

## **Decoding latency codes: a solution to the stimulus time problem**

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### **Abstract**

In many neural systems, there is evidence for a simple spike timing code, whereby stimulus information is conveyed by latency. However, measuring latency requires knowing the timing of stimulus application: can a downstream neural system read this code? We addressed this issue in rat somatosensory cortex, where the timing of the first post-stimulus spike contains all the information about the location of a whisker deflection on the snout. We found that a simple, biologically plausible decoder, based only on the timing of spikes pooled within-columns and without knowledge of stimulus time, not only affords 100%-correct decoding of stimulus identity but also permits reconstruction of stimulus time with 0.6 ms precision.

### **Introduction**

The nervous system codes many kinds of signal by fast (millisecond-scale) modulations of firing rate. In the simplest kind of such spike timing code, stimuli evoke responses with differing latencies [1-6]. For example, in the somatosensory system of the rat, deflection of a whisker evokes a rapid response in the topographically matching cortical column, whereas deflection of other whiskers evokes a slower response. However, since the subject does not have direct access to the time of stimulus onset, it is uncertain how response latency could be measured and used by the brain to decode stimuli.

The problem could be solved if the sensory input were generated in response to an active motor command, in which case the time of the command could constitute an estimate of stimulus time. For example, rodents make whisking movements that

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sweep their vibrissae across objects of interest. However, it seems unlikely that motor “efference copy” possess the necessary fine temporal resolution [7].

In this paper, we propose a solution to the stimulus time problem that uses only sensory cortex spiking activity to decode stimulus identity without any need for independent knowledge of stimulus time or motor signals. Our solution builds upon previous work on this subject [8,9], and is based on the columnar organization that characterizes sensory cortex. The essential idea is that downstream neurons use stored statistical knowledge of population responses of cortical columns to simultaneously estimate both the most likely stimulus and the most likely stimulus time. We illustrate the algorithm using data recorded from rat somatosensory cortex and show that it can be implemented by a simple integrate-and-fire mechanism.

## Experimental Methods

We analyzed the activity of single cells recorded from primary somatosensory cortex of barrel-columns of urethane-anesthetized rats in response to whisker stimulation [5,6]. Vibrissae C1, C2, C3, D1, D2, D3, E1, E2 and E3 were deflected one at a time, using a piezoelectric wafer controlled by a voltage generator. The stimulus was an up-down step function of 80 $\mu$ m amplitude and 100 ms duration, delivered once per second, 50 times for each vibrissa, 3mm from their base. Stimulus onset was defined as time = 0ms. We considered the responses of a population of 100 cells in each of barrel-columns D1, D2 and D3. Note that the cells were recorded in groups of 2-6 neurons simultaneously, while the population of 100 cells was generated by combining the responses of many groups of neurons recorded at different times.

## Maximum Likelihood Decoding

We constructed a Stimulus-Time-Free-Maximum-Likelihood (STFML) decoder as follows. First, we pooled the activity within each of the three cortical columns separately in 10ms bins within a window -500 to +100 ms around stimulus onset. The input to the decoder consists of these three (time-varying) pooled signals (Fig 1C-D). In previous studies on this dataset we demonstrated that more than 98% of the information conveyed by the population responses about stimulus identity can be reconstructed by a simple decoder based on a Poisson process [10]; (2) 99% of the information about whether or not the whisker topographically matching a certain column was stimulated is preserved if neurons within each column are “pooled” together [11]. Hence, for this data, little information is lost by pooling the responses of neurons and then decoding the stimulus on the assumption that spikes are generated according to a Poisson process with firing rate that depends on both stimulus time (when the whisker was deflected) and stimulus identity (which whisker was deflected).

The decoder receives input within a time window that preceded stimulus onset time by an amount that varied between 0 and -500 ms. On each trial, the decoder estimates both the most likely time for stimulus onset ( $\tau$ ) and the most likely whisker identity ( $s^p$ ):

$$(s^p, \tau) = \arg \max \left( P(s) \prod_{c=1,2,3} P_{\text{poisson}}^{(c)}(\{t_i + \tau\} | s) \right) \quad (1)$$

Here  $\{t_i\}$  is the set of spike times observed on a given trial, relative to stimulus onset.  $P_{\text{poisson}}^{(c)}(\{t_i\} | s)$  is the probability (according to a Poisson model) of observing this spike train in column  $c$  given stimulus  $s$  and  $P(s)$  is the probability of stimulus  $s$  occurring. For the results reported here, we considered a stimulus set consisting of four categories: D1, D2, D3, and any of the other 6 whiskers.

