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WHAT THE WHISKERS TELL THE BRAIN

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Abstract—A fundamental question in the investigation of any sensory system is what physical signals drive its sensory neurons during natural behavior. Surprisingly, in the whisker system, it is only recently that answers to this question have emerged. Here, we review the key developments, focussing mainly on the first stage of the ascending pathway – the primary whisker afferents (PWAs). We first consider a biomechanical framework, which describes the fundamental mechanical forces acting on the whiskers during active sensation. We then discuss technical progress that has allowed such mechanical variables to be estimated in awake, behaving animals. We discuss past electrophysiological evidence concerning how PWAs function and reinterpret it within the biomechanical framework. Finally, we consider recent studies of PWAs in awake, behaving animals and compare the results to related studies of the cortex. We argue that understanding ‘what the whiskers tell the brain’ sheds valuable light on the computational functions of downstream neural circuits, in particular, the barrel cortex.

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Key words: whisker system, somatosensory system, neural coding, trigeminal ganglion, barrel cortex, whisker mechanics.

INTRODUCTION

“It is extremely difficult to understand the visual cortex without understanding the retina and the lens. In the same way, it is difficult to understand the barrel cortex without understanding the follicle receptors and the whiskers”.

[Fox, 2008]

The interface between world and brain consists of sensory receptors that transduce physical signals (chemical, electromagnetic, thermal or mechanical) into cellular signals. Our knowledge of sensory systems is rooted in the ability to investigate how such physical variables translate into the responses of sensory neurons, and in the understanding of what information the spike trains of primary sensory neurons provide to downstream neural circuits, including the cerebral cortex.

The mechanoreceptors that form the basis of the somatosensory system are transducers of mechanical forces applied to the body. Forces due to body–object contact deform tissues within which mechanoreceptive nerve endings are embedded – in the case of the whisker system, the whisker follicle (Ebara et al., 2002; Mitchinson et al., 2004; Lottem and Azouz, 2011; Whiteley et al., 2015; Takatoh et al., 2017).

A long-recognized obstacle to the study of somatosensation is that the fundamental mechanical forces are very difficult to measure directly. Instead, many studies have investigated the encoding of directly measurable and controllable ‘kinematic’ quantities – measures of whisker position and its temporal derivatives. However, kinematic quantities do not necessarily relate to the underlying forces in any simple fashion. This is illustrated by classic work on primary afferents that innervate the primate hand (Phillips and Johnson, 1982). A ridged surface pressed into the fingertip deforms the skin and elicits robust firing in Slowly Adapting (SA) primary afferents. The pattern of skin deformation (the kinematics) caused by object contact is markedly different to the pattern of load force exerted by the object on the skin surface: SA activity correlates poorly with the kinematic indentation pattern, but well with the load force pattern.

It was first recognized by Johnson and colleagues that biomechanical modeling offers a potential way round the force measurement problem (Phillips and Johnson,

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1982). It is possible, using continuum mechanics, to make a biomechanical model of skin – that is, a system of equations that describes how the skin deforms upon application of a load force to its surface. If the skin is assumed to be a simple medium (elastic, homogeneous, isotropic and incompressible), the system of equations can be inverted to yield estimates of the load force (Phillips and Johnson, 1982; Sripati et al., 2006). The load force can, in principle, then be used to estimate tissue deformation (strain) inside the skin at the site of mechanoreceptive nerve endings. However, a substantial difficulty in taking this modeling approach further is that modeling the skin in a more realistic way has required finite-element simulations on supercomputers (Dandekar et al., 2003).

