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Algorithms of whisker-mediated touch perception

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Comparison of the functional organization of sensory modalities can reveal the specialized mechanisms unique to each modality as well as processing algorithms that are common across modalities. Here we examine the rodent whisker system. The whisker's mechanical properties shape the forces transmitted to specialized receptors. The sensory and motor systems are intimately interconnected, giving rise to two forms of sensation: generative and receptive. The sensory pathway is a test bed for fundamental concepts in computation and coding: hierarchical feature detection, sparseness, adaptive representations, and population coding. The central processing of signals can be considered a sequence of filters. At the level of cortex, neurons represent object features by a coordinated population code which encompasses cells with heterogeneous properties.

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Introduction

In the process that culminates in sensing and identifying an object, the starting point is the encoding of physical parameters by sensory receptors. A growing set of investigations focuses on transformations along sensory pathways as a means to understand the conversion from raw physical signals into sensations and percepts. A long-standing hypothesis is that those transformations are built up from a set of standard 'canonical' computations, implemented repeatedly [1] and combined to generate responses that are selective, specific and flexible [2]. Taking this hypothesis as a point of departure, this review aims to identify canonical computations, or algorithms, implemented in the rodent whisker system, an 'expert' system [3].

We focus on computations along the receptor-to-cortex ascending pathway; nevertheless a complete picture of

tactile sensation will only be achieved by understanding how sensory and motor computations are woven together [4,5].

Mechanical forces in the follicle

As in any sensory pathway, transduction from physical entities into action potentials constrains all later processing. Input signals — fluctuations in mechanical energy at the whisker base — are shaped by the interaction between the whisker's motion, its mechanical properties (e.g., compliance) and properties of the contacted object. The whisker-follicle junction is rigid, allowing robust transmission and readout of the forces induced by whisker motion [6**].

The form of whiskers (Fig. 1a) determines their mechanical behavior. Bending stiffness decreases from whisker base to tip due to taper [7**], and the concomitant increase in flexibility enables the slippage of whiskers during object exploration [8,9*]. Additional flexibility is achieved by their hollow structure [10].

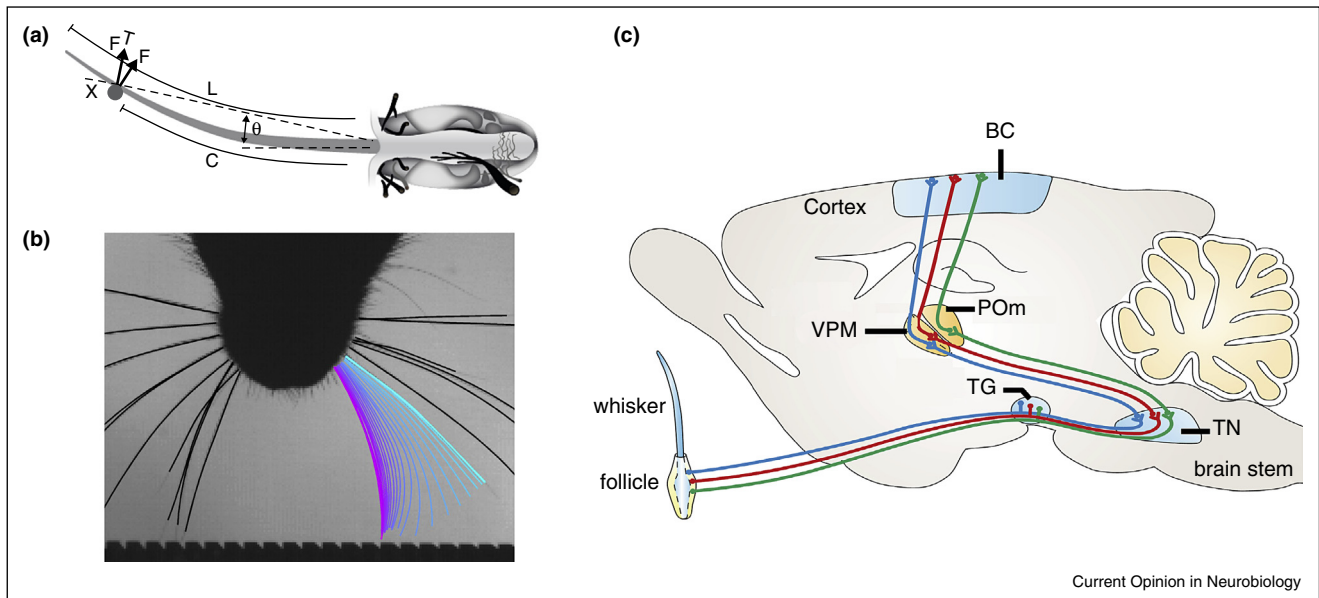
New methods for tracking whisker motion have allowed detailed analysis of how whiskers interact with objects [11,12]. The combination of whisker measurements with models of whisker deflection has begun to specify bending [9*,13] and changes in forces at the whisker base [6**,7**,9*,14]. Contact-induced whisker deformations can be decomposed into a slow bending component and a transient vibrational component [15]; the relative contributions of different components depend on the specific interaction [6**,7**,16]. Algorithms involving comparison of components require those components to be effectively transduced by mechanoreceptors.

