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Research Report

Mechanical resonance enhances the sensitivity of the vibrissa sensory system to near-threshold stimuli

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ABSTRACT

The representation of high-frequency sensory information is a crucial problem faced by the nervous system. Rodent facial vibrissae constitute a high-resolution sensory system, capable of discriminating and detecting subtle changes in tactual input. During active sensing, the mechanical properties of vibrissae may play a key role in filtering sensory information and translating it into neural activity. Previous studies have shown that rat vibrissae resonate, conferring frequency specificity to trigeminal ganglion (NV) and primary somatosensory cortex (SI) neurons during suprathreshold sensory stimulation. In addition to *frequency specificity*, a further potential impact of vibrissa resonance is enhancement of *sensitivity* to near-threshold stimuli through signal amplification. To examine the effect of resonance on peri-threshold inputs ($\leq$80 μm at the vibrissa tip), we recorded NV and SI neurons during stimulation at multiple amplitudes and frequencies, and generated minimal amplitude tuning curves. Several novel findings emerged from this study. First, vibrissa resonance significantly lowered the threshold for evoked neural activity, in many cases by an order of magnitude compared to stimuli presented at off-resonance frequencies. When stimulated at the fundamental resonance frequency, motions as small as 8 μm at the vibrissa tip, corresponding to angular deflections of less than 0.2°, drove neural firing in the periphery and cortex. Second, a closer match between vibrissal and neural frequency tuning was found for lower amplitude motions. Third, simultaneous paired recordings demonstrated that the minimal amplitude of resonant vibrissa stimulation required to evoke responses in SI increased significantly for recordings outside the primary vibrissa barrel column, providing additional evidence for somatotopically localized frequency columns. These data demonstrate that resonant amplification can increase the sensitivity of the vibrissa sensory system to an ecologically relevant range of low-amplitude, high-frequency stimuli.

1. Introduction

The meeting that inspired this collection of articles brought together researchers from many different levels of analysis, ranging from single cell recordings in culture to whole-head human EEG studies. A central theme throughout, highlighted by the theoretical position presented by Dr. Basar, was that an understanding of oscillatory biological phenomena is crucial

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to understanding biological information processing. The canonical example of this kind of process is frequency-defined states in the brain, which are correlated with the optimal performance of distinct behavioral tasks and have distinct impacts on action-potential activity. A second, different kind of oscillatory context discussed was the 'state' of non-neural systems (Basar and Guntekin, 2007). The vascular system, for example, can exist in a variety of self-generated oscillatory states, demonstrating myogenic rhythmicity in lower frequency ranges that can show global synchrony or local, independent generation (Basar and Weiss 1981). While the direct connection between these oscillatory phenomena and neural dynamics has not been determined, the local distribution of blood flow and volume regulated by functional hyperemia was discussed as a potential source of neural modulation, impacting the excitability of neurons and influencing signal transmission (Moore and Cao, 2007). This hemo-neural hypothesis suggests that the two oscillatory systems may be coupled.

The present paper explores a different kind of example of a non-neural component of a sensory system that may be a key to translating environmental signals into sensory information. Oscillatory phenomena in the nervous system are driven by many sources, ranging from the intrinsic resonance of single neurons (Giacomo et al., 2007) to the pattern of motor activity that supports active sensing (Carvell and Simons, 1990; Fee et al., 1997). A crucial question is how environmental signals in different frequency ranges are translated into patterns of neural activity that form sensory representations. Several examples exist of oscillatory sensory input that can drive oscillations in peripheral and central sensory representations, and these phase-locked signals may be crucial to encoding (Moore and Andermann, 2005; Cariani, 1997; Wever, 1949). An alternative, though not exclusive, form of representation derives from the transduction of sensory signals into differences in relative rates of neural activity, based on mechanical amplification at the point of entry to the system (Rinberg and Davidowtiz, 2000). A key example of this kind of transduction is the auditory system, where embodied mechanical properties of the cochlea (von Bekesy, 1960) differentially excite and drive increased firing rates in specific subsets of neurons, forming a spatial map of frequency (see Geisler, 1998 for a review).

