



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.

© 2012 Elsevier Ltd. All rights reserved.

Contents

1. Introduction	29
2. Whisker-mediated sensation as an “expert” capacity	29
3. Anatomical and functional organization of the pathway	30
3.1. Whisker and follicle	30
3.2. The ascending pathway	31
3.3. Connections of barrel cortex	31
4. Behavioral measures of tactile sensation	31
4.1. Quantification of behavioral performance: go: no-go discrimination task	31
4.2. Quantification of behavioral performance: two-alternative forced-choice design	31
5. Modes of operation	32
5.1. Active sensing	32
5.2. Generative and receptive modes	33

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.

6.	Receptor to decision in the generative mode	33
6.1.	Generative mode: perceptual capacities and characteristics of the behavior	33
6.2.	Whisker kinematics	34
6.3.	Neuronal responses to texture-induced whisker motion	34
6.4.	Decoding – trial to trial read out of the neuronal signal	34
6.5.	Object invariance	35
7.	Receptor to decision in the receptive mode	35
7.1.	Perceiving a sinusoidal vibration: behavioral capacities	36
7.2.	Perceiving a noisy vibration: behavioral capacities	36
7.3.	Neuronal responses to whisker motion in the receptive mode	37
8.	Beyond sensory cortex	37
8.1.	Pathways for intracortical processing	37
8.2.	Representation of touch at the end of the sensory pathway	38
8.3.	Challenges	39
	Acknowledgements	39
	References	39

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).

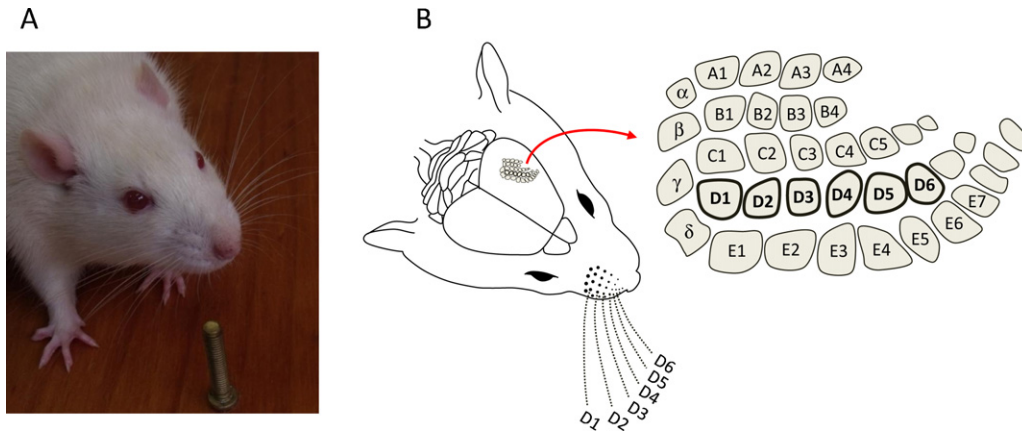


Fig. 1. (A) Close-up of a Wistar rat as it explores objects using its whiskers. Photograph courtesy of Mehdi Adibi. (B) Arrangement of the barrels in the left somatosensory cortex of a rat, with each barrel labeled by its corresponding whisker. Whiskers of the D row are shown full length with their corresponding barrels highlighted in the cortical map.

Modern research has shown that whisker touch (along with olfaction) represents the major channel through which rodents collect information from the nearby environment (Diamond et al., 2008c). They use their whiskers to recognize the positions of floors, walls and objects, particularly in dark surroundings.

Are the sensory systems of rodents suitable for the study of perceptual mechanisms? Until a few years ago, many neuroscientists would readily attribute perception to primates but not to rodents. This has changed as investigators have found that rodents can be trained to weigh sensory evidence (Kepecs et al., 2008), to assess reward statistics, to express their level of confidence in the outcome of their choices (Lavan et al., 2011), and even to generalize rules (Murphy et al., 2008), all in a primate-like manner. Rats spontaneously recognize views that differ by angle, size, and position as being instances of the same object (Tafazoli et al., 2012; Zoccolan et al., 2009); such generalization is a hallmark of true visual perception, and was once believed to belong only to primates. All the work cited above indicates that the rodent brain processes physical signals in order to build up representations of objects and things that are “out there” in the world, exactly the operation that Whitfield assigned to intracortical processing (Whitfield, 1979).

