The Functional Organization of the Barrel Cortex (Petersen, 2007)

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Introduction

Motivation for studying tactile somatosensory pathway in rodents:

● Tactile information from whiskers: build spatial representations, locate objects, perform fine-grain texture discrimination

● Motor control of whiskers: active sensory processing and sensorimotor integration
From Whisker to Cortex
Whiskers and Barrels
Thalamocortical Connectivity
Parallel Pathways

- Extralemniscal (caudal)
  - Pathway through ventrolateral strip of VPM to secondary somatosensory cortex and septal regions of S1

- Paralemniscal (rostral)
  - Projects to posterior medial (POM) nucleus of thalamus, which innervates layer 1 and 5A of somatosensory cortex, secondary somatosensory cortex, motor cortex
Corticocortical Connectivity
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<th>Method</th>
<th>Activity Measured</th>
<th>Advantages</th>
<th>Disadvantages</th>
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<td>Spatially ordered array of electrodes</td>
<td>Action potential firing</td>
<td>Receptive field mapping by sensory-evoked activity</td>
<td>Spatial resolution is limited by size of array</td>
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<tr>
<td>Intrinsic optical imaging</td>
<td>Changes in blood flow</td>
<td>Higher spatial resolution</td>
<td>Poor temporal resolution because physical basis is only indirectly related to neuronal activity</td>
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<td>Voltage sensitive dye (VSD)</td>
<td>Membrane potential changes</td>
<td>Millisecond temporal resolution, subcolumnar spatial resolution, sensitivity to subthreshold changes</td>
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Functional Mapping

Spatiotemporal dynamics measured with VSD:

- ~10 ms: Initial response localized to whisker’s corresponding barrel column
- Few ms after: Response increases in amplitude, propagates horizontally over barrel cortex
Functional Mapping

- Intrinsic signals at suprathreshold changes (localized)
- VSD signals dominated by subthreshold changes (distributed)
Functional Mapping

A. Multielectrode Arrays

10 x 10 array

C2 whisker stim

D2 whisker stim

B. Intrinsic Optical Imaging

cortex

C2 whisker stim

DAPI + Dil

C. Voltage-Sensitive Dye Imaging

500μm

12ms

16ms

20ms
Functional Mapping

● Somatotopic map
  ○ Pattern of activity across barrel map during whisker-guided exploration produces object “imprint”

● Texture map
  ○ Whiskers have different resonant frequencies -- possible role in texture discrimination
state dependent processing

- differences found in layer 2/3 of barrel cortex pyramidal neurons
  - quiet wakefulness = slow, large amplitude membrane potential changes
  - active whisking = slow oscillation disappears, variance lowers, neurons slightly depolarized.
  - not visible in firings of action potentials
state dependent processing
During quiet wakefulness, a passive whisker deflection results in a strong cortical sensory response.
During active whisking, same stimuli produced a weak response.
state dependent processing
Actively acquired information

- Trigeminal ganglion only fires when whisker is moved.
- During whisking without contact, low level of spiking activity.
- If contact is made with an object during whisking, high level of spiking activity.
Actively acquired information
Actively acquired information

- Single whisker active touch responses propagate across barrel map, similar to passively evoked responses during quiet wakefulness, but not like passive stimulus while whisking
Actively acquired information

- Sensory neurons of trigeminal nerve directly excite motor neurons responsible for whisker movement.
- When whisker encounters a real object, whisker is accelerated into that object, causing a loop.
- Similar to how we move our fingers across an object, whisker movements are likely to change.
Sensory information processing during learned behaviors

- Hutson and Masterson (1986)
  - use whiskers to detect a second platform
  - can be performed with a single whisker, depends on an intact barrel cortex
Sensory information processing during learned behaviors

Knutsen et al. (2006)
- rodents with a single whisker can discriminate position of a vertical bar
- in addition to contact with an object, the object's location is also encoded
Sensory information processing during learned behaviors

- Krupa et al. (2004)
  - rats were trained to detect width of an aperture using its whiskers
  - infragranular neurons fire before the rat’s whiskers touched the walls, indicating a
Sensory information processing during learned behaviors

- Carvell and Simmons (1990)
  - whiskers can determine textures as accurately as human fingertips
Barrel Column Mapping

● Direction-preference map
  ○ Clusters of nearby layer 4 neurons respond preferentially to similar directions of whisker deflection
  ○ Proposed: neurons responding to given direction of whisker deflection are closer to the neighboring barrel in the direction of the deflection
Synaptic Circuits

- Sensory information from single whisker deflection arrives in primary somatosensory neocortex from dense glutamatergic thalamocortical innervation of neurons in VPM
- Axon of VPM neuron innervates single layer 4 barrel
Synaptic Circuits

- Strong GABAergic feedback from reticular nucleus to the thalamus prevents prolonged depolarization of VPM neurons
  - Sharpen timing of input to cortex
- Structurally defined cortical columns by horizontal extent of layer 4 barrels
Synaptic Circuits

• Layer 2/3
  ○ Axonal arborization of pyramidal neurons → propagation of sensory response as glutamatergic output depolarizes neurons distributed across barrel cortex
  ○ Input to layer 5, which also receives and integrates input from thalamus, layer 4, and other pyramidal neurons in infragranular layers
Synaptic Circuits

- Long range corticocortical inputs from secondary somatosensory cortex and motor cortex
- POM thalamic input during certain behaviors
  - Arrives in layer 1 and 5A -- start of paralemniscal pathway
Somatotopic organization is genetically determined, refinement of somatotopic map is activity-dependent

Barrel cortex neurons
  - Early development: receive information relating to their principal whisker
  - Through experience: have broader tuning, more complex receptive field properties
Experience-Dependent Plasticity

Sensory deprivation

● Depression of evoked responses to deflection of trimmed whiskers

● Reduced efficacy of excitatory connection between layer 4 to layer 2/3
  ○ Presynaptic reduction in neurotransmitter release probability
  ○ Hebbian spike-timing-dependent plasticity
Experience-Dependent Plasticity

Sensory deprivation, continued

- Increased responsiveness to deflection of spared whiskers
- Reversal of effects when all whiskers regrow
- Single-whisker animals had smaller cortical representations of spared whisker when subject to exploration of new environments