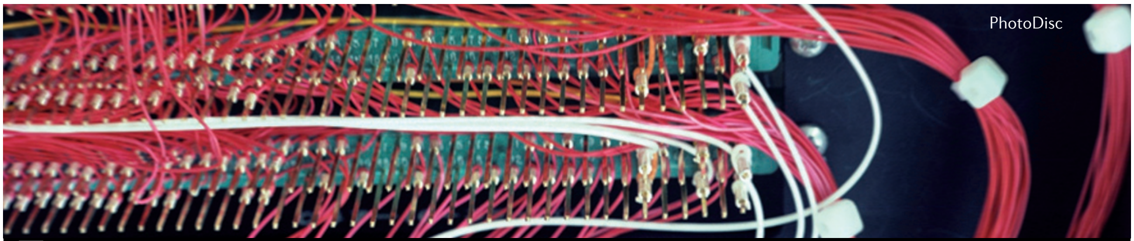

DENDRITES

Dendritic processors

“these studies show that active dendritic processing is a key component of neuronal computations in the visual system”

The expression of various voltage-gated ion channels in neuronal dendrites allows the initiation of local dendritic spikes in response to excitatory synaptic input and the back propagation of action potentials. The integration of active dendritic events is thought to contribute to neuronal computations, although clear evidence for this has been lacking. Now, two studies show that active dendritic spiking has a role in computations in the visual system.

Direction-selective retinal ganglion cells (DSGCs) fire action potentials when visual stimuli move across their receptive field in a particular direction (the ‘preferred’ direction), but are silent when the stimuli move in the opposing direction (the ‘null’ direction). Sivyer and Williams examined the contribution of active dendritic integration to direction selectivity in a subtype of DSGCs — namely, On-DSGCs — by recording from the soma and parent dendrites (the main branches of the dendritic tree) of these cells in rabbit retinal preparations that were exposed to moving light bars. Somatic recordings confirmed that On-DSGCs showed direction-selective responses. Interestingly, dendritic recordings made in the area of the dendritic tree that was first activated by light bars moving in the preferred direction showed that dendritic spikes preceded somatic responses, revealing that sensory input-induced dendritic spikes can drive action-potential firing.

Light-evoked excitation of DSGCs is mediated by bipolar cells, which form excitatory synapses onto DSGC terminal dendrites (which branch from the parent dendrites). The authors found that light evoked both large- and small-amplitude dendritic spikes, but only the former drove action potential generation. Thus, they reasoned that the small-amplitude spikes represent terminal dendrite spikes evoked by bipolar input that, in turn, trigger large-amplitude, parent dendritic responses.

To show that the small-amplitude spikes originated in terminal dendrites, they selectively excited areas of the On-DSGC dendritic tree with small light spots. Stimulation of an area including parent and terminal dendrites evoked both small- and large-amplitude spikes, whereas stimulation of terminal dendrites alone elicited only small-amplitude spikes. Importantly, the authors also showed that small-amplitude, terminal dendritic spikes were inhibited by null-direction light stimuli, indicating that the engagement and inhibitory synaptic control of active dendritic integration underlies the computation of direction selectivity.

Working *in vivo*, Häusser and colleagues sought to determine whether dendritic spikes are an essential component of synaptic integration during cortical visual processing. They presented lightly anaesthetized and awake mice with drifting square-wave gratings while recording from the apical dendrites and somas of layer 2/3 neurons of the mouse primary visual cortex, which exhibit orientation-tuned responses to visual stimuli. In response to stimuli in the preferred orientation, these neurons fired, and their dendrites showed high-frequency bursts of spikes. Back-propagating action potentials from the soma could also be detected in the dendrites, but these differed in their characteristics to the dendritic bursts. Two-photon calcium imaging of somatic and dendritic calcium transients, with simultaneous dendritic recordings, provided the most direct evidence of local dendritic spiking.

Local hyperpolarization of dendrites more strongly attenuated the dendritic bursts than isolated back-propagating action potentials, confirming the local origin of the bursting events. Cell-wide hyperpolarization attenuated subthreshold orientation tuning responses in the layer 2/3 neurons, indicating that dendritic bursting has a functional role in enhancing such responses.

Finally, the authors examined the mechanisms underlying the dendritic bursting. They included an NMDA receptor blocker in the pipette solution during whole-cell dendritic recordings from layer 2/3 cells, which blocked dendritic spikes, and during whole-cell somatic recordings, and found that, once the blocker had diffused throughout the dendritic tree, subthreshold orientation tuning was disrupted. Thus, NMDA receptor-mediated currents are crucial for dendritic bursting, and these dendritic bursts in turn shape orientation-tuned output.

Together, these studies show that active dendritic processing is a key component of neuronal computations in the visual system, both in the retina and in the primary visual cortex.

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ORIGINAL RESEARCH PAPERS Sivyer, B. & Williams, S. R. Direction selectivity is computed by active dendritic integration in retinal ganglion cells. *Nature Neurosci.* http://dx.doi.org/10.1038/nn.3565 (2013) | Smith, S. L. *et al.* Dendritic spikes enhance stimulus selectivity in cortical neurons *in vivo*. *Nature* http://dx.doi.org/10.1038/nature12600 (2013)