The ability of rats to use their whiskers to perform fine tactile discrimination rivals that of humans using their fingertips. Rats perform these discriminations rapidly and accurately while palpating the environment with their whiskers. This suggests that whisker-derived inputs produce a robust and reliable code in the whisker-trigeminal system. Here we show that whisker primary afferent neurons respond with highly reproducible temporal spike patterns to transient stimuli. We demonstrate that a single response train recorded from an individual neuron can reliably encode complex whisker deflection patterns, and that encoding is improved by combining responses from cells with opposite directional preferences.

Coding of sensory stimuli has been traditionally studied by analyzing changes in mean neuronal firing rates. However, sensory stimuli elicit very sparse spike patterns in many sensory systems, including the rodent whisker-trigeminal system. The limited number of spikes elicited in these systems, combined with the complex stimuli that the systems can distinguish, implies that a rate-based coding scheme is implausible. There is mounting evidence that sensory perception involves temporal coding schemes, in which the timing of individual spikes encodes information beyond that provided by a rate coding scheme. Temporal coding requires that a sensory stimulus elicit a highly reproducible pattern of spikes. Our first goal was to test the hypothesis that in the whisker-trigeminal system, sensory inputs evoke such reproducible spike patterns. We started by analyzing responses in whisker primary afferents of the trigeminal ganglion, because they necessarily constrain all subsequent processing.

To mimic whisker contacts that may occur during tactile discrimination, we deflected, in urethane anesthetized rats, an individual whisker in a complex patterns described by white noise waveforms, low pass filtered at 25, 125, or 625 Hz. We chose these frequency ranges because they encompass the range of frequencies rats are likely to encounter in their environment. We recorded extracellular spikes from individual trigeminal neurons in response to 50 trials of each stimulus. Because trigeminal neurons display a strong angular preference—they respond more robustly to whisker deflections at particular angles—we applied the stimuli in each neuron's preferred direction.

Responses to successive presentations of the same stimulus were highly reproducible, with most spikes and spike bursts occurring at precisely the same time in every trial. To quantify this reproducibility, we calculated, for each cell, the correlation coefficient between every pair of spike trains. The mean correlation coefficients ranged from 0.50 to 0.93 (mean=0.7±0.1).

These highly reproducible firing patterns suggest that an individual spike train may encode sufficient information to describe the stimulus features. Our second goal was to test this hypothesis by predicting the stimulus from individual trigeminal spike trains. We first computed a linear reverse filter for stimulus-response pairs recorded during the first second of the noise stimulus. Linear kernels were computed using the following equation:

$$K = \frac{CSD_{(spikes,stimulus)}}{PSD_{(stimulus)}}$$

where $CSD_{(\text{spikes, stimulus})}$ is the cross-spectral density of the spike train and the stimulus, and PSD is the power spectral density of the stimulus. We then convolved this kernel with the second half of each spike train to derive the stimulus prediction. We estimated the precision of the prediction by computing the cross-correlation coefficient between the actual stimulus and the prediction. Predictions computed from *individual* spike trains were significantly correlated with the original stimuli ($r \geq 0.7$). For each of these cells, we computed the coefficient of variation (CV) of the r for each trial as a measure of the variability of the predictions. We found that for all cells, the CV was < 10%, indicating that a spike train from *any* individual trial provides an equally accurate predicting the stimulus.

Trigeminal ganglion neurons and cells upstream in the whisker-to-barrel pathway respond more robustly to whisker deflections at high velocity or acceleration. We therefore asked whether encoding of velocity or acceleration is more robust than that of whisker position by reconstructing the velocity and acceleration of the stimulus. We compared mean r-values across all cells and found that predictions of stimulus velocity and acceleration were similar ($p=0.27$), but significantly more accurate than that of position ($p<0.01$). This finding indicates that the neural code best captures abrupt changes in whisker trajectories. Such changes occur when a whisker contacts an object or when it encounters changes in an object's shape or texture. Thus, whisker-based tactile discrimination appears to use a coding strategy similar to that of the visual system in which neurons are sensitive to changes in contrast, produced, for example by moving edges.

