Dendritic computations may contribute to contextual interactions in the neocortex

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The cerebral cortex is the single largest "organ" in the mammalian brain, and is astonishingly flexible: the same basic architecture has been tailored by evolution to perform sensory, motor, affective, and executive functions that contribute to a variety of behaviors. Our understanding of cortical computation remains primitive, however, even in the primary sensory areas, which have been the most intensively studied and where both the inputs and the tasks performed by the neurons are best understood. A striking feature of sensory cortex is that the main feedforward projection rising "vertically" from the input layer 4 to the next stage of processing in layer 2/3, which has primary responsibility for defining a layer 2/3 pyramidal neuron's (PN's) "classical" receptive field (CRF), accounts for only a small fraction of the excitatory contacts onto those cells (<10%, Binzegger et al. 2004). In contrast, 60-70% of the contacts onto layer 2/3 PNs arise from "horizontal" connections from other layer 2/3 pyramidal neurons (Binzegger et al. 2004; Boucsein et al. 2011).

Horizontal axons are a major feature of cortical organization, not only due to their sheer numbers, but because they provide a massive network for exchanging "contextual" information between PNs within a cortical area (Gilbert & Wiesel, 1979; Rockland and Lund 1982; Gilbert and Wiesel 1983; Martin and Whitteridge 1984; Gilbert and Wiesel 1989; Luhmann et al. 1990; Bosking et al. 1997; Schmidt et al. 1997; Angelucci et al. 2002a,b; Stettler et al. 2002; Chisum et al. 2003; Angelucci and Bressloff 2006; Boucsein et al. 2011). Little is known, however, regarding their functional roles in the cortex, the precise mathematical form of the classical-contextual interactions they engage in, or the biophysical mechanisms that underlie their modulatory effects.

To explore the role that nonlinear synaptic integration effects may play in mediating classical-contextual interactions in PN dendrites, we focused on the problem of contour detection in natural images. We compared two functions: (1) the probabilistic interaction between aligned edge elements in the classical and extra-classical "receptive fields", computed from the statistics of human-labeled natural contours, and (2) the NMDA-dependent interactions between proximal and distal excitatory inputs to PN basal dendrites, computed using compartmental simulations. We found the two functions, of very different origin, matched closely, suggesting that nonlinear multiplicative interactions between inputs to PN dendrites could contribute directly to the integration of classical and contextual information in the neocortex.

Given the variety of classical-contextual interactions that are likely to be needed in a structure with such diverse computing requirements as the cortex, our long-term goal is to map out the spectrum of nonlinear interactions that PNs are capable of producing in their dendrites, under variations of dendritic input location, peak synaptic conductance, spine neck resistance, diffuse vs. clustered activation, short-term synaptic dynamics (e.g. synaptic depression and facilitation), and NMDA/AMPA ratio. Examples will be given for some of the main types of interactions that can be achieved by varying these parameters.

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