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Strategies for Odor Coding in the Piriform Cortex

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Review of Suzuki and Bekkers (<http://www.jneurosci.org/cgi/content/full/26/46/11938>)

What we perceive in the olfactory world is different from what odor molecules are in the air. With hundreds or even thousands of aerosolized molecules present in any single environment, our brain must be able to simplify incoming information so that our perceptual categories, like rose, musk, or danger, represent more than a chemical laundry list. In the past decade, studies of the primary olfactory cortex, also called the piriform cortex, indicate that this brain region may be the first stop, on the way from the nose to perception, where information about the identity and concentration of odors are combined to form synthetic perceptual categories (Laurent, 2002; Stopfer et al., 2003; Wilson et al., 2006). However, how neurons of the piriform cortex function in such a circuit, and in turn how this circuit codes and transforms olfactory information, is still relatively unexplored.

Much effort has been made to dissect the ways in which odors bind to and activate olfactory receptors located on the dendrites of sensory neurons in the nose and how the mitral cells of the olfactory bulb (OB) process olfactory information. What has yet to be thoroughly described is how the piriform cortex receives and transforms information arriving from the OB via the lateral olfactory tract (LOT). Although the cell types present in the piriform cortex are known (Shepherd, 2004),

previous work has failed to differentiate between disparate electrophysiological profiles and synaptic contacts made between principal cells.

In a recent paper in *The Journal of Neuroscience*, Suzuki and Bekkers (2006) take an important step toward understanding the circuit in the piriform cortex by electrophysiological characterization of two classes of principal cells, the superficial pyramidal (SP) and semilunar (SL) cells (Fig. 1A). Both cell types receive excitatory input from the LOT, as well as input from associational and commissural fibers (Shepherd, 2004). The initial characterization of these two cell types revealed that SP cells have a lower input resistance, a faster membrane time constant, and a more negative resting membrane potential than SL cells. SP cells were more likely to generate bursts after stimulus initiation, with an instantaneous firing frequency that was approximately threefold higher than that of SL cells [Suzuki and Bekkers (2006), their Fig. 1B,C (<http://www.jneurosci.org/cgi/content/full/26/46/11938/F1>)], whereas SL cells fired regularly throughout the duration of the stimulus. Bursting in SP cells was, in part, attributable to a Ni^{2+} -sensitive Ca^{2+} current and to an afterdepolarization that followed the action potential [Suzuki and Bekkers (2006), their Fig. 2A,C (<http://www.jneurosci.org/cgi/content/full/26/46/11938/F2>)]. In contrast, SL cells exhibited a strong afterhyperpolarization after suprathreshold stimulation, such that subsequent EPSPs were less likely to elicit an action potential [Suzuki and Bekkers (2006), their Fig. 6 (<http://www.jneurosci.org/cgi/content/full/26/46/11938/F6>)].

Suzuki and Bekkers (2006) also found that strong paired-pulse facilitation was present only in SP cells in response to LOT stimulation. SL cells failed to exhibit facilitation, and stimulation of associational inputs (layer Ib) did not elicit facilitation in either cell type [Suzuki and Bekkers (2006), their Fig. 4 (<http://www.jneurosci.org/cgi/content/full/26/46/11938/F4>)]. Because SP cells were found to be more excitable than SL cells, the authors next investigated whether this was because of a difference in synaptic physiology. Addition of the NMDA open-channel blocker MK-801 [(+)-5-methyl-10,11-dihydro-5H-dibenzo[a,d]cyclohepten-5,10-imine maleate] suggested that projections to SP cells exhibited a lower presynaptic release probability [Suzuki and Bekkers (2006), their Fig. 5 (<http://www.jneurosci.org/cgi/content/full/26/46/11938/F5>)]. This raises the intriguing possibility that these cells receive input from a yet uncharacterized segregation of the output of the OB: either single fibers arising from the LOT can make synapses with diverse release probabilities, or different fibers can have different release probabilities. For instance, it is unclear whether subpopulations of mitral and tufted cells in the main olfactory bulb (MOB) project to different subclasses of piriform cortex neurons. Alternatively, the SP and SL cells may be instructive in shaping the physiology of their presynaptic partner, as has been shown in neocortical synapses (Koester and Johnston, 2005).

Next, the authors aimed to characterize how the distinct physiology of SP and SL cells influenced their firing properties. To do this, the authors designed *in vivo*-

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like stimulation paradigms that mimicked odor-evoked LOT activity (Fig. 1B). SP cells tended to fire in bursts at the onset of current injection and spiked at the frequency of the input stimulus. SL cells, in contrast, fired at a constant rate during current injection, and in response to patterned stimuli, they fire at a fraction of the stimulus frequency [Suzuki and Bekkers (2006), their Fig. 7 (<http://www.jneurosci.org/cgi/content/full/26/46/11938/F7>) and Fig. 8 (<http://www.jneurosci.org/cgi/content/full/26/46/11938/F8>)]. The authors conclude that SP and SL cells may implement different coding strategies for olfactory information.

