Features of whisker movement encoded by rat barrel cortex neurons

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Introduction

As nocturnal animals, rats depend on their vibrissal sensory system for object localization and for judgment of surface roughness or texture and of object size and shape. The present experiments were aimed at determining how neurons in rat somatosensory cortex generate representations of sensory events. Because of its anatomic and functional organization, the rat somatosensory system is particularly well-suited for examining how neuronal activity encodes stimuli. Recently there has been notable progress in revealing the temporal and spatial unfolding of barrel cortical neural activity in response to single-whisker deflections. From this evidence, it has been possible to unravel the functional circuitry underlying cortical activity, but most studies have not provided insights as to precisely what information is carried by neuronal activity. An exception is a report (Pinto et al., 2000; *J Neurophysiol* 83: 1158-1166) in which measurements were made of barrel cortex neural activity during ramp whisker deflections that varied in velocity and amplitude. The main finding was that cortical neuronal firing rate varied positively with whisker velocity. In the present study, we extend these findings by forming an experimental model for whisker stimulation that might more closely resemble the conditions under which rats naturally collect tactile information. The question that motivates our work is: What does a given pattern of neuronal activity report about the whisker stimulation? Thus, we aim to determine how specific features of whisker stimuli are encoded in neuronal activity (for a similar approach, see Petersen et al. in these proceedings).
Tactile sensation in the rat whisker system is an active process in which the rat sweeps its whiskers backwards and forwards through the air. We assume that during this "whisking" action, contacts with textured surfaces (which rats are known to be able to discriminate) produce vibrations in the whisker shaft: then the rat's judgment of texture stems from the neural encoding of these whisker vibrations. We thus delivered sinusoidal movements to the whisker shaft and analyzed neuronal activity to determine how the vibration parameters are represented in cortex.

Methods

In five experiments in urethane-anesthetized rats, a 100-microelectrode array was implanted in the whisker representation of somatosensory cortex. Electrode tips were about 600-1000 microns below the cortical surface, and response latencies to whisker stimulation were in the range 5-8 ms; both observations indicate that recording sites were in layers III or IV. The matrix of electrodes typically recorded from about 20 barrel-columns, and each electrode recorded the activity of a small cluster of neurons.
Resting the whisker shafts on bars extending from a piezoelectric wafer, the whole grid of large facial whiskers was moved together with a sinusoidal deflection. To explore cortical coding of the vibration, its frequency and amplitude on each trial varied across 7 values (frequency = 19, 30, 50, 81, 131, 211, 341 Hz; amplitude = 8, 12, 21, 33, 54, 87, 140 microns). The resulting 49 different frequency/amplitude combinations were presented in random order, with 200 trials per stimulus.

Results

We used raster plots and PSTHs to study responses. A sharp initial response about 5 ms after stimulus onset could be identified, peaking about 10 ms after stimulus onset. After a second, smaller rise in firing rate around 70 ms, the response settled to a plateau level, remaining there until stimulus offset. There was a small increase in firing rate when the stimulus ended. Thus, neurons typically showed two response phases which can be regarded as an early, rapidly adapting response (0-50 ms) and a subsequent, slowly adapting response (50-500 ms).
We then considered how vibration features were encoded in neuronal activity. Using firing rates averaged across the 500 ms stimulus duration as a first measure of neural responses, we observed a symmetric increase in response magnitude as either stimulus frequency or amplitude were increased. From these findings we concluded that neuronal activity encodes both frequency and amplitude, but decoding these features from neuronal firing rate would be ambiguous: a given activity level could, in principle, reflect an

infinite number of frequency/amplitude combinations. Was any feature of the vibration unambiguously encoded by neuronal activity?

The vibration features encoded by cortical neuronal activity can be best appreciated by constructing for each stimulus the quantity $E = A^2 * f^2$ proportional to the integrated kinetic energy, where A is vibration amplitude and f is vibration frequency. Energy is symmetrical with respect to changes in frequency or amplitude, and the stimulus set was such that different stimuli could possess equal Energy achieved by different frequency/amplitude combinations. We refer to these combinations as iso-Energy stimuli.

To allow direct comparison between stimulus energy (proportional to $A^2 * f^2$) and neuronal activity, we then examined neuronal responses within iso-Energy bands. Iso-Energy stimuli evoked very similar firing rates, even when differing drastically in frequency and amplitude. Moreover, firing rate changed from one iso-Energy stimulus set to its neighbor.

We next looked at PSTHs as a possible temporal code to disambiguate frequency and amplitude. PSTH profiles were clearly dictated exclusively by vibration energy, not by the frequency or amplitude that produced the energy.

To characterize neuronal encoding of vibration parameters for large neuronal populations, we simply summated the spikes recorded across all electrodes (range: 16-30 electrodes) and found that the pattern of response across the stimulus set was remarkably reproducible in different rats.

We also analyzed the data set in a manner aimed at determining whether a fast, temporal code might represent the stimulus features of interest. Specifically, we made whole-array spike counts by sliding a narrow temporal window. The algorithm, without specific knowledge of stimulus time, registered the peak firing rate encountered as the window slid. For all experiments, the encoding of stimulus energy by maximum, instantaneous spike density was nearly indistinguishable from that of a long-time window spike count.

Based on these observation we suggest that the feature of whisker vibrations that is most robustly encoded by cortical neurons is kinetic energy at the whisker shaft, and that the encoding of this feature is extraordinarily robust to the assumption of coding mechanism.