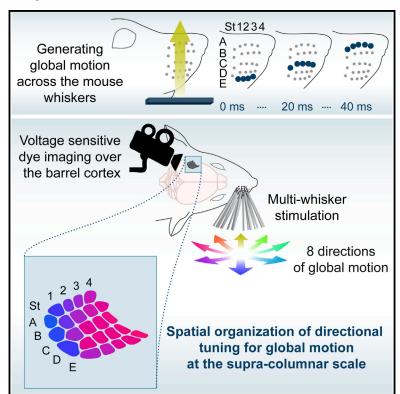
### **Cell Reports**

## **Supra-barrel Distribution of Directional Tuning for Global Motion in the Mouse Somatosensory Cortex**

#### **Graphical Abstract**



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#### In Brief

Using voltage-sensitive dye imaging of the mouse barrel cortex, Vilarchao et al. demonstrate the presence of direction selectivity to global motion generated by multi-whisker stimuli. Selectivity to global motion is spatially organized at the supracolumnar scale with an overrepresentation of selectivity to caudo-ventral directions.

#### **Highlights**

- Multi-whisker stimuli generating global motions activate the entire barrel cortex
- Responses are sublinear and depend upon the direction of the global motion
- Overall, the barrel cortex responds preferentially to caudoventral global motions
- Directional tuning for global motion varies gradually over the barrel map







# Supra-barrel Distribution of Directional Tuning for Global Motion in the Mouse Somatosensory Cortex

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#### **SUMMARY**

Rodents explore their environment with an array of whiskers, inducing complex patterns of whisker deflections. Cortical neuronal networks can extract global properties of tactile scenes. In the primary somatosensory cortex, the information relative to the global direction of a spatiotemporal sequence of whisker deflections can be extracted at the single neuron level. To further understand how the cortical network integrates multi-whisker inputs, we imaged and recorded the mouse barrel cortex activity evoked by sequences of multi-whisker deflections generating global motions in different directions. A majority of barrel-related cortical columns show a direction preference for global motions with an overall preference for caudo-ventral directions. Responses to global motions being highly sublinear, the identity of the first deflected whiskers is highly salient but does not seem to determine the global direction preference. Our results further demonstrate that the global direction preference is spatially organized throughout the barrel cortex at a supracolumnar scale.

#### INTRODUCTION

Layer 4 of the rodent primary somatosensory cortex contains anatomical structures named "barrels" topologically organized as the whiskers on the animal's snout. Since their description by Woolsey and Van der Loos (1970), the barrels are considered as the prototypical morphological manifestation of the functional columnar organization of the cerebral cortex. Each neuronal column associated with a barrel processes primarily the information coming from its corresponding whisker (Feldmeyer et al., 2013; Petersen, 2003, 2007). However, when rodents explore their environment, they contact objects with the whole array of whiskers, inducing complex sequences of multi-whisker deflections. Although the topographic organization of the whisker-to-barrel cortex pathway suggests a parallel processing of the inputs orig-

inating from distinct whiskers, it also contains the neural bases for the integration of more complex interwhisker information (Armstrong-James and Callahan, 1991; Arnold et al., 2001; Ego-Stengel et al., 2005; Narayanan et al., 2015).

The principal candidates for integrating complex spatiotemporal sequences of tactile inputs are neurons with multi-whisker receptive fields (RFs). It has been shown that, in the supra- and infragranular layers of the barrel cortex, single neurons receive inputs from their principal whisker (PW) and from several surrounding whiskers (Brecht and Sakmann, 2002; Brecht et al., 2003; Manns et al., 2004; Moore and Nelson, 1998; Zhu and Connors, 1999). The structure of these multi-whisker RFs is stimulus dependent. They differ according to the direction of the whisker deflection (Le Cam et al., 2011). In addition to multi-whisker thalamic input, the cortico-cortical connections have profound effects on the RFs and the spread of subthreshold activity. For example, intracortical circuitry shows anisotropy toward within-row connectivity (Kim and Ebner, 1999; Petersen and Sakmann, 2001; Simons, 1978). A morphometric study revealed a much higher degree of horizontal connectivity than originally reported in the rat barrel cortex, with a majority of excitatory neurons projecting their axon far beyond their cortical column (Narayanan et al., 2015). Altogether, these observations suggest that complex interactions are likely to take place in the barrel cortex and might be essential for the integration of multi-whisker contacts.

Understanding how the barrel cortex can extract the emergent properties of such complex tactile inputs requires the use of multi-whisker stimuli that are locally invariant but differ by their global coherent properties. This is the case of "global motion" stimuli (Jacob et al., 2008), which consist in sequences of 24 whisker deflections presented in spatio-temporal orders mimicking front edges crossing the whisker pad in eight different directions. Single-unit recordings from the C2 barrel-related column in rat barrel cortex have shown that a majority of neurons are able to extract directional information from global motions independently of the local direction of deflections of individual whiskers. Preferred direction for global motions in regular spiking units presented a bias for caudo-ventral directions in the C2 barrel-related column (Jacob et al., 2008).

Whereas the spatial mapping of stimulus features, like the direction of a local stimulation, has been documented in the



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