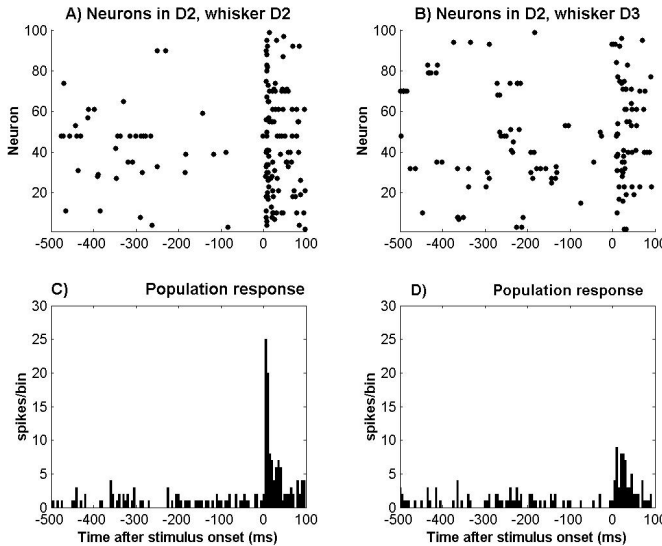
The performance of the decoder in reconstructing stimulus identity was assessed in Information Theoretic terms, as follows. We computed  $Q(s^p | s)$ , the fraction of trials in which an actual stimulus  $s$  elicited a predicted stimulus  $s^p$ . As detailed in [9], the information extracted by a decoder is:

$$I_{\text{decoded}} = \sum_{s, s^p} P(s) Q(s^p | s) \log_2 \frac{Q(s^p | s)}{Q(s^p)} \quad (2)$$

The entropy of the stimulus set, and hence an upper bound on  $I_{\text{decoded}}$ , was 1.42 bits.

## Results

Figure 1A shows the responses of neurons in column D2 to deflection of whisker D2. 9-10 ms after stimulus onset, there was a sharp, synchronous increase in firing rate. By 50 ms after stimulus onset, activity had returned to baseline level. Responses of these neurons to deflection of a different whisker (D3) are shown in panel 1B. Figure 1C-D shows the pooled activity of column D2 units in response to deflection of these two whiskers. The response to the topographically matching whisker is stronger, shorter latency and is more precisely timed.



**Figure 1.** Panels *A* and *B*: responses of 100 neurons in barrel column D2 to deflection of whiskers D2 and D3 respectively on a single trial. Each row represents a different neuron and each dot represents an action potential. Panels *C* and *D*: time course of the within-column population response in the same trial (10-ms binned spike count histogram).

These results are the key to understanding why simultaneous time-identity decoding is possible. If a transient burst of intense firing occurs in barrel-column Y, followed a few milliseconds later by weaker, more diffuse firing in other barrel-columns, it is highly likely that whisker Y was deflected 9-10 ms prior to the column Y burst.

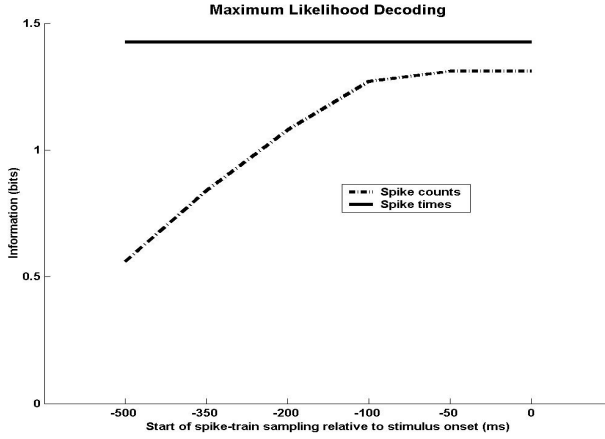
We counted the number of spikes that occurred in the interval 10-15 ms after stimulus onset on each trial for each whisker. In this case the distribution of spike counts following deflection of whisker D2 (range 15-35 spikes/bin; median 26 spikes/bin) was totally separated from that to deflection of whisker D3 (range 1-11 spikes/bin; median 5 spikes/bin). There was instead considerable overlap between the spike count distributions when spikes were counted in long time windows. For the interval -500 to +100 ms, the corresponding responses were in the range 125-210 spikes/bin for whisker D2 and 109-175 spikes/bin for whisker D3. In long time windows, the spike counts get “diluted” by spontaneous firing and latency differences are lost. These data illustrate in a simple way that differences in spike timing were much more important than differences in spike number. Thus it is crucial that the decoding is based on precisely timed spike trains, not merely on the spike count in a long time window.

