Good Vibrations. Focus on “Texture Signals in Whisker Vibrations”

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Roughly 20 years ago Valentino Braitenberg published a book on vehicles—a treatment of the amazingly complex behavior of a variety of very simple machines (Braitenberg 1984). This approach was inspired by the “law of uphill analysis and downhill invention.” Accordingly it is easier to design a mechanism to do something from scratch than to figure out just how nature has contrived to do it. Although the book is still widely cited in the robotics and artificial intelligence community, only a few neuroscientists followed Braitenberg’s path of “synthetic psychology” and tried to understand brain performance by rebuilding it.

In this issue of the Journal of Neurophysiology (p. 1792–1799), Hipp and colleagues provide a beautiful example of how we can learn a lot about a sensory system by trying to reinvent what it does (Hipp et al. 2006). The authors are fascinated by the ability of rodents to perform very fine texture discriminations with their whiskers. Rather than confronting the problem with classical neurophysiological tools (inserting microelectrodes, etc.), the investigators chose to build an artificial whisker system to identify the whisker vibration signals that allow such fine sensory discriminations. Thus they analyzed vibration signals both from artificial metal whiskers and real whiskers, then developed a classification algorithm that successfully matched the vibration frequency spectra of single trials to the texture, which induced it. It appears real whisker signals provide more information than metal whisker vibrations, but this point deserves further investigation, as the test conditions were not strictly comparable. But how do whisker vibrations allow discrimination? Analyzing whisker vibration spectra, the authors identify two critical features in whisker signals. The first one is the modulation power (which increases with texture coarseness), the power in the part of the spectrum that represents the modulation due to the texture surface. The second one is the modulation centroid (which decreases with increasing texture coarseness), a measure related to the center of gravity within the power spectrum. These two features of whisker signals provide most of the vibration information because restricting whisker signals to these two parameters allows performance that is three-fourths of the optimal performance.

Whisker mechanics is a relatively novel but very active area of research. Interest in this topic was kindled by the vibrissa resonance hypothesis (Moore and Andermann 2005; Neimark et al. 2003). Accordingly, the resonance properties of whiskers, which vary systematically with whisker length along whisker rows, will mediate texture discrimination. Different whiskers would be tuned to different frequencies and thus breakdown vibrational signals into labeled frequency lines. Consistent with this idea it was found that both trigeminal ganglion cells (the 1st-order whisker neurons) and cells in the somatosensory cortex can show tuning to vibrissa resonance frequencies (Andermann et al. 2004). The vibrissa resonance concept is very intuitive, but to what extent it explains whisker-based texture discrimination is unclear as yet. When different stimulation frequencies are applied to whisker shafts in population recordings across the plane of barrel cortex, a systematic frequency tuning of barrel cortex neurons along whisker rows is not evident (Arabzadeh et al. 2004). Instead neurons across barrel cortex seem to respond proportionally to the product of frequency and amplitude (Arabzadeh et al. 2004), i.e., they respond to stimulus velocity as reported previously (Pinto et al. 2000). In line with earlier findings (Arabzadeh et al. 2005), the study by Hipp et al. (2006) shows that individual whiskers provide information about a broad range of vibrational frequencies. More importantly the study proves that even in an individual whisker different textures induce spectrally different signals—reflected in the modulation centroid—that allow for texture discrimination. These results do not rule out that rats use resonance-based signals and across whisker comparisons for texture discrimination (Neimark et al. 2003), but they at least indicate that a whisker should not be conceptualized as a narrow-band frequency filter for vibrational information.

Systematic length variation along the whisker row is an evolutionary conserved and therefore probably a functionally significant feature of the vibrissae array. While the length of neighboring whiskers in different rows (i.e., along arcs of the whisker array) varies unsystematically across species, neighboring whiskers within a row show a precisely exponential increase in length from anterior to posterior in most mammals (Brecht et al. 1997). Originally, it was suggested that the different length whiskers of a row might form a distance detector (Brecht et al. 1997). However, at least one behavioral test of this hypothesis in which whiskers from rows and arcs were systematically removed while rats had to estimate the width of an aperture did not support the concept (Krupa et al. 2001). Similar arc versus row whisker removal experiments could probably tell us much about the significance of vibrissa resonance for texture discrimination. Although there is so far no evidence that removal of whisker arcs and whisker rows have different behavioral consequences, there is converging evidence that spatial integration across multiple whiskers plays a prominent role in the vibrissal system. This finding was not only made here by Hipp and colleagues (Hipp et al. 2006) in their artificial whisker system but also holds in behavioral experiments with rats in aperture tasks (Krupa et al. 2001) and texture discriminations (Simons 1995).

While major questions about of whisker mechanics remain unresolved, the good vibrations predominate. What is refreshing about vibrissal research is the pace by which novel research
approaches like artificial whisker systems (Hipp et al. 2006), mechanics (Arabzadeh et al. 2005; Neimark et al. 2003), robots with whiskers (Fend et al. 2003), and behavioral experiments enrich what used to be an almost exclusively neurophysiological/neuroanatomical domain.

REFERENCES