Available data about anterior piriform cortex principal cells indicates that olfactory stimulation evokes spatially distributed and infrequent firing. Previously, it has been suggested that SP cells in the piriform cortex act as coincidence detectors of tightly timed inputs from the MOB mitral cells (Laurent, 2002; Franks and Isaacson, 2006). The report by Suzuki and Bekkers (2006) highlights the capacity of SL cells to represent the intensity of incoming activity. If one assumes that SP and SL cells receive identical input from the OB, then their differing physiology would act on a patterned stimulus and distribute it in time. In this scenario, SP cells would respond to the fine temporal features of the stimulus, and SL cells would respond to its intensity, very similar to temporal coding and rate coding strategies.

The anatomy of the anterior piriform cortex has been well studied (Haberly, 2001); however, there remain many unanswered questions about its circuit physiology. These include the role of different classes of interneurons on the output of the principal cells, the importance of principal cell recurrent collaterals on spatio-temporal coding, and the importance of centrifugal modulation. Additional characterization of the relationship of MOB output to piriform output, building on Suzuki and Bekkers' (2006) characterization of SP and SL cells, will more firmly establish the rules of rate and intensity coding in the piriform circuit. For instance, it is not known how odor concentration or odor identity is represented in the firing of OB mitral cells, making it more difficult to address this issue in the piriform cortex. Under what conditions will more LOT axons be recruited? Future experiments will undoubtedly move to *in vivo* preparations to test piriform circuitry with odor stimulation,

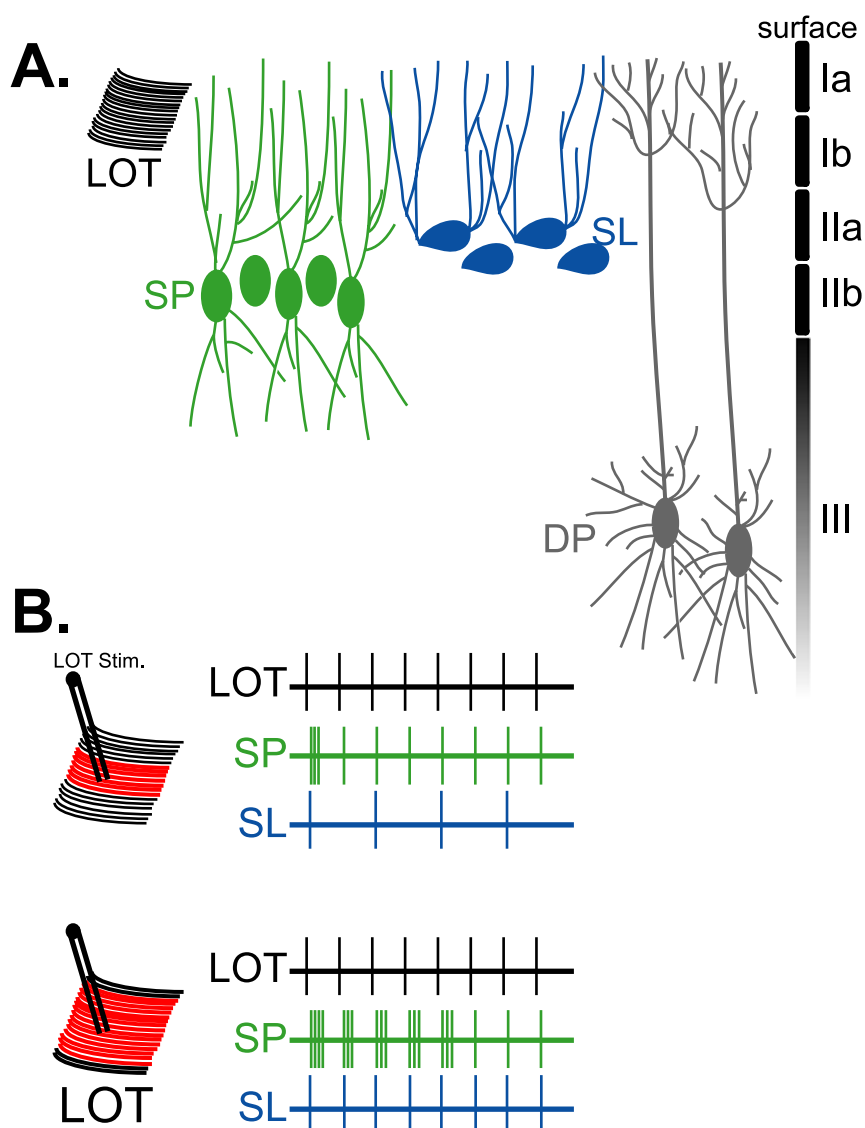


Figure 1. Principal cells in the piriform cortex. **A**, Schematic of the piriform cortex, including the somata and dendrites of the three types of principal cells: SP (green), SL (blue), and deep pyramidal (DP; gray). The activity of DP cells was not addressed by Suzuki and Bekkers (2006). The LOT, a bundle of mitral and tufted cell axons, projects from the MOB to the piriform cortex and makes synapses with the principal cells in layer I. **B**, LOT nerve stimulation (Stim.). The SP and SL cell output is related to the strength of the stimulus. Top, When the LOT is stimulated just above threshold, a small subset of LOT fibers is recruited (shown as red fibers). Although the SP cell fires with each LOT action potential, the SL cell does not. Bottom, At a higher stimulus intensity, the SP cell fires more frequently, whereas the SL cell closely follows the stimulus frequency.

thereby testing hypotheses about coding rules in the context of behavior and during modulation from other sensory and nonsensory modalities.

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