Progress in Neurobiology 103 (2013) 28–40

Contents lists available at SciVerse ScienceDirect

Progress in Neurobiology

journal homepage: www.elsevier.com/locate/pneurobio

Whisker sensory system – From receptor to decision

Mathew E. Diamond [a,1,*], Ehsan Arabzadeh [b,2]

[a] Cognitive Neuroscience Sector, International School for Advanced Studies, Trieste, Italy
[b] School of Psychology, University of New South Wales, Sydney 2052, New South Wales, Australia

ARTICLE INFO

Article history:
Received 15 February 2012
Received in revised form 11 May 2012
Accepted 15 May 2012
Available online 6 June 2012

Keywords:
Vibrissa
Sensory coding
Perception
Tactile
Texture
Vibration
Sensory cortex

ABSTRACT

One of the great challenges of systems neuroscience is to understand how the neocortex transforms neuronal representations of the physical characteristics of sensory stimuli into the percepts which can guide the animal's decisions. Here we present progress made in understanding behavioral and neurophysiological aspects of a highly efficient sensory apparatus, the rat whisker system. Beginning with the 1970s discovery of "barrels" in the rat and mouse brain, one line of research has focused on unraveling the circuits that transmit information from the whiskers to the sensory cortex, together with the cellular mechanisms that underlie sensory responses. A second, more recent line of research has focused on tactile psychophysics, that is, quantification of the behavioral capacities supported by whisker sensation. The opportunity to join these two lines of investigation makes whisker-mediated sensation an exciting platform for the study of the neuronal bases of perception and decision-making. Even more appealing is the beginning-to-end prospective offered by this system: the inquiry can start at the level of the sensory receptor and conclude with the animal's choice. We argue that rats can switch between two modes of operation of the whisker sensory system: (1) *generative mode* and (2) *receptive mode*. In the generative mode, the rat moves its whiskers forward and backward to actively seek contact with objects and to palpate the object after initial contact. In the receptive mode, the rat immobilizes its whiskers to optimize the collection of signals from an object that is moving by its own power. We describe behavioral tasks that rats perform in these different modes. Next, we explore which neuronal codes in sensory cortex account for the rats' discrimination capacities. Finally, we present hypotheses for mechanisms through which "downstream" brain regions may read out the activity of sensory cortex in order to extract the significance of sensory stimuli and, ultimately, to select the appropriate action.

Contents

Abbreviations: A, amplitude; CA1, Cornu Ammonis area 1; ERH, entorhinal cortex; f, frequency; FC, dorsal medial prefrontal cortex; Hi, hippocampus; ms, millisecond; SI, primary somatosensory cortex; SII, secondary somatosensory cortex; VI, primary visual cortex; PER, perirhinal cortex.

* Corresponding author. Tel.: +39 040 3787236; fax: +39 040 3787549.
E-mail addresses: diamond@sissa.it (M.E. Diamond), ehsan@unsw.edu.au (E. Arabzadeh).

[1] The authors contributed equally.

[2] Tel.: +61 02 9385 3523; fax: +61 02 9385 3641.

0301-0082/$ – see front matter © 2012 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.pneurobio.2012.05.013

1. Introduction

Our goal here is to characterize a chain of events that occurs when a rat acts upon signals received through the whiskers. We address four questions. (i) What are the behavioral capacities supported by the whiskers? (ii) How does whisker motion specify the external stimulus? (iii) What neuronal codes are present in sensory cortex? (iv) How is sensory information transformed in subsequent stages of processing?

Why the focus on cortical processing? In the late 19th century, Hermann Munk proposed that the cerebral cortex is responsible for the difference between seeing elementary forms and perceiving objects (Munk, 1881). His subjects were dogs that received either a lesion restricted to the posterior pole of the occipital lobe or else a lesion elsewhere, including regions farther anterior and lateral (angular gyrus). Those with bilateral occipital lobe ablation showed complete blindness, bumping into tables and walls. Those with more anterior lesions, sparing the occipital pole, showed what Munk called "psychic blindness" – they did not collide with furniture, yet they did not recognize by vision previously familiar objects.

By the late 20th century, behavioral methods had become more precise and quantitative. We take the ideas expressed by Whitfield (1979) as a conceptual framework. After analyzing the behavioral effects of lesions in the auditory system, Whitfield noted that animals can perform fine sensory discriminations even after ablation of sensory cortex, provided the task does not require them to transform "sensory data" into "objects." For instance, a cat with its auditory pathway ablated above the level of the brain stem can localize sound; it can be trained to lick when a sound is presented to its right, and to inhibit licking when a sound is presented to its left. Thus, the brain stem can transmit left/right differences in neuronal firing pattern to the centers that control licking. But the same decorticate animal cannot be trained to approach a sound source, once localized, on the other side of the room (Neff and Diamond, 1958). Without cortex, the acoustic waves are accessed only as a neuronal activity pattern within the brain, not as a sound emanating from somewhere in the surroundings. Extending this notion beyond the auditory system, Whitfield postulated that even with sensory cortex ablated, animals can act on the information present in subcortical centers provided the task can be solved by reading out the elemental physical characteristics of a stimulus (tone, wavelength, vibration frequency). A deficit appears when the animal is required to endow simple sensations with the quality of belonging to objects. Whitfield concluded, much like Munk, that the cortex transforms physical characteristics into the percept of real things that are "out there" in the world (p. 146).

A second function is implicit in the essay of Whitfield; the cortex is critical for the storage and recall of previous sensory experiences. The neuronal activity that encodes elemental sensory data can gain meaning only when it is integrated with memories of previous encounters with the same or different stimuli. Many behaviors require sensory information to be retained, whether in long term or short term (working) memory. Whereas neuronal activity in the ascending pathways to cortex and in primary sensory cortex itself subsides rapidly when a stimulus is removed, later stages of cortex seem to have a special capacity for retaining salient information (see Romo and de Lafuente, 2012). Recently, this second fundamental function of neocortex has begun to be studied in the tactile modality in rats and we will highlight some novel findings.

2. Whisker-mediated sensation as an "expert" capacity

Understanding *how* the neocortex transforms physical characteristics into the percept of real things that are "out there" in the world has long been a challenge. A productive approach has been to investigate "expert" cortical processing systems, ones that accomplish complex transformations in a fast and reliable manner. The efficiency of the primate visual system in extracting meaning from visual scenes is well-known. For instance, in a task where subjects must decide whether a briefly flashed photograph of a natural scene contains a target category such as an animal or food, monkeys can accurately respond as early as 160 ms after stimulus presentation, and humans around 220 ms (Thorpe et al., 1996). While the phenomenon of fast, precise perception can be convincingly shown in the visual system, the mechanisms are hard to unravel. The neuronal representation of simple features is not completely clear even in VI and the large number of dimensions in the stimulus space makes it difficult to quantify neuronal selectivity to higher-order features (Yamane et al., 2008). Even when the stimulus features that drive a neuron can be defined, the workings underlying such selectivity occupy the realm of abstract modeling (Kouh and Poggio, 2008). A mechanistic account for *visual* object recognition remains beyond the grasp of contemporary cognitive neuroscience, but building a comprehensive characterization of the neuronal basis of behavior in simpler sensory systems might be possible.

Mice and rats were adopted as laboratory animals for reasons having little to do with integrative neuroscience, but we now know that they, too, possess "expert" sensory processing systems. In nature, they are active in dark environments and have poor vision; their survival depends on the sense of touch. A classic study in 1912 illustrated that a rat's ability to navigate through a raised labyrinth depends on the use of its whiskers (Vincent, 1912).