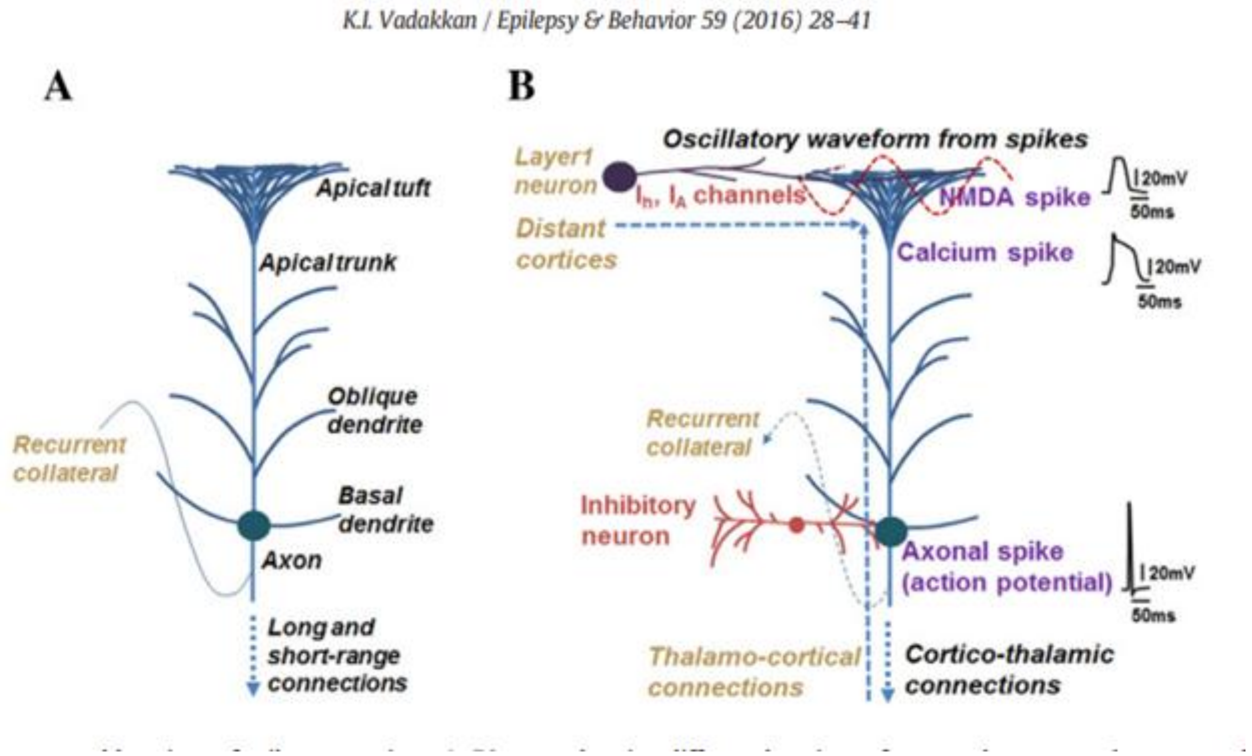

Figure 2. Anatomy of pyramidal neurons and locations of spike generations. A: Diagram showing different locations of neuronal processes that are capable of producing regenerative potentials (spikes). These include apical tuft, apical trunk, oblique, basal, and axon. Synapses in distal dendrites produce EPSP of amplitude more than 10 mV; whereas those proximal to the soma produce EPSP amplitude of 0.2–0.3 mV. The EPSPs from distal dendrites attenuate from nearly 10 millivolts (mV) to nearly 0.014 mV (more than 900-fold attenuation) as they reach the soma (Spruston, 2008). B: Diagram showing the locations of spike generation and inhibitory mechanisms to regulate spike propagation. In the apical tuft, oblique, and basal dendrites, several dendritic conductance contributed by regenerative NMDA receptor current trigger dendritic plateau potentials with a rapid initial sodium spikelet followed by a plateau phase that collapses abruptly (Schiller et al., 2000). At the apical trunk, calcium spikes are generated. Axonal spikes (action potentials) are generated at the axon initial segment. Inhibitory inputs can regulate the net potential reaching the

soma. Both recurrent collateral and thalamo–cortical inputs control the generation and propagation of the spikes at different locations. Layer 1 cortical neurons that are mostly GABAergic send horizontal processes interconnecting several postsynaptic terminals of apical tufts. Representative traces of different spikes are shown (figure modified from Vadakkan, 2015).

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