Next, we studied how well the stimulus could be identified using the Maximum Likelihood decoder. In order to assess the role of stimulus time, we varied the size of the peri-stimulus time window available to the algorithm (from X ms preceding stimulus onset to 100 ms after stimulus onset). X=0ms corresponds to highly precise knowledge of stimulus time, X=500 ms to very coarse knowledge. Figure 2 compares the performance of our decoder when precise spike timing was available (solid line) to when only total spike count was available (dashed line). The performance of the spike count decoder was poor. Despite the fact that 100 neurons were available in each of three barrel-columns, good decoding was achieved only when very precise stimulus time information is available. This is due to the fact that slow time scale spike counts differentiate poorly between stimuli (see above). In contrast, the spike timing decoder performed at 100% accuracy even for the largest time window. Again, this can be attributed to the precisely timed response of cortical neurons to whisker deflection (Fig 1). In fact, the only purpose of the time window in this case was to differentiate the stimulus into separate trials. Thus, whereas spike count decoding requires precise knowledge about stimulus time, spike timing decoding can essentially be done without it.

The appeal of the Maximum Likelihood algorithm is that it bounds the performance of any decoder operating on the pooled spike train data. Thus the poor performance of the spike count decoder is not due to the decoding being inefficient. However, it might still be objected that spike timing information can only be exploited by highly sophisticated decoding algorithms that real neurons are not able to implement.

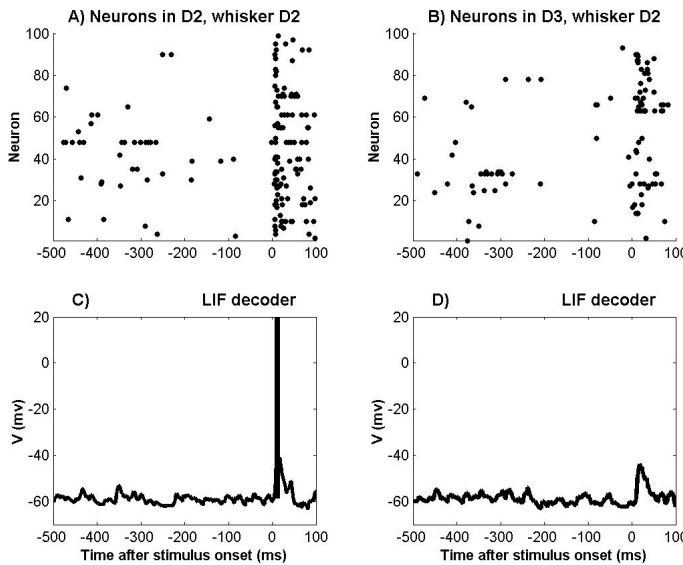
In fact, an extremely good approximation to the Maximum Likelihood decoder can be obtained in a neurally plausible manner, based on the Leaky Integrate and Fire (LIF) neuron model. We constructed a set of three LIF units, each of which integrated spike trains from one column (D1, D2 or D3). As shown in Figure 3, the LIF unit in

column D2 was able to use neuronal activity in the three columns to accurately identify deflection of D2 whisker and gave only a sub-threshold response to deflection of D3 whisker. This was true for a wide range of model parameters. The LIF model was 100% reliable: that is, the LIF unit integrating the spikes of a particular column fired in all trials in which the whisker principal to that column was deflected. The LIF neurons hence decoded 100% of the information that was decoded by the spike time STFML decoder in Fig. 2 (not shown).



**Figure 2:** Information decoded by the Stimulus-Time-Free Maximum Likelihood algorithm based on spike timing (solid line) and spike counts (dashed line).

We considered the variability of the timing of the LIF unit spike response across trials. We found that the standard deviation of the time jitter of the integrate-and-fire spike in response to principal whisker stimulation was 0.6 ms. This shows that the first-spike-latency of the columnar activity provides not only a substrate for stimulus-time-free decoding of stimulus identity, but also allows reconstruction of stimulus timing directly from the neuronal activity with sub-ms precision.



**Figure 3.** . Panels A and B: responses of neurons in barrel column D2 and D3 respectively in a single trial in which whisker D2 was deflected. Panel C. Membrane potential of the column D2 LIF unit in

response to whisker D2 stimulation. *Panel D.* Membrane potential of the LIF unit integrating spikes from neurons in column D2 in response to whisker D3 stimulation. All afferent synapses in this model were excitatory and evoked post-synaptic responses modelled as zero-delay decaying exponentials with a time constant of 5ms and synaptic reversal potential 20mV. The membrane capacitance was 0.5nF, membrane conductance 100nS. Membrane resting potential was - 60 mV and firing threshold – 40mV.

Our new decoding algorithm extends previously developed stimulus-time-free decoding algorithms [8,9], by taking into account the relative time of columnar activity rather than that of single neurons. An advantage of the present algorithm is its robustness with respect to lack of information about stimulus time: as shown above, it works even when long pre-stimulus time windows are considered.

In conclusion, provided that precise spike timing is available, the identity of a whisker stimulus can be accurately identified based purely on the pooled activity of neurons in primary somatosensory cortex. The decoding mechanisms outlined here allow stimulus features (the identity and time of the stimulus) to be extracted without precise knowledge of stimulus time.

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