

What Makes Whiskers Shake? Focus on “Current Flow in Vibrissa Motor Cortex Can Phase-Lock With Exploratory Rhythmic Whisking in Rat”

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As one researcher once put it—“to beat the night with sticks” (D. Kleinfeld, personal communication)—might be only option for a small mammal to find its way through the dark holes it is living in. Rats employ such a strategy and explore their environment by fast rhythmic whisker movements. Whisking is generated by a highly specialized (Dörfl 1982) fast-muscle-fiber-dominated (Jin et al. 2004) musculature. It is a relatively simple movement in that it is restricted to only a single dimension (back and forth); multiple joints are absent and load plays a minor role. Such simplicity makes whisking an attractive model for the study of motor control. In this issue (p. 1700–1707), Ahrens and Kleinfeld analyze the cortical control of whisking behavior by a set of technically challenging experiments on awake behaving rats. The authors assess vibrissa movements with electromyograms (EMGs) of the whisker musculature, while simultaneously recording electrical activity in the somatosensory and motor cortices. Current source density analysis of these local field potentials shows that electric activity throughout the depth of motor cortex covaries with whisker EMGs and hence with the whisker rhythm. By applying spectral analysis techniques, the authors elegantly pinpoint the relationship between cortical activity and rhythmic motor output. The correlation between cortical activity and whisking persists after deafferentation, demonstrating that it does not simply result from sensory feedback to motor cortex. This novel finding ties in nicely with other evidence from the same laboratory, which demonstrates that rhythmic electric stimulation of vibrissa motor cortex can evoke whisking-like movements (Berg and Kleinfeld 2003) and vibrissa motor cortex neurons show tuning for frequencies around the whisking rhythm (Kleinfeld et al. 2002). Covariation of motor cortical activity and whisking, whisking evoked by intracortical stimulation, and sensory tuning for whisking frequencies in motor cortex, all support the idea the vibrissa motor cortex might be able to act as a rhythm generator for whisking.

This view of vibrissa motor cortex as a potential rhythm generator for whisking may not be surprising to the naïve reader, but it deviates substantially from previous views of how whisker movements are controlled. Like just about everything in the study of whisking behavior, thinking about whisking motor control goes back to the encyclopedic study of Welker (1964). This study on the kinematics, multisensory coordination, ontogeny, and neural control of whisking also indicated that decorticated animals display seemingly normal whisking behaviors. Although more recent studies demonstrated alterations in whisking after cortical lesions (Gao et al. 2003;

Semba and Kommisaruk 1984), the persistence of whisking after removal of the entire cerebral cortex primed researchers to look for a subcortical whisking generator. Thus anatomical (Hattox et al. 2002) and physiological/pharmacological (Hattox et al. 2003) studies delineated brain stem circuits involved in the control of whisking. Brain stem neurons, including serotonergic cells, that provide inputs to whisking motor neurons in the facial nucleus may form a brain stem pattern generator for whisking. In addition, behavioral and deafferentation data suggested that whisking may be generated in a feedback-independent manner, i.e., by a relatively autonomous “central-pattern-generator” (Gao et al. 2001). Finally, earlier unit-recording studies in vibrissa motor cortex (Carvell et al. 1996) did not observe a 1:1 relationship between cortical activity and the whisking cycle. These results together with the evidence on “whisking brain stem circuits” led to a motor control model where the vibrissa motor cortex merely gates the brain stem whisking generator.

To decide conclusively if vibrissa motor cortex functions by gating a brain stem generator or can act itself as a pattern generator for whisking may require additional experiments and further rigorous analysis. In my view, however, it seems most likely that there will be no decision among these opposing views of the role of motor cortex in the control of whisking. Instead it appears plausible that a model, in which vibrissa motor cortex can control whisking in multiple ways—either by a sweep-to-sweep fine control of the movement pattern or more globally by simply turning on and off whisking—could reconcile the opposing views of motor cortex function. Such a multitude of functions is in line with the results of intracellular stimulation in vibrissa motor cortex, which show that layer cortical 5 cells can reset the whisker rhythm, whereas cortical layer 6 cell stimulation evokes movements without resetting the rhythm (Brecht et al. 2004). The fact that movement patterns evoked from vibrissa motor cortex are highly state dependent may also reflect the potential for functional diversity of cortical motor commands (Berg and Kleinfeld 2003). Vibrissa motor cortical neurons are large in number (~1,000,000 according to a rough estimate), but at the same time, individual cells are quite effective in evoking movements (Brecht et al. 2004). The cortical output converges via a variety of synaptic pathways on a small number of facial nucleus vibrissa motor neurons—on the order of 1,000–2,000 cells (Klein and Rhoades 1985)—through which all whisking behavior is expressed. Given these apparently disproportionate numbers one cannot help but think that a hidden functional richness is buried in vibrissa motor cortical circuits. Thus experiments like those of Ahrens and Kleinfeld that study cortical activity in awake behaving animals by sophisticated analysis techniques are likely to continue to surprise us.

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