Effects of adaptation on information coding in rat somatosensory cortex

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Adaptation is a fundamental feature of sensory processing. Sensory responses typically have dynamic ranges several orders of magnitude smaller than those of the stimulus parameters they encode. The solution to this problem adopted by neural systems (and found in every sensory modality where it has been sought) consists of the continuous modulation of neuronal input-response relationships, thus matching response dynamic range to stimulus context. Indeed, the meaning that we give to any signal from our environment is modulated by the context within which it appears.

The functional effects of adaptation on sensory information coding have been extensively studied in the sensory periphery. On the other hand, despite the intuitive appeal of adaptation as a principle for neocortical processing, there is little understanding of its functional effects on sensory coding in the cortex (perhaps excepting primary visual cortex). For instance, in the primary somatosensory cortex of the rat, whisker stimulation with repeated high-frequency pulses depresses neuronal responses more than stimulation with low-frequency pulses, and the circuit mechanisms responsible for this effect have recently been described (Chung et al., *Neuron* **34**, 437 (2002)). Although such stimuli are ideal for evoking adaptation in cellular responses, their relationship to natural environments is unclear. No characterization exists of how cortical sensory representations change in time with shifts in the statistics (i.e. the context) of more ecologically relevant stimuli. Is adaptation present during exposure to such stimuli? If so, what is its functional role –how does it affect sensory representations? Does it imply information about fast changes in stimuli or about their context, and does it alter the stimulus properties encoded by spikes?

Such questions have recently been addressed for H1 motion-sensitive visual neurons in the blowfly (Fairhall et al., *Nature* **412**, 787 (2001)). These neurons adapt their responses not only to the average but also to the variance of the recent distribution of stimuli. While the neuronal transfer function adapts to rapid stimulus variations, slower changes in spike train statistics encode information about stimulus context. Thus, in this invertebrate system, the phenomenology of adaptation can be related to its functional significance for information processing. In mammalian neocortex, do ensembles of neurons use adaptation in a similar way?

The somatosensory modality of the rat is an excellent system for addressing this problem. A rodent's vibrissae ("whiskers") are crucial to its perception, and confer tactile discriminative abilities similar to those of human fingertips. The topographic arrangement of rat "barrel" (primary somatosensory) cortex allows one to record simultaneously from several regions (cortical barrel-columns) corresponding to particular vibrissae. Adequately large samples of spiking responses can be recorded in this way, enabling application of the methods of information theory to analyses of the dynamics of cortical responses to sustained stimuli in vivo. Recent results from our laboratory (Petersen et al., Arabzadeh et al., this meeting) indicate that single units and clusters of neurons in barrel cortex encode stimulus kinetic energy. Because stimulus frequency and energy are important parameters for tactile stimuli in the rat and across species (including apes and humans), we used them as test variables in sets of stimuli designed specifically for testing adaptation.

Stimulus Design

Two types of sinusoidal vibration stimuli were created:

(1) Several (3-5) predefined frequency levels (range 50-100 Hz) were selected in pseudorandom sequence. Each frequency level was maintained for 5 seconds, long enough to evoke an "onset" response and a later "steady state / adapted" response. The pseudorandom sequence was such that each possible step from one level to

another (e.g. 50 Hz to 100 Hz, or 0 to 50 Hz) was presented a minimum of 100 times, and each level was presented 100-150 times.

(2) Instantaneous frequency values were independently drawn from a Gaussian distribution, over a broadband range of frequencies known to be appropriate for driving barrel cortex neurons (~ 90 Hz with 20-50 Hz standard deviation). The resulting time series was smoothed (100 ms) to give a trajectory of instantaneous frequency values (duration 30-60 sec). A sinusoidal stimulus was then constructed using these time-varying frequencies. An ensemble of 100 such stimuli was generated, drawn from the same distribution. In order to have two different "contexts" for adaptation, stimuli were generated with two different frequency variances (for instance, 30 Hz and 50 Hz).

Stimulus set (1) was designed to permit evaluation of the influence of different stimulus properties on barrel cortex neuronal responses throughout a period of sustained but varying stimulation. Analysis was based on peri-stimulus time histograms (PSTHs) and spike counts: stimulus properties examined included stimulus onset and offset, values of kinetic energy and frequency, and changes in kinetic energy and frequency. Set (2) allowed spike-triggered averaging and reverse correlation analyses of responses to be performed, in order to estimate the neuronal transfer function.

Physiological Methods

We performed acute recordings in urethane-anesthetized adult rats using a 100-microelectrode array implanted in barrel cortex, allowing parallel recording of vibrissae responses from many neuronal clusters (see e.g. Petersen and Diamond, *J. Neurosci.* **20**, 6135 (2000)). Stimuli were administered jointly to all caudal vibrissae, using a piezoelectric wafer and a custom-made ladder frame on whose rungs vibrissae were placed ~ 1-2 mm from their base.

Results

At present, our preliminary results are as follows. Barrel cortex "steady state" or "adapted" neuronal responses to a fixed frequency sometimes remain above baseline level. However, the main factors influencing response magnitudes (i.e. being coded for) are stimulus onset and changes in frequency or energy. Sudden changes in frequency and energy are more robustly and informatively encoded than stable values or smooth changes in frequency and energy. Increases in energy always evoke increases in spike counts, both when stimulation is previously present (ongoing stimulus) and when it is not (stimulus onset). Taken together, these results suggest that response adaptation plays a role in tactile stimuli encoding in primary somatosensory cortex. Barrel cortex neuronal clusters behave as detectors of "surprise" or "novelty", i.e. of changes in stimulus parameters. Further analyses will be presented at the meeting.