Active sensing mediated by multiple motor-sensory-motor loops

Sensation is an active process. For example, while viewing and touching, the eyes and hands are constantly moving. These movements prevent receptor adaptation, but also optimize sensory processing. Studying the computational basis of such active sensing is difficult, because of closed-loop interactions between motor control and sensory processing. Thus, most research on sensory processing and motor control is conducted in an “open loop” condition, in which either motor control or sensory processing is eliminated.

Sensory information is encoded by both spatial and temporal cues, and accurate representations of the world depend on both types of information. Rats move their whiskers repetitively to explore the environment, and to detect, localize and identify objects. Sensory information, in turn, affects future motor movements. How this motor-sensory-motor functional loop is implemented across neuronal loops of the whisker system is not yet known. Our present focus is on the principles of motor control of sensor movements; peripheral encoding induced by sensor movements, and central decoding of the sensory information.

Whisking and object localization

During exploration, localization and identification of objects rats actively move their whiskers back-and-forth, in a stereotypical pattern termed whisking. Recently, we developed methods of characterizing this behavior in detail in freely-moving and behaving animals (Knutsen et al, 2005). We found that rats control whisking variables, such as amplitude, velocity and duration, separately and in a context dependent manner. We have designed perceptual paradigms in order to assess the acuity with which rats can localize objects using their whiskers. We have found that whisking behavior is important for localization, and that it is not merely sufficient for rats to contact objects to determine their locations: the whiskers must be able to move, independently of head movements, in order for rats to accurately localize. Future studies will be aimed at understanding how whisking facilitates the encoding of object location, and how it relates to neural activity.

**Fig 1. Whisking behavior during object localization**

**A.** Movie frames from a localization trial. The rat was trained to determine which of the two vertical poles was more posterior. **B.** The behavioral setup. **C.** Whisker movements were tracked from high-speed video frames and the angle of the whiskers relative to the head plotted. The angles of the right and left C2 whiskers are plotted; thick line indicates moments a whisker contacted the poles.
Loop via the lemniscal pathway (Fig. 2, Yu et al., in press). The pathways, and object identification along a further higher-order localization along a higher-order loop via the extralemniscal low-order loop that includes the paralemniscal pathway, object localization along nested motor-sensory-motor loops, organized hierarchically. In the case of vibrissal processing, our results raise a novel possibility for hierarchical processing: Instead of a separate path, the functional segregation we observed since each of these pathways project to a different target in cortex-to-periphery hierarchical motor processing, as current dogmas suggest, the brain might implement the processing of periphery-to-cortex hierarchical sensory processing which leads to the level of activity or the frequency of its repetition, but rather on the nature of the sensory information that is conveyed by that activity.

**Encoding of active vibrissal touch in trigeminal ganglion**

Using artificial whisking in anesthetized rats, we found that vibrissal information is carried by three types of neurons in the trigeminal ganglion: Whisking cells, Touch cells and Whisking/Touch cells, which convey specific signals related to active whisking and touch: whisking motion, contact timing, and combined whisking-touch information. We found that the horizontal coordinate of object location is encoded primarily by spike timing (Szwed et al., 2003), the vertical by neuron identity, and the radial primarily by firing rate (Szwed et al., 2006).

**Parallel processing in thalamus**

To understand how these signals are processed by the brain to localize and identify objects, we recorded from individual neurons from the three major thalamic nuclei of the whisker system, each belonging to a different afferent pathway – paralemniscal, a recently discovered pathway (extralemniscal), and the lemniscal pathway. We found that different sensory signals related to active touch are conveyed separately via the thalamus by these three parallel afferent pathways. The paralemniscal conveys sensor motion (whisking) signals via the POM, the extralemniscal conveys contact (touch) signals via VPMvl, and the lemniscal pathway conveys combined whisking-touch signals via VPMdm. Since each of these pathways project to a different target in the brain, and eventually closes the sensory-motor loop along a separate path, the functional segregation we observed raises a novel possibility for hierarchical processing: Instead of periphery-to-cortex hierarchical sensory processing which leads to cortex-to-periphery hierarchical motor processing, as current dogmas suggest, the brain might implement the processing of active touch along nested motor-sensory-motor loops, organized hierarchically. In the case of vibrissal processing, our results suggest that sensor-motion control is implemented along a lower-order loop that includes the paralemniscal pathway, object localization along a higher-order loop via the extralemniscal pathway, and object identification along a further higher-order loop via the lemniscal pathway (Fig. 2, Yu et al., in press).

**Layer-specific responses in cortex**

While studying cortical representations of active touch and object location, we found that the dynamics of neuronal responses were affected by the presence of an object in a layer specific manner. In both Whisking and Touch conditions, deep neurons (layers 4 and 5a) exhibited facilitation during the whisking train, while superficial neurons (layer 2/3) exhibited depression. In layers 2/3 and 4, responses were stronger during touch trials than during whisking in air. In layer 5a response strengths were similar for both conditions. Overall, our results indicate that, in the cortex, adaptation does not depend only on the level of activity or the frequency of its repetition, but rather on the nature of the sensory information that is conveyed by that activity.

**Selected publications**


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