Mechanisms of Active Sensing

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Active sensing and sensory-motor loops

Sensation is an active process whereby sensory organs continuously and actively sample the external world, usually by physical movements. Thus, to acquire meaningful information about the surrounding, the brain must integrate sensory signals with information about the active movement that induced them.

We study how sensor motion and sensory signals interact to produce perception, focusing on the rat vibrissal system. Rats generate actively-controlled sweeping movements of their facial whiskers ("whisking") to locate and identify objects in their immediate environment. Their whiskers are embedded in nested sensory-motor loops at several levels of the brain, from the brainstem up to neocortex (figure 1), whereby rhythmic whisking behavior is exquisitely modulated by sensory feedback, allowing precise positioning of the vibrissae in a manner that maximizes information uptake.

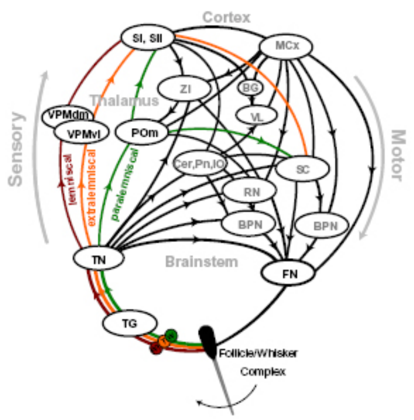

Fig. 1 Hierarchy of nested sensory-motor loops in the vibrissal system.
Sensory signals related to active vibrissal touch are conveyed by multiple pathways trough the sensory regions of the brain, and feed-back to motor circuits. Whisking signals (W) conveyed by the paralemniscal pathway involving whisking control; Contact signals (T) conveyed by the extralemniscal pathway involving processing of object location; and combined whisking-touch signals (WT) conveyed by the lemniscal pathway involving processing of object identity.

Sensory processing of active vibrissal touch

Using artificial whisking in anesthetized rats, we found that whisker information is carried from the whisker follicle via the trigeminal ganglion and to the thalamus by three parallel afferent pathways: the paralemniscal pathway, processing self-generated motion of the whiskers, extralemniscal pathway, processing contact signals which contain information about object location, and the lemniscal pathway, integrating whisking and touch information, perhaps for processing object identity (Szwed et al., 2003; Szwed et al., 2006; Yu et al., 2006).

These three pathways begin to integrate in the primary and secondary somatosensory cortices (S1 and S2) (Derdikman et al., 2006; Yu et al., unpublished). Specifically, the deeper layers of S2, which are the major anatomical target of the extralemniscal and paralemniscal pathways, contain a

