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Active sensing: What do the rat's whiskers tell the rat's brain

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Sensation usually involves active sampling of the physical world. Every second, the environment bombards us with myriad stimuli. Our senses pick up those that appear to be crucial for our well-being. For example, our eyes are in constant motion, even when focusing on an object. We call such motor-induced sensation active sensing. Sensory information acquired in such a way is encoded both in space and in time, because a stimulus is determined not only by which receptors are activated but also when they are activated. In what follows, these two encoding schemes are referred to as spatial encoding and temporal encoding.

We are interested in temporal encoding of information and its subsequent decoding by the brain. Experimental results are derived from the tactile system, though our working hypotheses cover both tactile and visual modalities.

Encoding of active vibrissal touch

The vibrissal system of the rat is a convenient model for studying active sensing. To detect, localize and perceive objects, rats scan the environment with their whiskers. Recently, we demonstrated that horizontal object location in this system is encoded in time (Szwed et al., 2003). These findings were obtained in anaesthetized animals from recordings of individual first-order (trigeminal ganglion) neurons during epochs of artificial whisking against an object. In these experiments, we found that vibrissal information is carried by several types of neurons: Whisking cells, which respond only to whisking and fire the same way regardless of whether the whisker touches an object or not; Touch cells, which fire only when whiskers encounter objects during whisking; and Whisking/Touch cells, which fire during whisking and fire additional spikes upon touch.

Whisking and Whisking/Touch cells fire in specific phases of the whisking cycle, reporting the actual

whiskers' position with high precision (Fig 1B). Touch cells can be divided to three main subtypes: Contact cells, which fire briefly upon contact; Pressure cells, which fire continuously during touch; and Detach cells, which fire upon detaching from the object (Fig. 1A). Contact cells encode horizontal object location in their firing onset times, where more anterior locations are encoded by increased onset latencies, relative to protraction onset.

How do awake rats use these cells in a real-life situation? How do they move their whiskers to optimize information pickup? Experiments in which awake animals perform an object location task are currently under way.

Possible decoding mechanisms

Our recordings from NV show that horizontal object position is encoded by (i) coincident firing of individual Whisking and Contact cells, and (ii) the temporal interval between firing onset of Whisking cells and firing of Contact cells. These findings suggest two basic algorithms for decoding horizontal object location.

1. Spatio-temporal decoding. Temporal coincidences between Whisking and Contact cells could be detected by an array of coincidence detectors, (Fig. 2, left). When fed by an array of Whisking cells (Fig. 2, lower-left 'W') and by Contact cells (Fig 2, lower-left 'C'), this array of detector cells should generate an output whose spatial firing profile would be specific for every contact position (Szwed et al' 2003).
2. Temporal decoding. The same input could be decoded by neuronal phase-locked loops (NPLLs, Ahissar 1998) of the paralemniscal system (Fig. 2, upper-right). NPLLs would receive the summed activity of Whisking and Contact neurons, detect the temporal interval between these activities, and translate it into a spike-count code.

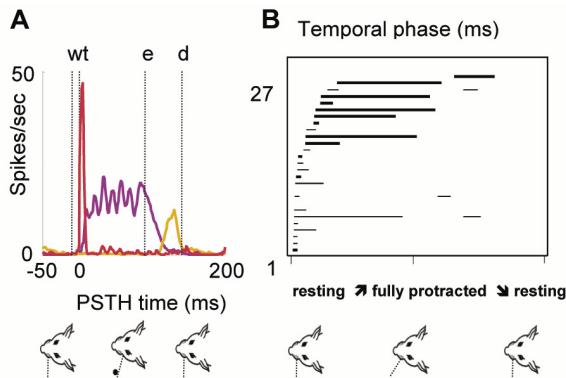


Fig. 1 (A) Touch Cells. Average PSTHs of Contact (red, $n=8$), Pressure (magenta, $n=11$), and Detach (orange, $n=6$) cells, triggered on whisker-object contact. Vertical lines denote time of whisking onset (wt), touching of object by the whisker (t), end of muscle contraction (e), and detachment of whisker from object (d). (B) Whisking and Whisking/Touch Cells. Each horizontal line represents temporal phases along the free-air whisking cycle in which a Whisking (thick line) or Whisking/Touch (thin line) cell was active.

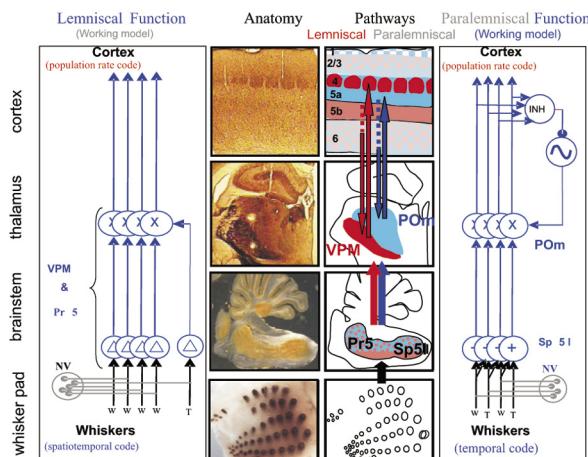


Fig. 2 Afferent pathways to the cortex. Simplified schematic outlines of the afferent pathways in the vibrissal system and of our working models for decoding horizontal object location. Anatomy: coronal and parasagittal cuts through the whisker pad and the three processing stations. Pathways: scheme of the anatomical connections, with the lemniscal pathway on the left in blue and the paralemniscal on the right in black. Functions: our working models for lemniscal and paralemniscal processing of horizontal object location. Δ , relay; +, integrator; X, AND-gate (phase detector); INH, inhibitory neurons; \sim , oscillatory neurons. Whether lemniscal phase detectors (X) reside in Pr5, VPM, or cortex is currently unknown.

Parallel pathways and parallel processing

Vibrissal information is conveyed to the barrel cortex via two parallel pathways, the lemniscal and paralemniscal (Fig. 2). In the paralemniscal system, latencies are more variable, responses are weaker, receptive fields are larger and cortico-POm feedback is exceptionally strong. These observations are consistent with temporal decoding by a NPLL-like mechanism. In contrast, in the lemniscal system, latencies are fixed and spatial resolution is better. We assume that the lemniscal system is tuned for decoding of spatially-encoded signals, while the paralemniscal system is tuned for decoding of temporally-encoded signals.

Selected Publications

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