Sensorimotor strategies and neuronal representations of whisker-based object recognition in mouse barrel cortex

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Rodents use their whiskers to identify objects in their environment. In this study, we developed a novel curvature discrimination task that challenges mice to discriminate concave from convex shapes. We asked which sensorimotor features are important for this task. We found that the cumulative number of contacts per trial for each whisker was informative about the stimulus and choice identity. In contrast, task history and precise contact timing across whiskers were much less important. We recorded neuronal populations in the whisker representation in primary somatosensory cortex (barrel cortex) and found that they were driven by sensorimotor (e.g., whisker motion and touch) and cognitive (e.g., reward history) variables. Interestingly, non-linear interactions of these variables had a significant modulatory effect on neuronal activity, suggesting that one of the roles of the barrel cortex is to provide a high-dimensional representation of the task space to downstream areas.

Keywords: barrel cortex; somatosensory; decision-making; encoding models; neuronal representations.

Humans and other animals can identify objects by active touch – coordinated exploratory motion and tactile sensation (Davidson 1972; Diamond et al., 2008). Rodents, and in particular mice, scan objects by active whisking, which allows them to form an internal representation of the physical properties of the object. In order to elucidate the behavioral and neural mechanisms underlying this ability, we developed a novel curvature discrimination task for head-fixed mice – *curvature discrimination* – that challenges the mice to discriminate concave from convex shapes. On each trial, a curved shape was presented into the range of the mouse's whiskers, and they were asked to lick left for concave and right for convex shapes. Whisking and contacts were monitored with high-speed video. Mice learned the task well, but because the task is challenging, their performance plateaued at 75.7% correct on average, still significantly above chance (50% correct).

Because most previous work has relied on mice detecting the presence or location of a simple object with a single whisker (O'Connor et al., 2010), it is *a priori* unclear which sensorimotor features are important for more complex tasks such as curvature discrimination. To characterize them, we trained a classifier to identify either the stimulus identity or the mouse's choice on each trial using the entire suite of sensorimotor variables that could potentially drive behavior (whisker position, contact timing and position, contact kinematics, *etc.*), as well as task-related variables that could affect behavior in ways complementary to the gathered sensory information. By increasing the richness of the set of features used to perform the classification of stimulus and choice, we identified which features were most informative to

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perform the task and which features were driving the animal's decision, respectively. We found that the cumulative number of contacts for each whisker separately was informative about the stimulus and choice identity on each trial. Surprisingly, precise contact timing within a trial for the different whiskers and previous history of the task were much less important in either case. Angular position was highly predictive of stimulus identity but less predictive of the mice's trial-by-trial choices, suggesting that the mice's behavior was not fully optimal.

In order to identify how barrel cortex contributes to transforming fine-scale representations of sensory events into high-level representations of object identity, we recorded neural populations in mice performing this task. We fit a generalized linear model (GLM) to each neuron's firing rate as a function of both sensorimotor (e.g., whisker motion and touch) and cognitive (e.g., reward history) variables. Neurons responded strongly to whisker touch and, perhaps more surprisingly for a sensory area, to whisker motion (Curtis and Kleinfeld, 2009). We also observed widespread and unexpected encoding of reward history and choice. Because this analysis regresses out sensorimotor variables, this result cannot simply be explained by changes in motor patterns or sensory input. In addition, we also compared different encoding architectures and found that models with non-linear interactions (multilayer feedforward networks) among input features were associated with higher predictive performance than pure linear models. This effect was consistent across laminar location and cell type. Overall, these results suggest that the barrel cortex is involved in providing a mixed and high-dimensional representation of the task-related variables to areas located downstream of the decision-making pipeline, a representation that has been shown to optimize information transmission in scenarios with several input channels (Barak, Rigotti, & Fusi, 2013; Rigotti et al., 2013).

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