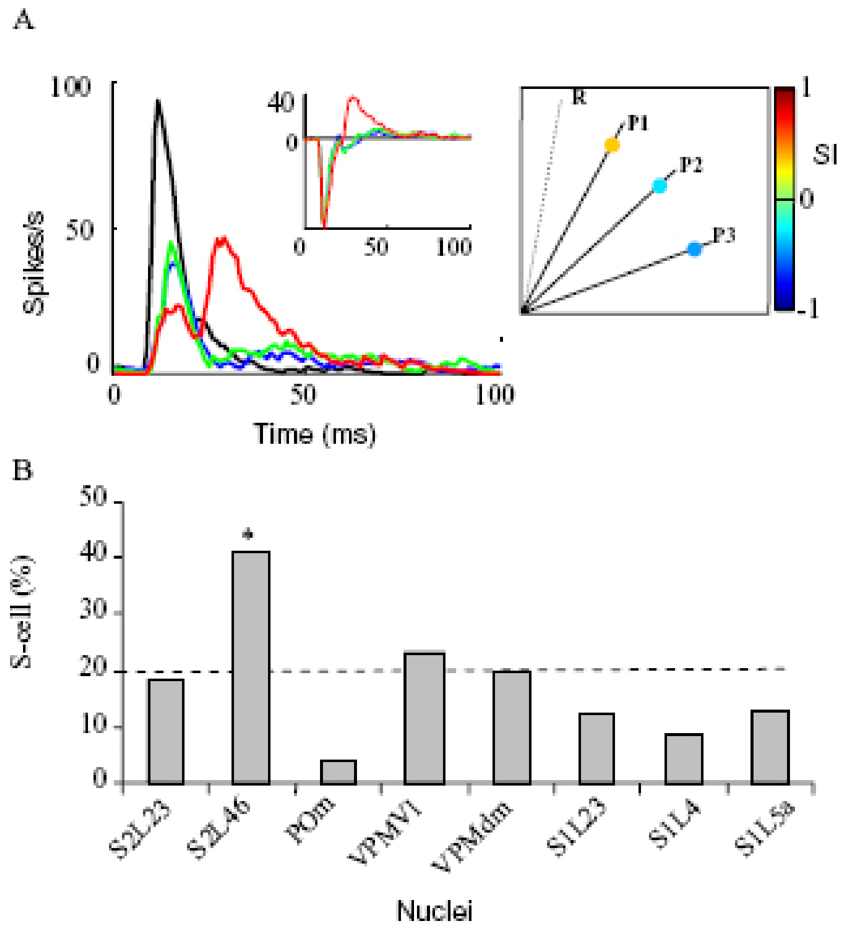

***Fig. 2** Location-selective neuronal responses in the thalamus, S1 and S2.*
A, Responses of one S2 (deep layer) neuron at steady state during active whisking. Left, PSTHs at steady state during protraction. Inset shows PSTHs after subtracting the PSTH in free-air. Right, selectivity index (SI) values of this neuron at three object positions (from posterior to anterior: P1, P2 and P3) are indicated in a color code.
B, Percentages of location-selective cells in S2, S1 and thalamic nuclei

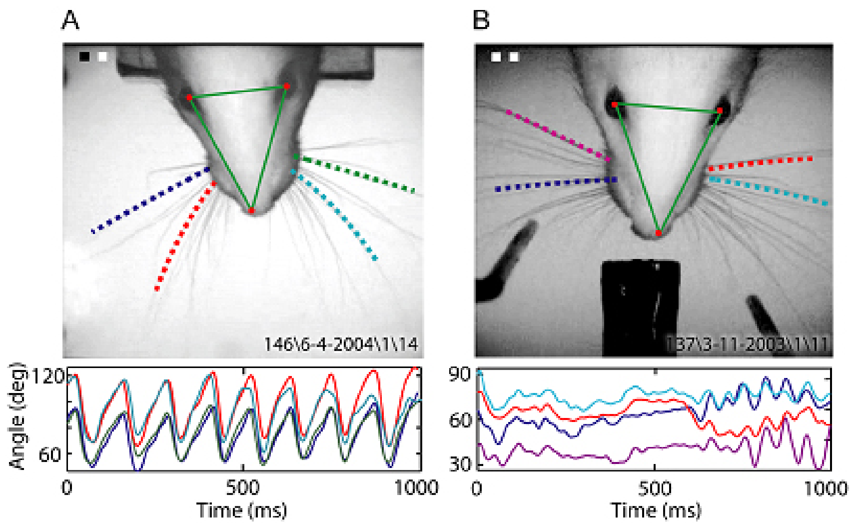

***Fig. 3** Whisking patterns produced by freely exploring and task engaged rats*
top snap-shot pictures taken from high speed videos (1000 frames/ sec) of a rat whisking in free air (A) and during object localization task (B). Bottom traces show tracking (angle in time) of four whiskers (traces colors correspond to whisker markers). Note the typical periodicity and bilateral symmetry in free air versus complexity of a highly-trained task-engaged rat.

relatively large proportion of neurons (41%) which are selective to specific horizontal locations of contacted objects, compared with at most half of this proportion in other thalamic and cortical areas (figure 2). This functional differences between layers in S1 and S2, taken together with related response latencies and dynamics, suggest that there are at least two cortical streams that process object information in parallel. These parallel streams are probably part of a multiple-level network of parallel and nested motor-sensory-motor loops that control active touch.

