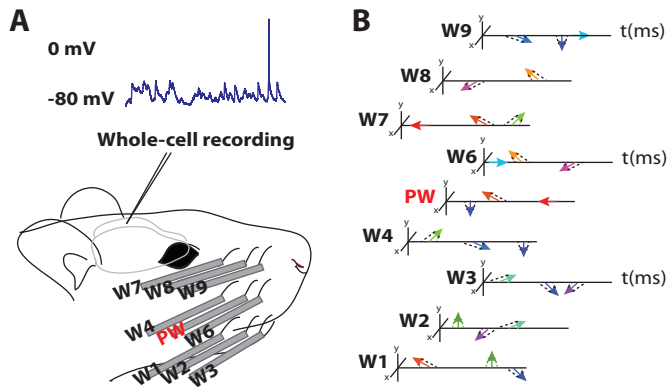


**Title:** Laminar differences in cortical receptive fields measured by reverse correlation of intracellular recordings.

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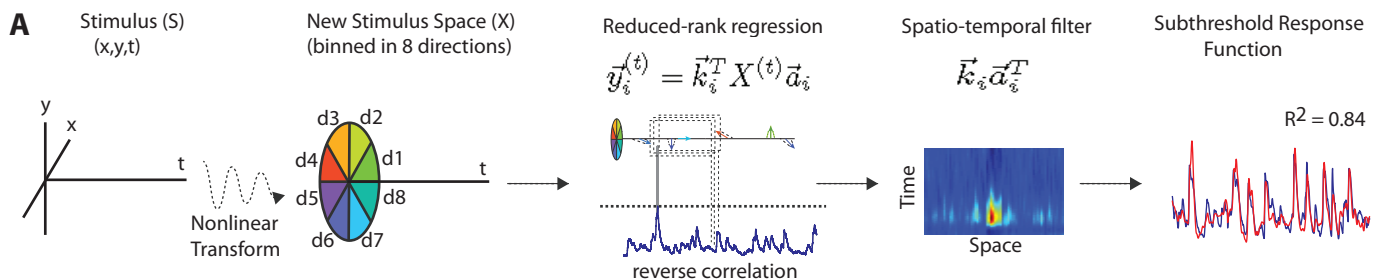
**Summary:** Our knowledge of receptive fields and sensory transformations in rodent barrel cortex (S1) lags behind other sensory systems. Firing rates of neurons in S1 can be low, making reverse correlation of high-dimensional stimuli challenging. Additionally, most researchers rely on simple single-whisker laboratory stimuli for receptive field mapping, which are neither ethological nor capable of revealing spatiotemporal complexity. Here we use a novel multi-whisker stimulator system that moves 9 whiskers independently in arbitrary directions, exploring a vastly larger stimulus space than conventionally examined. By recording intracellularly rather than extracellularly, we can additionally access information available in the subthreshold response to calculate receptive fields even for neurons with little or no spiking activity. After exploring a number of stimulus-response models, including conventional Linear-Nonlinear models as well as quadratic models, we found that a filtered input nonlinearity model (of the form discussed in Ahrens et al, 2008) provided an effective and parsimonious representation of the responses. In this model, the whisker deflections are mapped through a static nonlinearity that re-represents the whisker movements binned into an 8-directional space, before being temporally filtered, weighted across whiskers, and summed to predict the voltage response. The static nonlinearity, temporal filters, and linear weights are all estimated simultaneously using rank-penalized regression methods. Our model is able to predict neural responses to novel stimuli with a correlation coefficient as high as 0.84. Furthermore, through repeated presentations of identical stimuli, we show that our model captures ~ 90% of the predictable variance (Sahani and Linden 2003), suggesting that the main nonlinearities are spike-threshold rather than network nonlinearities. Analysis of the spatiotemporal receptive fields across layers and cell-types reveals the emergence of unique spatial and temporal features encoded in the supra- and infra-granular layers, and serves as a useful comparison to similar studies from the visual and auditory systems.

