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REPRESENTATION OF TACTILE SCENES IN THE RODENT BARREL CORTEX

LUC ESTEBANEZ, ISABELLE FÉRÉZOU, VALÉRIE EGO-STENGEL AND DANIEL E. SHULZ *

Unité de Neuroscience, Information et Complexité (UNIC), Centre National de la Recherche Scientifique, FRE 3693, 91198 Gif-sur-Yvette, France

Abstract—After half a century of research, the sensory features coded by neurons of the rodent barrel cortex remain poorly understood. Still, views of the sensory representation of whisker information are increasingly shifting from a labeled line representation of single-whisker deflections to a selectivity for specific elements of the complex statistics of the multi-whisker deflection patterns that take place during spontaneous rodent behavior – so called natural tactile scenes. Here we review the current knowledge regarding the coding of patterns of whisker stimuli by barrel cortex neurons, from responses to single-whisker deflections to the representation of complex tactile scenes. A number of multi-whisker tunings have already been identified, including center-surround feature extraction, angular tuning during edge-like multi-whisker deflections, and even tuning to specific statistical properties of the tactile scene such as the level of correlation across whiskers. However, a more general model of the representation of multi-whisker information in the barrel cortex is still missing. This is in part because of the lack of a human intuition regarding the perception emerging from a whisker system, but also because in contrast to other primary sensory cortices such as the visual cortex, the spatial feature selectivity of barrel cortex neurons rests on highly nonlinear interactions that remained hidden to classical receptive field approaches.

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Key words: barrel cortex, whisker stimulation, naturalistic stimulus, sensory responses, neural coding.

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INTRODUCTION

In this Review, we describe the wide repertoire of whisker movement features that are coded by barrel cortex neurons in the anesthetized rodent preparation. We start from the low-dimensional properties described with simple single-whisker deflections that can be combined into a linear model of barrel cortex neurons. We then discuss the impact of several elements of the sensory context, such as the stimulation density and the effect of an immediately preceding stimulus, which both affect neuronal responses in ways not predicted by the linear model. These observations reveal the existence of numerous intrinsic nonlinearities of cortical neurons.

Neuronal selectivity for global tactile properties of the surfaces contacted by multiple whiskers cannot be available from any single-whisker contact alone. We describe recent efforts to understand how neurons in the vibrissal system analyze simultaneous whisker deflections and how the barrel cortex extracts collective properties of complex stimuli.

A RECEPTIVE FIELD ANALYSIS OF BARREL CORTEX NEURONS FUNCTION

To identify the functional properties of neurons, the traditional approach in sensory physiology has been to explore the sensory periphery and find the limits of the area of the periphery that triggers a neuronal response. Delineating this area – the so called receptive field (Hartline, 1938) – has been a dominant research strategy in the study of the barrel cortex, inspired by the earlier studies of the visual system (Hubel, 1959; Hubel and Wiesel, 1962) that were highly informative of visual functional properties. In the whisker system, the relevant stimulus space includes not only the identity of the stimulated whiskers (Welker, 1971), but also a number of additional parameters of the whisker deflection – including the direction and amplitude of the whisker stimulation – that are encoded by the highly specialized tactile sensors in whisker follicles (Rice, 1993; Rice et al., 1993; Mosconi et al., 1993).

*Corresponding author.
E-mail address: daniel.shulz@unic.cnrs-gif.fr (D. E. Shulz).

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Multiple tunings to specific whisker deflection properties

With the advent of the first controlled single-whisker stimulators, several studies have demonstrated that barrel cortex neurons encode specific properties of whisker deflections. These features include the amplitude of the peripheral movement, either in position, speed or acceleration (Simons, 1978; Simons, 1983; Arabzadeh et al., 2003), the frequency of an oscillatory input (Simons, 1978; Arabzadeh et al., 2003; Andermann et al., 2004; Ewert et al., 2008), the interval between repetitive stimulations (Simons, 1985; Ahissar et al., 2001; Webber and Stanley, 2004) and the direction of deflection (Simons, 1978; Bruno and Simons, 2002; Wilent and Contreras, 2005). These studies have mostly focused on responses to movements of the principal whisker (PW), which is classically defined based on the latency and/or strength of the neuronal response to a standard ramp-and-hold whisker deflection. Similar response properties are observed for stimulation of the surround whiskers that elicit a response, albeit with reduced amplitude and dynamical characteristics.

Among these tuning properties, direction selectivity has been one of the most thoroughly studied, perhaps because it represents the most obvious feature of the input space that can be parameterized and is also a prominent feature of barrel cortex neuronal responses. For example, Fig. 1A shows intracellular recordings of a layer 4 neuron in the anesthetized rat in response to deflection of its principal whisker in eight randomly interleaved directions (Wilent and Contreras, 2005). Robust synaptic responses were observed, occasionally leading to one or two spikes. The selectivity to the direction was larger for the spike output than for the synaptic potentials, highlighting the contribution of intracellular mechanisms and spike thresholding to information processing.