Our findings demonstrate that a linear reconstruction method accurately predicts complex spatiotemporal stimuli from a single spike train. However, we were not able to fully reconstruct all stimulus features. Whereas single-trial reconstructions accurately predicted upward stimulus deflections (*i.e.,* stimuli applied in the cells' preferred direction), they did not optimally predict downward deflections (stimuli at the cells' null direction). We postulated that in order to obtain a more accurate prediction of the stimulus, it might be necessary to combine spike responses from 2 cells that are oppositely tuned. To mimic recording from two cells with opposite angular tuning, we presented the original stimulus to a cell and then reversed the stimulus and presented it to the same cell. We then computed new kernels as described above, and obtained predictions of the stimulus from these integrated spike trains. Reconstructions were significantly improved by integrating spike trains in this manner (see Fig. 1).

Our main findings are: (1) trigeminal spike patterns elicited in response to complex time-varying stimuli are highly reproducible; (2) single spike trains provide accurate predictions of complex whisker stimuli; (3) predictions are improved by combining information from pairs of cells with opposite angular preferences.

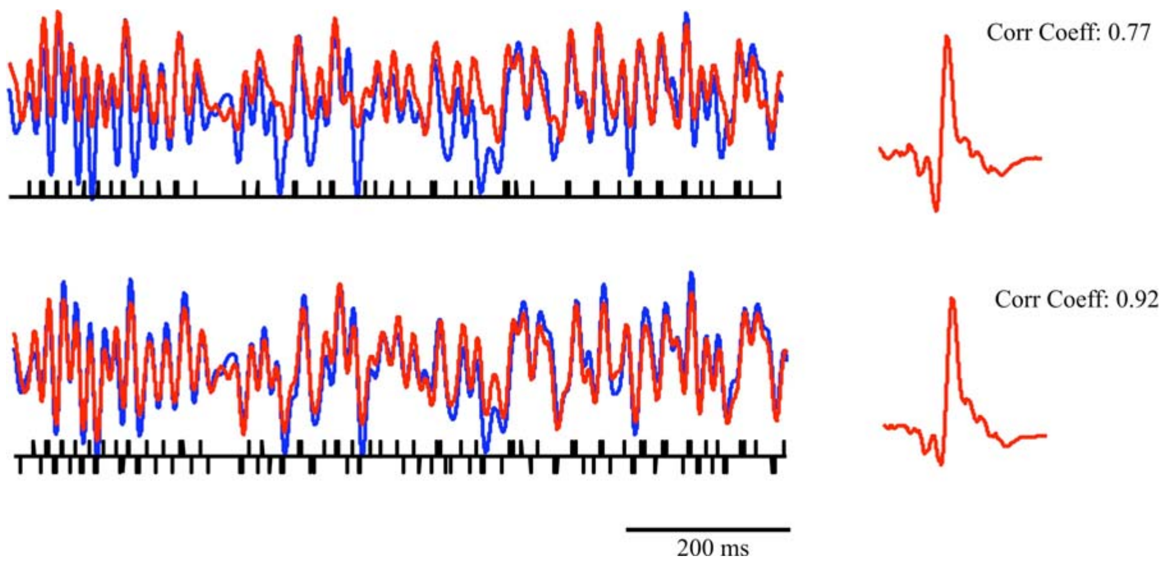

Figure 1

Top: Prediction (red) of whisker displacement (blue) created by convolving the kernel (at right) with the single spike train below (black).

Bottom: Prediction (red) of whisker displacement (blue) created by convolving the kernel at right with the combined spike train below (black) constructed from a single response to the original stimulus (positive spikes, as in top trace) and a single response to the inverted stimulus (negative spikes).