The vibrissa sensory system is widely employed for studies of neural processing and behavior. Several lines of inference suggest that small-amplitude, high-frequency 'micromotions' are a key sensory signal in this system (Carvell and Simons, 1990; Neimark et al., 2003; Arabzadeh et al., 2003), and recent studies have detailed these micromotions in the awake, freely-behaving animal (Ritt et al., 2008). At the point of entry to the system, the mechanical properties of the vibrissae likely impact the transduction of these sensory signals. For example, recent studies have shown that vibrissae resonate, generating a several-fold increase in motion amplitude when stimulated at their fundamental resonance frequency (Neimark et al., 2002; Hartmann et al., 2003; Neimark et al., 2003; Andermann et al., 2004; Mehta and Kleinfeld, 2004; Moore and Andermann, 2005; Ritt et al., 2008). This pattern of frequency-specific transduction has recently been observed in animals freely sampling a variety of surfaces with their vibrissae (Ritt et al., 2008). In this context, resonance tuning was robust during contact with rough and smooth surfaces, and during more ballistic and more periodic signal transmission, indicating that these embodied mechanical properties shape representation during the transduction of a variety of types of tactual 'natural scenes' (Ritt et al., 2008).

Resonance-dependent amplification by the vibrissae confers band-pass neural tuning to rat trigeminal ganglion (NV) and SI neurons (Andermann et al., 2004). Further, because vibrissa resonance is dependent on vibrissa length (Hartmann et al., 2003; Neimark et al., 2003), and length varies systematically from caudal to rostral across the vibrissa pad (Brecht et al., 1997), a map of frequency-tuned neurons is overlaid on the somatotopic representation of vibrissa position. Along a dorsal–ventral arc, vibrissae have similar lengths and in turn similar frequency tuning, generating isofrequency 'columns' that span multiple vibrissa-related barrel columns in SI (Andermann et al., 2004). Based on these findings, we hypothesized that resonance may contribute to the specificity of vibrissa-based frequency discrimination, by generating frequency tuning in peripheral and central neurons, and by selective engagement of regions within somatotopic maps. Further, mechanical amplification due to resonance may facilitate the detection of high-frequency information, transforming small inputs that would otherwise not surpass the sensory neural threshold into suprathreshold stimuli (Neimark et al., 2003; Moore and Andermann, 2005). In the present study, we tested the impact of frequency-specific mechanical amplification on the likelihood of driving a significant neural response and, more generally, on the amplitude of sensory responses relative to input strength. To address these questions, we presented a large range of sinusoidal stimuli varying in frequency and amplitude to a vibrissa while recording neural activity, permitting the construction of minimal amplitude tuning curves (MATCs), as commonly employed in the auditory system.

We observed several-fold decreases in response thresholds for neural firing at frequencies near the vibrissa fundamental resonance frequency (FRF), and enhanced gain of suprathreshold responses. In addition, we found that threshold amplitudes for effective resonant stimuli in SI increased sharply for recordings outside the principal barrel column, underscoring the spatial localization of frequency tuning in SI (Andermann et al., 2004). Taken with previous findings, these results suggest that vibrissa resonance can substantially impact the neural representations that mediate the detection and discrimination of low-amplitude, high-frequency stimuli.

2. Results

2.1. *Minimal amplitude frequency sensitivity in NV*

Neurons in NV demonstrated sharp frequency tuning for small-amplitude stimuli. In Fig. 1A, firing rate responses of an NV unit and corresponding C2 vibrissa motion amplitudes are shown for stimuli applied in 5 Hz intervals at 15 frequencies surrounding the FRF (a 265 Hz range). In this example, MATCs with a well-defined 'characteristic frequency' (CF: the