Somatosensory System Organization and Texture Sensation in Rats and Mice

The Whiskers of Mice and Rats

How do impulses from skin receptors eventually lead to the sensation (i.e., the registration of the elemental properties) and perception (i.e., recognition of the identity and meaning of the sensation) of the things that we contact? As a first example, we use the sensory pathways originating in the whiskers of mice and rats to illustrate the main principles of the organization and function of touch. We then show how these principles apply to sensation and perception in primates.

Mice and rats are active in dark environments and have poor vision; their survival depends on the sense of touch. Through the whiskers, the brain builds up percepts of objects: their position, size, shape, and texture. The heart of the tactile system is an array of some 35 long whiskers on each side of the face, thick hairs that the animal flicks forward and backward (there are also shorter, and less mobile hairs packed densely around the nose and lips that the animal can use to collect additional information). Contact with an object activates mechanoreceptor terminations located in the whisker follicles, giving rise to neuronal signals (see Figure 21.2B). The first study to utilize the whiskers as an object of research was carried out by S. Vincent in 1912 for her Ph.D thesis at the University of Chicago (using rats captured in the city!). She built an elevated labyrinth and found that the time required to run from the start to the end of the maze and the number of errors (for example, stepping into dead-end arms) increased dramatically when whiskers were clipped. The rats were slowed by the need to feel the edge of the platforms with their feet rather than with their whiskers.

Magnification Factor

The behavioral importance of the rodents’ whiskers goes hand in hand with the richness of the skin innervation. The whisker pad is the most densely supplied skin area of the body studied so far—about 200 trigeminal ganglion neurons innervate each whisker follicle. In Figure 21.6A, it is evident that the primary somatosensory cortex occupies a greater territory

![Figure 21.6](image-url)
than do the primary sensory fields for vision and audition. And within primary somatosensory cortex, the whisker field is disproportionately large. Although this can be interpreted as a greater magnification of the whiskers’ cortical representation with respect to that of other body parts (i.e., in terms of square millimeters of skin projecting to square millimeters of cortical surface), it can also be interpreted as conservation, across body areas, of the relationship between receptor density and cortical territory. In other words, the number of tactile receptors projecting to each square millimeter of cortical surface is held constant. As a result, the richly innervated whisker follicles gain a large territory.

**Topographic Map of the Whiskers and Columnar Organization**

To visualize the organization of the mouse somatosensory cortex, Woolsey and van der Loos separated the cerebral cortex from the underlying structures. Then, they flattened the curved cortex between two slides and sectioned the slab in a tangential plane that yielded a large horizontal expanse of layer IV in a single section. Once the tissue was stained, distinct clusters of densely packed neurons were visible. The grid-like arrangement of the 35 clusters resembled wine casks, calling out for the name *barrels* (Figure 21.6B). The insight of Woolsey and van der Loos was that the spatial arrangement of the barrels replicates exactly the spatial arrangement of the whiskers on the snout. The authors concluded that the barrel field is a map of the whiskers on the contralateral snout. Every whisker on the snout was given a label (e.g., D3) and could be readily matched with one cortical barrel (again, D3). Within a few years, the prediction of a connection from each whisker to its own cortical barrel was extended from mice to rats and confirmed by many physiological studies. Thus, the receptive fields of the neurons in barrel D3 are centered on the so-called *principal* whisker, D3. Whiskers surrounding the principal whisker may also excite cells to a lesser degree. Neurons in the layers above and below layer IV, which receive their main sensory input from layer IV, also receive a strong input from the principal whisker. So, the neuronal population extending through all layers forms a cortical column associated with a single whisker, a functional unit anchored by the layer IV barrel.

Because two whiskers that are adjacent to each other on the animal’s face are represented in adjacent cortical barrels, the barrel field constitutes a **topographic map** (Figure 21.6C). Beyond the special case of whiskers, it is common to refer to a brain representation as a “map” whenever the spatial relationship among sensory receptors is conserved in the central representation of the sense organ. A historical note on the discovery of cortical somatosensory maps is given in Box 21.1.

The map of cortical columns serves to organize the storage of sensory experiences. One demonstration is provided by an experiment in which, to begin, all whiskers except one were trimmed from the snout of the rats (Figure 21.7A). Then, the animals were trained, in the dark, to perch on one platform, extend the intact whisker across a gap to touch and, thus, localize a second platform, and jump across the gap to reach a reward. Next, the *trained* whisker was clipped off and a previously clipped whisker was fixed with glue to a different whisker stub (Figure 21.7B). When retested, the number of trials necessary to reacquire the task was found to increase as a function of the distance between the site of the trained whisker and the new (i.e., attached) whisker (Figure 21.7C). Moreover, the transfer of learning between any two whisker locations was perfectly explained by the spatial distribution of physiological activity within the barrel field map (Figure 21.7D). This experiment suggests the presence of a sensory memory trace governed by the precise topography of the sensory receptors.

**Map Development and Plasticity**

When a strain of mice is bred to have different numbers of whiskers, the barrel field differs in precise correspondence with the face; thus, extra whiskers (or missing whiskers) are accompanied by extra (or missing) barrels in the matching part of the barrel field. Destruction at birth of a whisker follicle will cancel that whisker’s module from all maps in the ascending sensory pathway. But once the anatomical connection between one whisker and its corresponding cortical barrel is established a few days after birth, that barrel remains fixed throughout life.

The topographic map at the level of cortex is not generated ad hoc from a disordered input—rather, all along the pathway, the neighboring relations are received in an orderly manner from the preceding level (the descending feedback projections mentioned earlier in the chapter respect the same topographic order). Each barrel receives input from a discrete barreloid in the ventroposterior medial nucleus of the thalamus; each thalamic barreloid receives input from a barrelette in the brainstem trigeminal nucleus; and each barrelette receives input from a whisker. During development the modular clustering appears in a temporal sequence from periphery to cortex.24

Although the principal input to a given barrel is its topographically matched whisker, neurons do respond to stimulation of neighboring whiskers, particularly in the column of neurons above and below the layer IV barrel. These inputs form the surround receptive