## Additional Detail:



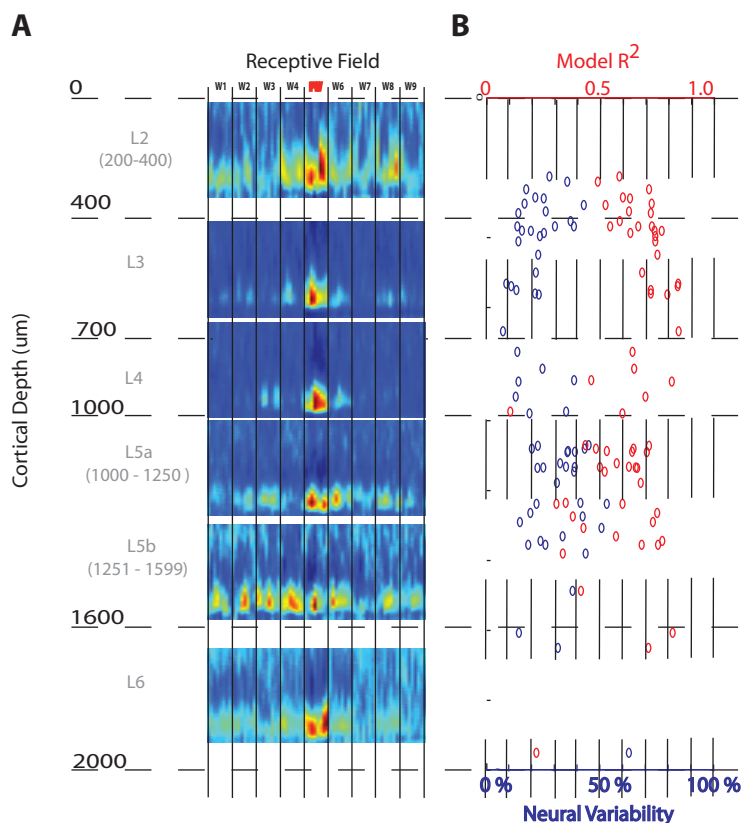
## Figure 1. Experimental Design

(A) Blind whole-cell recordings were made from neurons spanning all depths of a single barrel column while simultaneously stimulating the whisker pad. During recordings rats were kept in an unanesthetized, lightly-sedated state using fentanyl. (B) Stimulus delivery was performed using a novel whisker stimulator system that moves 9 whiskers independently in arbitrary directions. Stimuli consisted of complex, sparse noise pulses (peak velocity 2200° / second) in random directions and random times.



## Figure 2. Schematic of model (rank 1)

(A) A filtered input nonlinearity model is used to calculate the spatiotemporal filter and predict responses to novel stimuli. Whisker deflections are first passed through a static nonlinearity that re-represents the stimulus features into 8 angle-bins. In the new feature space, the reduced-rank regression model estimates parameter weights for vectors  $k_i$  and  $a_i$  simultaneously using rank-penalized regression methods. The spatiotemporal receptive field can then be expressed as outer product of the vectors ( $k_i * a_i$ ). The response of the neuron is the linear sum of weights after passing the stimulus through the spatio-temporal filter. Neural responses to novel stimuli can be predicted with an  $R^2$  as high as 0.84.



## Figure 3. Spatiotemporal receptive fields and model performance by depth.

(A) Representative example of spatiotemporal receptive fields (STRFs) for neurons in layers 1- 6. STRFs increase in complexity from granular to supragranular to infragranular layers, paralleling that seen in the visual (Martinez et al, 2006) and auditory systems (Atencio et al, 2009). L5 neurons may be important for detecting structural features encoded by temporal delays between whiskers. (B) Model  $R^2$  (red dots) and neural variability (blue dots) as a function of neuronal depth. Model performance peaks in L4 and L3 and drops in L2 and L5. Neural variability is inversely related to model performance, suggesting that weak performance in L2 and L5 is largely a function of neural noise rather than an inadequate model.