Most natural whisker deflections occur at very high speed and acceleration (Ritt et al., 2008), and particularly during discrete stick then slip events (Wolfe et al., 2008) that occur when a whisker is rubbed against a surface. Neuronal recordings have been performed during such events (Jadhav et al., 2009). In a 20-ms time window following slip events, particularly those with high acceleration, the firing rate of the neuron recorded in an awake head-fixed rat is increased (Fig. 1B). Even more system-

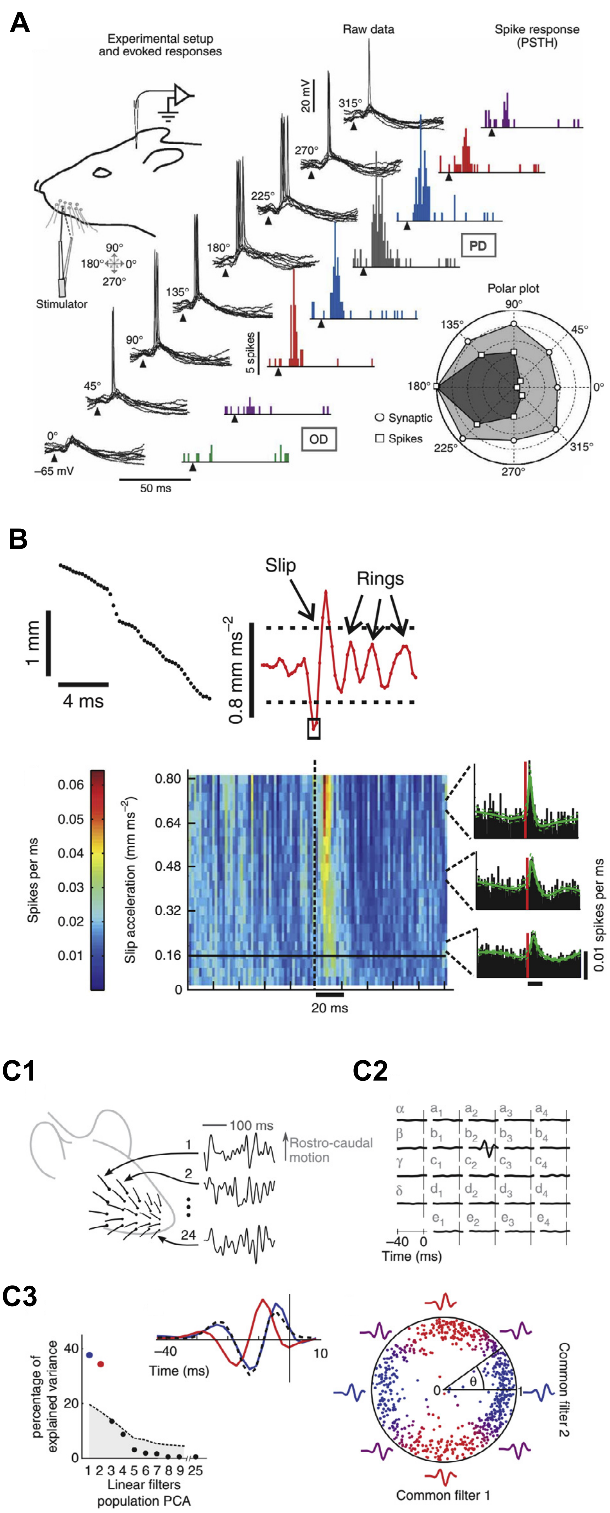

Fig. 1. Response properties of barrel cortex neurons to movement features of the principal whisker. (A) Direction selectivity in a layer 4 neuron recorded intracellularly in an anesthetized rat, while its principal whisker was deflected in eight different directions. The membrane potential and spike histograms are shown for 8 trials for each direction (PD: preferred direction, OD: opposite direction). The average responses are plotted in polar coordinates, revealing a significant directionality, larger for the spike output than for the synaptic response (from Wilent and Contreras, 2005). (B) Spiking response to slip-stick events in a barrel cortex neuron recorded in the awake rat. Top, Example of whisker motion on a coarse sandpaper (left, position; right, acceleration) revealing a high-acceleration slip event. Bottom, Time course of the response as a function of peak whisker acceleration, revealing strong tuning of the neuron to the slip events (from Jadhav et al., 2009). (C) Neuronal filters revealed by probing rat barrel cortex neurons with white noise as the input (C1). Spike-triggered covariance analysis for this neuron reveals the recurrence of a specific deflection profile on whisker B2 before each spike (C2). Population principal component analysis (PCA) showed that neuronal filters are surprisingly similar, and can be described as linear combinations of two generic filters (red and blue traces, C3) (from Estebanez et al., 2012).

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