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Current Opinion in Neurobiology

Whisking mechanics and active sensing

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We describe recent advances in quantifying the three-dimensional (3D) geometry and mechanics of whisking. Careful delineation of relevant 3D reference frames reveals important geometric and mechanical distinctions between the localization problem ('where' is an object) and the feature extraction problem ('what' is an object). *Head-centered* and *resting-whisker* reference frames lend themselves to quantifying temporal and kinematic cues used for object localization. The *whisking-centered* reference frame lends itself to quantifying the contact mechanics likely associated with feature extraction. We offer the 'windowed sampling' hypothesis for active sensing: that rats can estimate an object's spatial features by integrating mechanical information across whiskers during brief (25–60 ms) windows of 'haptic enclosure' with the whiskers, a motion that resembles a hand grasp.

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Current Opinion in Neurobiology 2016, **40**:178–188

This review comes from a themed issue on **Systems neuroscience**

Edited by **Don Katz** and **Leslie Kay**

http://dx.doi.org/10.1016/j.conb.2016.08.001

Introduction

The rodent vibrissal-trigeminal system is one of the oldest models for the study of active sensing in the field of neuroscience [1–5]. The past five years have seen several breakthroughs in the field of vibrissal research, including the discovery of the central pattern generating circuits responsible for rhythmic whisking [6] and their close association with sniffing behavior [6,7], as well as the elucidation of differential processing along parallel thalamocortical pathways [8,9]. However, we still do not fully understand how to interpret the signals in these central structures, in part because we do not yet fully understand the inputs: the tactile signals that drive the responses of primary sensory neurons in the trigeminal ganglion.

Recent advances in three-dimensional (3D) whisker mechanics [10,11••,12,13•] offer the opportunity to compute the complete set of tactile inputs transmitted by the vibrissae during active tactile exploration. The goal of the present paper is to review recent literature so as to establish a unified framework for describing the geometric and mechanical variables relevant to whisking behavior. Specifically, we develop formalisms for head-centered and whisker-centered reference frames, and compare them with the more traditional resting-whisker reference frame. The whisker-centered reference frame is well suited to describing mechanical information about the external world transmitted by the whisker, but it is geometrically unintuitive. The resting-whisker reference frame is well suited to describing the location of an object relative to a particular whisker, but is ill suited to describing mechanical variables and mechanoreceptor deformation.