Motor control and behavior

Sensory processing stations along the all afferent pathways project to motor areas, thereby affecting whisking. In order to analyze and model sensory-motor control of whisking, our lab applies theoretical and computational approaches and integrates behavioral and neurophysiological data. Beyond predictions that are tested in experimental paradigms, modeling work has also produced tools for artificial generation of whisking, thereby contributing methodologically and conceptually to our understanding of sensory-motor loops functional implementation and to biomimetic robotics.

Careful examination of whisking behaviors shows that to facilitate solving of different tasks rats choose from a repertoire of motor strategies: While exploratory whisking, aimed to detect object in the rat's path, is repetitive and periodic, whisking produced by task-engaged rats is highly complex and task-adapted (figure 3). Careful examinations of whisking patterns suggest that whisking motorics is an integral part of whisker sensation, and is often the first available tool for adapting sensation to new conditions.

In rats, three dimensional reconstruction of the whisker path revealed that whisker motion is not confined to the horizontal and elevation axes, but includes torsional movement, where whiskers rotate around their own axis (figure 4). While the functional relevance of torsional motion is yet to be systematically demonstrated, such motion may explain phase specificity shown by sensory whisking neurons, and may suggest a mechanism that exploits directional selectivity in texture processing.

Human motor strategies of active sensing

Studying motor strategies and sensory feedback as means to learn about active perception, we expand our research beyond rats and examine whisking humans. Our lab has developed whisker-like probes adjusted for human psychophysical tactile tasks, similar to those preformed by rats. We found that human and rats share several motor-sensory strategies and perhaps encoding mechanisms. Furthermore, we observed that humans can reach superb motor coordination between hands to increase sensory acuity. We expect that understanding the key features of tactile motor strategies and perception limitations may direct applicative research towards developing adequate sensory substitution instruments to

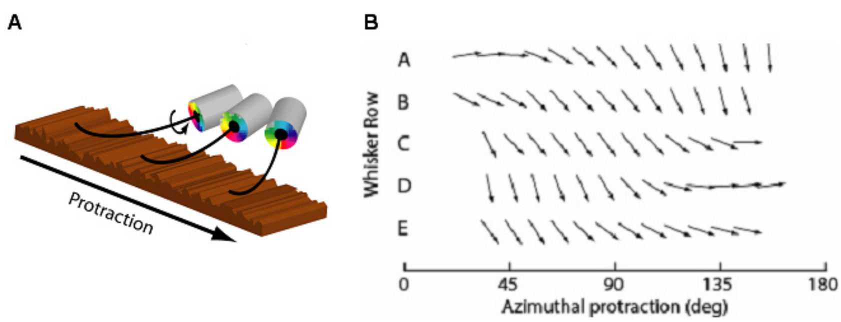

***Fig. 4** Torsional motion of the whiskers in behaving rats*
A, 3D schematic of follicle and whisker orientation during scanning of a textured surface
B, Averaged orientation of the whisker plane for each whisker row as a function of azimuthal angle. The azimuth angle was averaged in bins of 10 deg in individual trials, and then averaged across all whiskers of the same row across all experiments. Arrows indicate the orientation of the whisker plane. Horizontal arrows indicate that the plane of the whiskers was parallel to the eye-nose axis.

assist the blinds.

To further explore algorithms for sensory substitution, we investigate motor strategies of vision. By recording eye movements at high resolution we investigate the dependency of vision on miniature eye movements occurring during fixation, without which vision is not possible. We also study the amount of control exerted by the brain on these movements. Whereas the degree of control of the smallest eye movements (drift and tremor) is not yet clear, we observed significant control of the higher-amplitude type of fixational eye movements – microsaccades.

Whiskered robots

Our lab participates in an international initiative, bringing together nine research groups from Europe, the USA and Israel, whose aim is to use understanding of active touch in rats for robotics. Whiskered robots, that will be able to quickly locate, identify and capture moving objects, will be used primarily in rescue and search tasks in areas where vision is limited. This project will advance technology on the one hand, and will help gain a better understanding of the brain on the other. We suggest that it is the multiple closed feedback loops that are the key features giving biological systems an advantage over robotic systems. We will also use the robot as an experimental tool, by building a brain-like system, step-by-step, thus gaining insights into the workings of the brain's inside components.

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