



Action Potential Propagation and Inhibitory Synapses in Secondary Dendrites of Mitral Cells

proposition by Xiong and Chen is that recurrent inhibition in the proximal region of the secondary dendrite will have a direct effect on the firing pattern of the output neuron while inhibition in distal regions will have a greater role in lateral inhibitory effects on other cells.

These results could be summarized in the following manner (see Figure). A single action potential can travel throughout the length of the secondary dendrite of an MC (1). In the slice preparation, a single action potential rarely induces an IPSP, unless Mg^{2+} ions are removed, to allow NMDA receptor activation. A stronger activation of the cell will produce an IPSP as the action potentials propagate along the dendrite (2). Since each GC can have dendrodendritic contacts with other MCs, GCs are able to inhibit action potential propagation in the secondary dendrites of neighboring MCs (3). This lateral inhibition is thought to play an important role in olfactory discrimination (Mori et al., 1999) as it can suppress weak responses in neighboring MCs. Another way these action potentials can be gated is by IPSPs produced by direct activation of the GC, either by axon collaterals from MCs (4) or by incoming fibers from other brain regions (i.e., olfactory cortex, not shown). In addition, recent studies have indicated that spillover of glutamate can activate autoreceptors in the MC secondary dendrites (Isaacson, 1999). It has been proposed that this excitation may allow synchronous activity of mitral cells *in vivo* (Isaacson, 1999; Schoppa and Westbrook 2001). The interplay between this self-excitation and dendrodendritic inhibition, which in turn could lead to olfactory oscillations, may have a relevant role in olfactory processing and awaits further studies (Laurent, 1999).

Optical recordings of stimulus-induced activity show

patterns of glomerular excitation that range over wide areas of the olfactory bulb. It seems likely that the microcircuitry of the cells, and in particular the involvement of the widely projecting lateral dendrites of MCs, play a critical role in correlating and refining this relatively raw input from the periphery, enabling us to make sense of the more than 500 chemical components that constitute the smell of coffee.

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Should Bad Workmen Always Blame Their Tools?

In this issue of *Neuron*, Beauchamp and colleagues (2002) differentiated brain regions in humans that are selectively responsive to viewing motion: (1) of humans, (2) of tools/utensils, and (3) in general. Active regions were the superior temporal sulcus, middle temporal gyrus, and MT/V5, respectively. This study provides impetus for future work in motion perception and its relationship to apraxia.

Both human and nonhuman primates possess excellent high-level motion processing skills, including the ability to infer the actions not only of their conspecifics, but also those of other species. These neural mechanisms are not only essential for survival (i.e., aiding in the evasion of predators and achieving successful procreation), but are also the cornerstone in the ability to form and maintain successful social relationships (reviewed by Adolphs, 1999; Allison et al., 2000). Human primates have also evolved considerable skills not only with the use of tool and utensils, but also with their manufacture as well, quite unparalleled in nonhuman primates.

Single-unit electrophysiological studies in nonhuman

primates demonstrate clearly that the monkey superior temporal polysensory area (STPa) has neurons that respond to animate motion and effectively integrate form and motion information (Oram and Perrett, 1996). Recent functional magnetic resonance imaging (fMRI) studies in humans have identified the temporoparietal cortex, namely, regions near the posterior superior temporal sulcus (STS), as being crucial for the processing of such complex visual displays (reviewed by Allison et al., 2000; Blakemore and Decety, 2001). Human neural responses to viewing motion of the face, hand, and body occur within 200 ms of motion onset in the bilateral temporal scalp, as studied by event-related potentials (ERPs) (Wheaton et al., 2001). To date, the response properties of these brain regions to viewing different types of complex animate and inanimate motion have not been thoroughly studied.

In this issue of *Neuron*, Beauchamp and colleagues (2002) present a set of three well-designed functional neuroimaging experiments where differences in human brain activation, as studied by fMRI, are assessed in response to viewing mobile humans versus mobile tools and utensils. Overall, these experiments were designed to: (1) delineate the response properties of high-order motion processing centers in temporoparietal cortex, and (2) differentiate them from lower-order centers that respond to motion per se. Specifically in Experiment 1, viewing human motion produced activation in the cortex around the superior temporal sulcus (STS) and superior temporal gyrus (STG), whereas viewing the motion of tools or utensils preferentially activated cortical regions centered on the middle temporal gyrus (MTG). Importantly, general motion processing regions, i.e., MT/V5, did not show this differential activation pattern, responding equally robustly to all forms of presented motion. Experiment 2 demonstrated that the lateral temporal cortex responded to the *motion* of humans and utensils and not to the *categories* of presented object. This was unlike the response properties of ventral temporal cortex studied in the same experiment where an equally robust response was elicited to *both* static and moving images of humans and utensils. Finally, Experiment 3 investigated the influence of *articulation* on STS versus MTG responses. Humans are able to produce a virtually limitless set of movements because body parts can move without having to necessarily maintain a consistent arrangement in space relative to one another (made possible by our articulated joints and known as articulated motion). On the other hand, tools and utensils, e.g., a pair of scissors, are usually capable only of nonarticulated motion. Human motion can consist of both articulated and nonarticulated movements, but tool or utensil motion usually involves nonarticulated motion. In Experiment 3, Beauchamp and colleagues (2002) tested for differences in activation to observing articulated versus nonarticulated human motion. In this elegant experimental manipulation, the results clearly indicate that the STS is responsive to complex articulated human motion, whereas the MTG is driven more by unarticulated motion, of both tools/utensils and humans. These findings build on the study of Grezes and colleagues (2001), who reported a nonrigid versus rigid motion activation difference, with nonrigid motion being processed in the STS (and intraparietal cortex), whereas

rigid motion activation loci occurred posterior to the STS activation.

The Beauchamp et al. (2002) study has highlighted additional specialization in the human motion processing pathway and raises a new set of questions about complex visual mechanisms. How do the STS and MTG motion sensitive regions relate to frontal "mirror" neurons (Rizzolatti et al., 2001) observed in monkeys and humans that are active in observing and executing grasping behaviors? Given that tools and utensils are ostensibly used by the (human) hand, what is the differential functional significance between frontal versus temporal regions in human subjects? Given that limb apraxias constitute a series of impairments consisting not only of the inability to recognize, but also to imitate or execute a skilled, learned movement (Leiguarda and Marsden, 2000), does the STS/MTG form a crucial part of a network for praxis? Are these regions purely visually sensitive or are they multimodal (Calvert et al., 2000)? How do the STS and MTG regions respond to other forms of inanimate motion involving man-made objects that are not classed as tools or utensils?

So at the end of the day, we have to conclude that bad workmen shouldn't really blame their tools—it may just be that their high-level motion processing and praxis systems just don't cut the mustard!

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