When whiskers sweep across a textured surface (Fig. 1b), they are trapped and released by surface ridges and grains [17–19,20**] (reviewed in [21]). These brief (~2 ms) 'stick-slip' events cause transient, high-frequency vibrations [18]. The consequent sequence of fluctuations in mechanical energy provides a signature of texture [17,18]. Stick-slip events excite primary sensory neurons and their targets [17,18,20**,22]. However, differences in 'stick-slip' events across trials are not well-correlated with trial-to-trial choices in a texture discrimination task [20**]; other features of whisker motion may also contribute.

Transduction of touch into neuronal signals

Transduction is carried out at the terminals of neurons whose cell body resides in the trigeminal ganglion (TG; Fig. 1c). The many mechanoreceptor types, distributed

Figure 1



Input forces to the sensory system and the ascending pathway. **(a)** The force acting upon a whisker during contact, and thus transmitted to the receptors in the follicle, is illustrated. The object at position X strikes a whisker of length L at a distance C from the skin and at angle θ away from the whisker's resting angle, inducing a force F . **(b)** Illustration of a single large stick-slip event. One frame from a high-speed (1000 frames/s) video is shown in gray scale. The whisker traces have been enhanced to increase their visibility. While the rat palpated the surface to judge the groove spatial frequency, one whisker was tracked through a sequence of frames and the traces, from violet to light blue, show the whisker position over 1 ms timesteps. The whisker tip was blocked in a groove and then sprung free as the rat retracted the whisker shaft in the posterior direction. **(c)** Principal sensory pathways to the cortex are illustrated schematically. TG neurons send a peripheral branch to the skin and a central branch into the trigeminal nuclei (TN) of the brainstem. Axons from TN cross the midline to reach the thalamus, terminating in VPM and the posterior medial nucleus, POm. Thalamic neurons project to BC. Blue, red, and green lines represent parallel pathways that carry different sorts of tactile information, as reviewed elsewhere. (a) Adapted personal communication from A. Hires and K. Svoboda; (b) adapted from [20**]; (c) adapted from [5].

differentially across the follicle, have diverse response properties and are best activated by distinct forces with particular time courses. Given the diversity of receptor types and spatial distributions, it is not surprising that both of the principal functional classes of primary afferent neurons, slowly and rapidly adapting (SA and RA), in fact comprise a rich variety of feature combinations. Thus, each neuron displays distinct sensitivity to the location, direction and velocity of whisker displacements evoking lateral forces [17,23–26], to the pattern of axial forces [25], to whisking phase [27–29] and to contact, detachment or their combinations [24,27].

As a population, TG neurons represent the space of dynamical features of one whisker through a high-dimensional code (~ 200 , counting each neuron as a dimension) (see Section 'Feature selectivity') [30**]. This permits rapid information encoding: specific patterns of forces (e.g., [7**]) may engage subsets of neurons to 'label' the stimulus. Whisker motion patterns are richly represented by the TG population, allowing several population-based decoding schemes for any task. For example, information present across the population probably permits instantaneous comparison of the relative magnitudes of

different force components (see Section 'Mechanical forces in the follicle'). Intriguingly, each TG neuron projects to multiple target neurons within a column of the principal trigeminal nucleus ('barrelette'), and individual barrelette neurons receive convergent inputs of different afferent types (SA, RA): thus, TG population signals are decoded in a 'one-to-many' and 'many-to-one' manner [31*].

A requirement for TG to implement a fast population code based on relatively small numbers of spikes is that spike generation be precise. Indeed, TG neurons respond with highly reliable firing patterns [17,23,32,33] and are among the most temporally precise neurons yet discovered in the animal kingdom [17,30**,32]. The minimal sequential pathway from receptors to cortex (Fig. 1c) requires just three synapses — very short compared to other sensory systems.

To summarize, TG neurons convey information packaged in a high-temporal precision code where different neurons encode diverse physical properties. The speed of peripheral encoding is reflected in the finding that cortical neurons carry texture information within 20 ms after

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