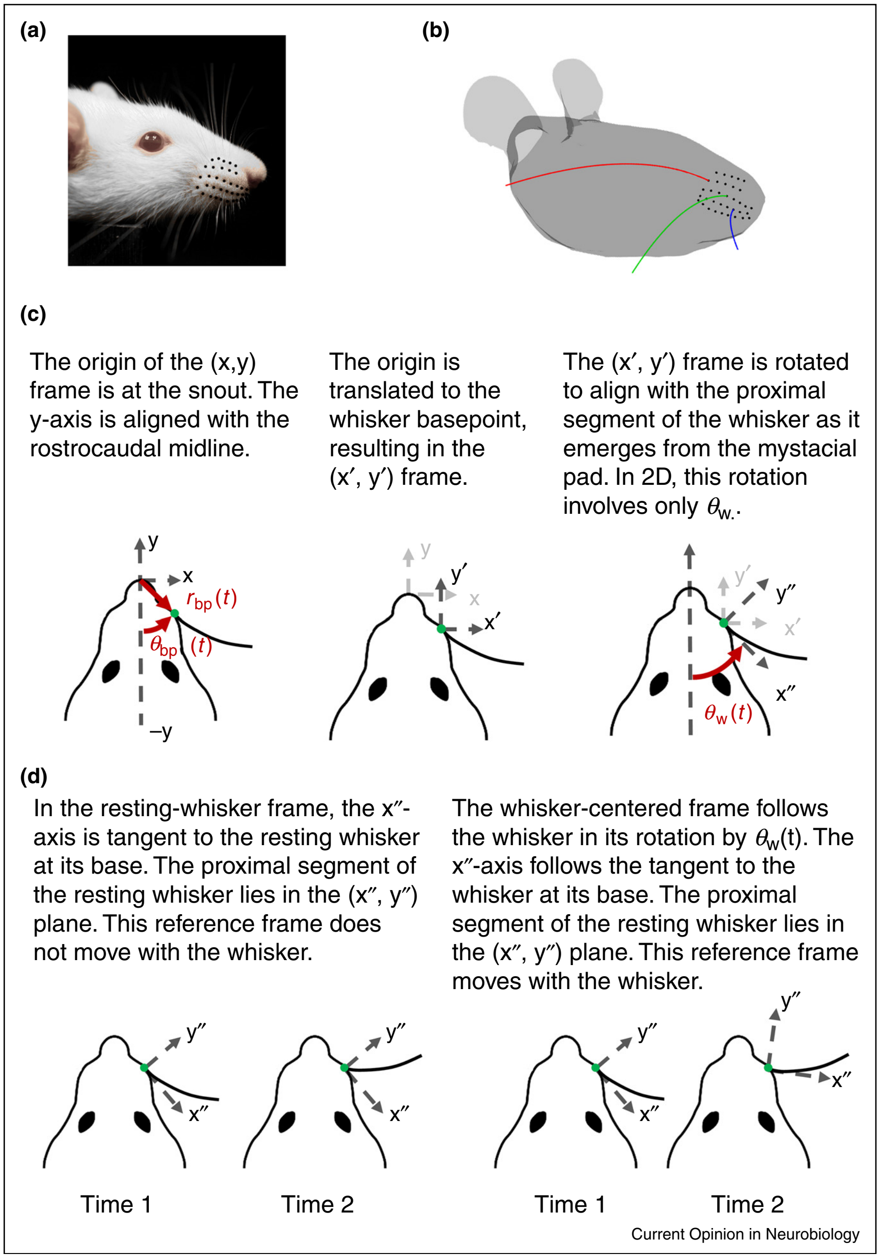
By carefully distinguishing between these reference frames, we argue that a whisking rodent will face two separate problems during tactile exploration. The first is how to localize an object in head-centered coordinates based on tactile information that originates in whisker-centered coordinates ('where' is the object). The second is how to integrate information across multiple whiskers to estimate the object's contour, independent of its location in head-centered coordinates ('what' is the object). In this review we focus on the rat whisker system, but the framework also applies to mice and other rodents.

The geometry of whisking

Whiskers are arranged in a regular array (rows and columns) on the rat's face, and decrease in length from caudal to rostral (Figure 1a,b). Each whisker has an intrinsic curvature that follows from approximating its proximal shape by a parabola [12,14]. Intrinsic curvature varies systematically across the array (Figure 1b); shorter whiskers tend to have larger curvature than longer whiskers and also a more variable curvature [15].

Each whisker is held tightly within a follicle at its base [16,17]. Each follicle is packed with mechanoreceptors, and is actuated by both intrinsic and extrinsic muscles [18–23]. Whisking behavior allows rodents to move their whiskers independently of the head, and it is therefore important to distinguish between head-centered and whisker-centered reference frames.

Figure 1



Arrangement of the whiskers on the mystacial pad and reference frames relevant to whisking mechanics. **(a)** The whiskers of the rat mystacial pad are organized in rows and columns. **(b)** Whisker length and curvature vary systematically across the array. **(c)** Panels illustrate a two-step process to transform between head-centered, resting-whisker, and whisker-centered reference frames. The translation moves the origin from the snout to a whisker basepoint with polar coordinates (r_{bp}, θ_{bp}) in the head-centered reference frame; θ_{bp} is measured counterclockwise from the midline. The rotation results in a new reference frame in which the proximal segment of the whisker lies in the x''–y'' plane and is tangent to the x''-axis at its base. The y''-axis is perpendicular to the x''-axis, with positive defined as the direction in which the tip curves concave. **(d)** The resting-whisker reference frame does not rotate with the whisker. In contrast, the whisker-centered reference frame rotates with θ_W(t).

Because each whisker is held tightly by its follicle [16], and because the base of a whisker is relatively stiff [15,24–28], the follicle and the proximal segment of the whisker move approximately as a single unit (a rigid body) relative to the head. Figure 1c describes the time-dependent position and orientation of this unit in a head-centered reference frame.

The two-step process depicted in Figure 1c — namely, a translation of the head-centered reference frame to the