Journal Club

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Rat Whisker Psychophysics

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Review of Stüttgen et al. (<http://www.jneurosci.org/cgi/content/full/26/30/7933>)

Like the digits of the human hand, the whiskers on the mystacial pad of rodents are used for fine tactile discriminations. During manual actions such as typing or piano playing, human fingers display fine and dexterous movements. Similarly, whisker movement kinematics are dynamic, and changes in whisking behavior correlate with performance on tactile discriminations (Carvell and Simons, 1990; Harvey et al., 2001). These behavioral similarities make the rodent whisker system useful in the investigation of the neural mechanisms underlying somatosensory and motor function. An added advantage of studying whiskers is that each whisker is represented by a discrete population of neurons at subcortical structures and in a unique column of neurons in primary somatosensory cortex (barrel cortex).

There exists a rich literature on the transformation of peripheral sensory stimulation into neuronal activity along the whisker-to-barrel pathway in anesthetized rats. Using well controlled whisker deflections, these studies have revealed that both deflection velocity and amplitude are reliably encoded by neural impulses throughout the whisker-to-barrel pathway (Pinto et al., 2000; Shoykhet et al., 2000; Ito and Kato, 2002). Few studies, however, have detailed the psychophysics of whisker-based tactile discriminations

in behaving animals, and the biologically relevant parameters of whisker stimulation remain unknown. In a recent study in *The Journal of Neuroscience*, Stüttgen et al. (2006) address these issues, revealing psychophysical detection thresholds of whisker deflections and their putative neural correlates in primary afferents.

Using awake, head-restrained rats, Stüttgen et al. developed an operant conditioning task to determine the amplitude and velocity detection thresholds of precisely controlled whisker deflections [Stüttgen et al. (2006), their Fig. 1 (<http://www.jneurosci.org/cgi/content/full/26/30/7933/F1>)]. To initiate the delivery of a water reward, rats were trained to lick a water spout after detection of a whisker deflection. To keep rats "honest," Stüttgen et al. (2006) imposed a time-out penalty in the event of random licking and included "catch" trials without any stimulation. With these procedural parameters in place, unsignaled lick responses were kept well below chance levels (12–18%). During testing, whisker deflections of varying amplitude (1–12°) and velocity (62–1500°/s) were presented and lick responses were recorded [Stüttgen et al. (2006), their Fig. 2 (<http://www.jneurosci.org/cgi/content/full/26/30/7933/F2>)].

Behavioral data were quantified by computing the probability of observing a lick response to a given whisker deflection. These data indicated that the detection of whisker deflections is determined by at least two kinematic parameters: amplitude and velocity. Specifically, rats reliably detected low-velocity whisker deflections (<750°/s) of sufficiently high

amplitude (>3°) [Stüttgen et al. (2006), their Fig. 3 (<http://www.jneurosci.org/cgi/content/full/26/30/7933/F3>)]. Conversely, low-amplitude deflections (<3°) were detected but only when presented at high velocity (<750°/s) [Stüttgen et al. (2006), their Fig. 4 (<http://www.jneurosci.org/cgi/content/full/26/30/7933/F4>)]. Stüttgen et al. propose that these data are indicative of two psychophysical channels: one sensitive to large amplitudes and slow velocities (W1), and the other sensitive to low amplitudes and high velocities (W2).

In search of the neural substrates of W1 and W2, Stüttgen et al. (2006) performed microelectrode recordings from the trigeminal ganglion (TG), the first station in the whisker-to-barrel pathway. The authors sampled from both slowly adapting (SA) and rapidly adapting (RA) neurons in the TG. In response to the same stimulation parameters used during behavioral testing, RA neurons responded to all amplitudes of whisker stimulation when presented at high velocity (>750°/s) [Stüttgen et al. (2006), their Fig. 5 (<http://www.jneurosci.org/cgi/content/full/26/30/7933/F5>)] as required by a putative W2 channel. Conversely, SA neurons responded to all velocities when deflections were of sufficient amplitude (>3°) [Stüttgen et al. (2006), their Fig. 6 (<http://www.jneurosci.org/cgi/content/full/26/30/7933/F6>)], as needed by a putative W1 channel. Quantitative comparisons of psychophysical results with neural data demonstrate that the responses of single RA neurons can account for the W2 channel, whereas single SA neurons can account for the W1 channel

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[Stüttgen et al. (2006), their Fig. 7 (<http://www.jneurosci.org/cgi/content/full/26/30/7933/F7>)]. These data make a strong case for the tuning of RA and SA neurons as the physiological substrates of the psychophysical detection curves and support a two-channel model.

Combining behavioral and *in vivo* physiology, the results described by Stüttgen et al. (2006) are quite convincing and extend our understanding of the coding of sensory stimulation along whisker-to-barrel circuits. Nevertheless, the current findings must be evaluated in relation to “natural” whisker stimulation parameters. For example, unlike passive whisker stimulation used in most studies, rats actively sweep their whiskers across a surface to generate contacts during exploration. Thus, in contrast to passive stimulation in which whiskers are being pushed, whiskers may push against an object during active touch. Despite the inherent differences between natural active whisking and the passive stimulation used by Stüttgen et al. (2006), the range of deflection amplitudes tested (1–12°) are within the range of average deflection amplitudes observed previously on object contact in a

texture discrimination task (mean of ~9° for protraction; 12° for retraction) (Carvell and Simons, 1990). Moreover, the range of velocities tested by Stüttgen et al. (2006) (62–1500°/s) includes the average deflection velocities produced during contact (mean protraction of ~578°/s; mean retraction of 702°/s) (Carvell and Simons, 1990). Thus, the deflection parameters tested are behaviorally relevant to object detection in whisking rats, emphasizing the significance of these results to our understanding of the mechanisms of somatosensation.

Stüttgen et al. (2006) have introduced a well controlled experimental task for addressing important psychophysical and physiological questions. For example, recordings from thalamus and/or barrel cortex during presentation of these same stimuli will reveal how the two sensory channels of neural activity are propagated along the whisker-to-barrel pathway. Likewise, minor modifications of stimulation parameters will help answer how deflections at different angles are encoded psychophysically as well as physiologically. Finally, perceptual deficits that take place after sensory deprivation can be ex-

amined in animals that have undergone whisker trimming or facial nerve lesion. Thus, both the methods and results described by Stüttgen et al. (2006) make a significant contribution to the study of the rat whisker system.

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