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Figuring space by time

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Sensory information is encoded both in space and in time. Take a moving stimulus, for instance. Its position and trajectory across an array of sensory receptors is determined by which receptors are activated and when they are activated, respectively. In what follows, these two coding schemes are referred to as spatial encoding and temporal encoding. Accurate representations of the world depends on both types of encoded information. Our present focus is on the principles of temporal encoding induced by movements of sensory organs and decoding of this information by the brain. Experimental results are derived from the tactile system, though our working hypotheses cover both tactile and visual modalities.

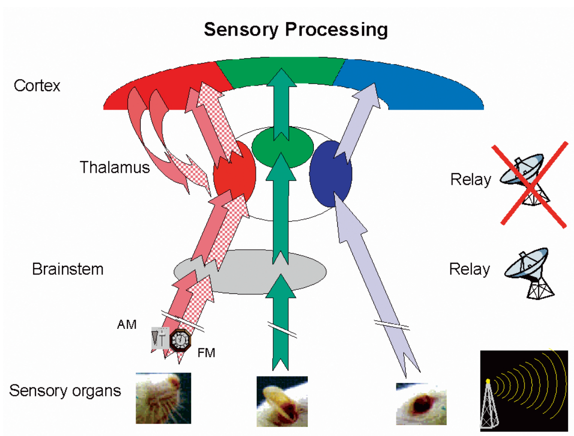

Fig. 1 *Tactile information is processed in parallel via lemniscal and paralemniscal pathways, using amplitude and frequency modulations. Decoding is accomplished by thalamocortical circuits.*

Temporal encoding-decoding in the tactile system

To perceive stationary objects the sensory organ must move. Primates move their fingers, and rodents, such as rats, move their whiskers when they localize and identify objects. The rat whisker system is an accessible model system in which to study spatial and temporal coding schemes. The rat has about 35 large whiskers arranged in a 5 by 7 array. Whiskers along the same arc scan different horizontal trajectories, while whiskers of the same row scan the same trajectory. An object's vertical location can be extracted from the identity of activated whiskers along arcs: an example of spatial coding. The identity of active whiskers, however, does not provide information about horizontal location. This information is available in the timing of whisker activation, as the temporal interval between whisker movement onset and moment of touch is proportional to the distance covered by the whisker during this period. Encoding by temporal intervals is an example of temporal encoding.

Neuronal mechanisms have been identified that could decode temporally-encoded whisker information. The rat whisker system contains two afferent pathways: the lemniscal and paralemniscal. We have measured neuronal responses to passive whisker movements in three stations along these pathways (brainstem, thalamus and cortex) and found that (i) the two pathways use different coding schemes to process input from the whiskers and (ii) the thalamus is an active player in the decoding process (Fig. 1). Comparison of these results with predictions of theoretical modeling suggest that the paralemniscal system is involved in temporal decoding and the lemniscal in spatial decoding.

Temporal encoding-decoding in the visual system

The eye is often compared to a camera and the retina to a surface dotted with photosensitive material like photographic film. As such, signals from the retina are spatially encoded, and the image reconstructed from identities of active ganglion cells. The eyes are, however, never completely still. During fixation they move back and forth so that the visual image will be swept across several photoreceptors, at rates much higher than the integration period of individual photoreceptors. These uninterrupted fixational eye movements introduce important constraints on how visual information is encoded. Consider the following: two ganglion cells are excited by a single horizontal spatial offset (such as two mis-aligned vertical lines). During a lateral eye movement a burst of spikes is triggered in each cell as the RFs cross the stimulus edge. If the decoding circuit was to rely on spatial coding, and only on the output of these two cells, then the spatial offset would not be sensed. That the neurons fired only indicates that they faced a luminance change: there is no additional information in the spatial code about the presence, direction or magnitude of the spatial offset. This information is contained solely in the temporal dimension as the onset of one burst is delayed relative to the other. The interval between bursts in the two cells represents the spatial offset. To properly represent spatial offset, the readout circuit must decode this temporal delay.

Fixational eye movements introduce a spatial-to-temporal transformation, similar to that encountered in tactile systems. It is clear that the visual system must identify the onset of each burst and measure the interval between them. While there are several possible solutions to this task, one seems especially attractive to us. From electronic solutions to similar computational tasks, and our own measurements, we know that temporal intervals can be estimated by predictive phase-locking between sensory input and local oscillators acting as a processing clock. Phase-locking with the fixational eye movements would synchronize these oscillators with the input and provide the mechanism to accurately measure temporal intervals.

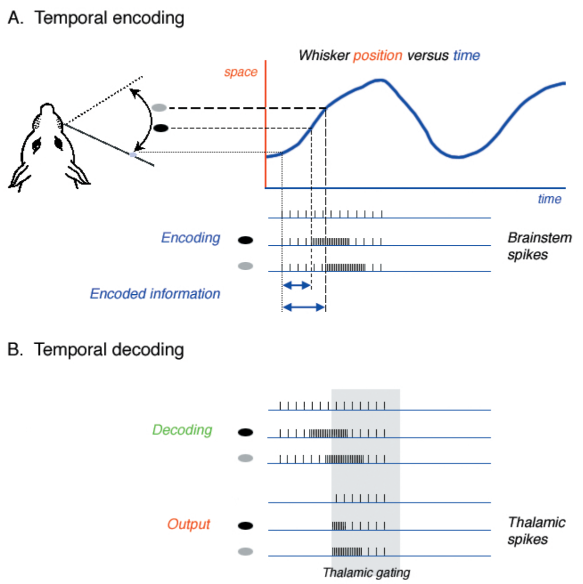

Fig. 2 *Hypothesis for temporal encoding-decoding in the whisker system. Temporal decoding by thalamic gating ensures that more anterior objects generate higher spike-counts by delayed touch-bursts and hence more spikes passing the gate.*

Proposed coding schemes for tactile and visual systems

We propose a novel encoding-decoding scheme for the tactile and visual systems. In this scheme, spatial encoding is induced by spatial arrangements of receptors and temporal encoding is induced by the movements of the sensory organs. Decoding of temporal information requires phase-locking to sensory organ movements. In the whisker system, temporal and spatial coding seem to be used by the paralemniscal and lemniscal pathways for processing horizontal and vertical coordinates, respectively. We also propose that temporal and spatial coding are used for fine and coarse tactile texture analysis, respectively. In the visual system, temporal coding is facilitated by fixational eye movements and is decoded, as in the whisker system, by phase-locking to internal, neuronal oscillators. Further, we propose that temporal decoding is used for fine feature analysis (what), and spatial coding for coarse feature analysis and absolute localization (where).

Selected Publications

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Acknowledgements

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For additional information see:

www.weizmann.ac.il/neurobiology/labs/ ahissar/ahissar.htm