One of the lesser known beauties of the whiskers as a model system is that the force-kinematics relationship is much simpler than that for the hand. The two simple, but crucial, differences are that whiskers protrude from the skin and that they are near-conical objects, typically 10 times longer than their base width (Williams and Kramer, 2010; Hires et al., 2016). First, this allows a whisker's motion and shape to be directly measured, accurately and non-invasively, in the awake, behaving animal, by high-speed imaging. Second, the mathematical problem of how a long, thin rod deforms under an applied load is much simpler than the analogous problem for an arbitrary 3D body. There are simple, but powerful, results (detailed below) that express the relationship between the force applied to a rod and how much it bends (Birdwell et al., 2007; Pammer et al., 2013). By making appropriate measurements of whisker shape from imaging data, estimates of the mechanical forces acting on the base of the whisker shaft can be derived. These procedures were first applied “ex vivo” using plucked whiskers mounted on motors (Birdwell et al., 2007), later in vivo (O'Connor et al., 2010; Bagdasarian et al., 2013; Pammer et al., 2013; Huet et al., 2015; Wallach et al., 2016) and, in a significant recent advance, to awake, behaving animals where neuronal activity is simultaneously measured (O'Connor et al., 2010b, 2013; Petreanu et al., 2012; Chen et al., 2013; Hires et al., 2015; Peron et al., 2015; Bush et al., 2016; Campagner et al., 2016; Severson et al., 2017).

It is the primary purpose of this article to review these developments and how they have advanced our knowledge of neural coding in primary whisker afferents (PWAs). The wider significance of this work is that it clarifies the computational problems of touch that downstream neural circuitry, including barrel cortex, have evolved to solve, and provides an essential baseline for investigation of the perceptual algorithms implemented in neural circuitry (Marr, 1982; Maravall and Diamond, 2014). We start by reviewing a general framework for whisker mechanics.

MECHANICAL FRAMEWORK FOR WHISKER-BASED SENSATION

In the absence of contact (“whisking in air”), whisker mechanoreceptors are potentially susceptible to diverse forces, reflecting inertia of the whisker, contraction of

facial muscles and viscoelasticity of the whisker pad tissue within which the follicle is anchored. When a time-independent force is applied to a whisker, force onset triggers high-frequency vibration of the whisker (Neimark et al., 2003; Hartmann et al., 2003; Ritt et al., 2008; Wolfe et al., 2008; Boubenec et al., 2012), which rapidly decays to a static equilibrium, where the whisker bends against the object (Birdwell et al., 2007). In steady state, the degree of bending depends on both the applied force and the whisker's stiffness. During active whisking against an object, the relative importance of the dynamic and static effects depends on the material properties of the whisker, the whisker motion, the shape/texture/material of the object and where along the whisker shaft the motion of the whisker is measured. Since mechanoreceptors sense stresses at the base of a whisker, it is motion here, rather than at the tip, that is most relevant to neural coding in PWAs. Whisking against a rough surface elicits dynamic ‘slip-stick’ effects that evoke neuronal responses (Arabzadeh et al., 2005; Wolfe et al., 2008; Jadhav et al., 2009), but whisking against a smooth surface such as a metal pole generally elicits only weak dynamic effects at the whisker base (Quist et al., 2014).

For whisking against smooth objects, a whisker's shape can, aside from occasional slips, be approximated as a continuously changing steady state, where the shape at any given time depends on the applied force at that time. This ‘quasi-static’ case is not universally applicable (e.g., rough textures) but, as detailed in the next section, it is the basis for a mechanically rooted experimental paradigm that has given substantial novel insight into somatosensation. Unless stated to the contrary, the following discussion assumes the quasi-static case.

Forces at the whisker base

Suppose a time-independent force is applied to a whisker. Such a force exerts a rotatory effect on the whisker (‘moment’), which makes it bend around a pivot near its base. In steady state, the applied force and the moment are balanced by reaction force and reaction moment at the whisker base. In general, both the forces and moments are 3D, implying a total of 6 mechanical variables acting at the whisker base. However, 3D forces/moments are challenging to estimate (for progress, see Huet et al., 2015; Loft et al., 2016) and almost all studies to date have considered experimental conditions where whisker motion and whisker forces/moments are predominantly planar. Whisking motion occurs largely, but not entirely, in the horizontal plane defined by the two eyes and the nose (Bermejo et al., 2002; Knutsen et al., 2008). Thus, when a rat/mouse whisks against a vertical surface, such as a pole, whisker-object contact force and whisker bending is largely in the horizontal plane: these effects can be measured by imaging in this plane. In this 2D case, whisker-object contact is characterized by 3 mechanical variables at the whisker base: a 2-component applied force \vec{F} directed at some angle in the horizontal plane and a moment M_o directed about the vertical axis, normal to the horizontal plane (see Fig. 1).

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