3. Anatomical and functional organization of the pathway

Inspection of the rat's snout reveals the grid-like layout of about 35 long and thick facial hairs known as vibrissae or whiskers (Fig. 1A). These constitute an array of highly sensitive detectors that project outwards and forwards from the snout to generate and collect tactile information. The sensory pathway passes through the brain stem and thalamus before reaching the primary somatosensory cortex (Fig. 1B). In this section we provide a brief overview of this exquisite system.

3.1. Whisker and follicle

Whiskers are hollow, tapered shafts; the cuticle of the whisker consists of flat scales, overlapping like roofing slates (Voges et al., 2012; Williams and Kramer, 2010). Another characteristic of whiskers that differentiates them from ordinary hairs is the large follicle, densely populated with various types of nerve endings (Diamond, 2010; Ebara et al., 2002). Whisker motion transmits mechanical energy to the follicle (Birdwell et al., 2007) which is transduced into trains of action potentials by sensory receptors – the terminals of trigeminal ganglion cells. Follicles are arranged in five horizontal rows (A to E). There are 4 follicles in rows A and B,

and 9–12 follicles in rows C, D and E. All follicles of row A and B and the first 7–8 follicles of rows C to E contain big whiskers also known as macrovibrissae (Brecht et al., 1997). Each whisker is identified by a unique letter-number combination corresponding to its row and arc (e.g., row D, arc 2, or D2).

The vibrissa follicle (Fig. 2) is populated by receptors with assorted morphologies and locations (Ebara et al., 2002; Rice et al., 1986). Among the most prominent are Merkel endings. Other populations include lanceolate endings, which are a form of free nerve ending. The relations between the morphology and location of a receptor and detailed neuronal response properties remain unknown; to date, ganglion cell responses have been studied without knowledge of the cell's terminal structure. It is known that many neurons in the trigeminal ganglion are sensitive to features

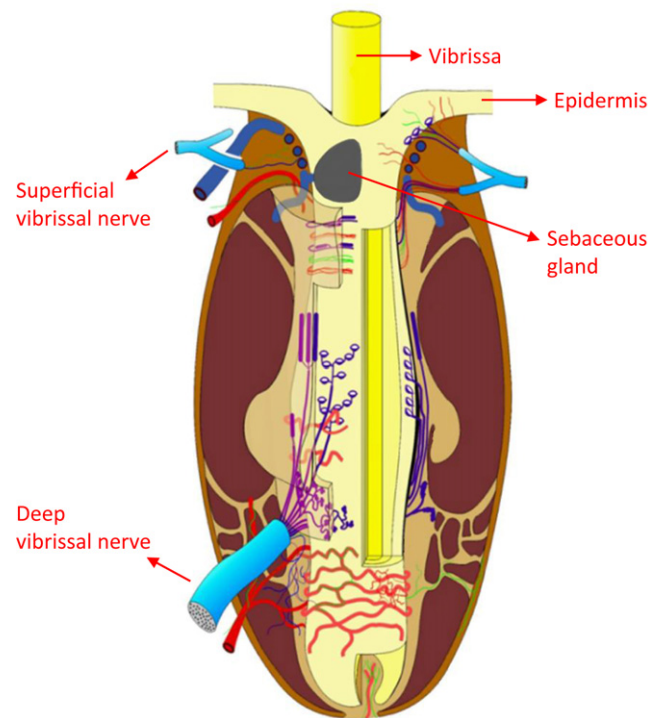


Fig. 2. Schematic view of the whisker follicle of a rat or mouse. Nerve terminations enter through the superficial vibrissal nerve and the deep vibrissal nerve to occupy different locations within the follicle, and their positioning is likely to be closely related to type of hair movement that excites them (vibration, bending, pulling, etc.). Picture courtesy of Frank Rice.

of whisker motion, such as velocity and acceleration (Arabzadeh et al., 2005; Jones et al., 2004; Shoykhet et al., 2000). Other ganglion cells are slowly adapting and appear suited to encode whisker position (Lichtenstein et al., 1990; Shoykhet et al., 2000).

Recently, Mitchinson and colleagues (Mitchinson et al., 2004, 2008), followed by Lottem and Azouz (2011), proposed mechanical and mathematical models of transduction in the whisker follicle. The most recent of these models is notable because it uses a single parameter that determines the time course of the interaction between whisker and receptor. In spite of the complex anatomical structure and the variety of receptor types that exist within the vibrissa follicle, this model successfully predicted the responses of sensory receptor neurons to a number of complex tactile stimuli (Lottem and Azouz, 2011).

3.2. The ascending pathway

Trigeminal ganglion cells emit a process that divides near the cell body to form a peripheral branch and a central branch. The sensory receptor endings described above are the terminals of the peripheral branch (see details in Nicholls et al., 2012). About 200 ganglion cells innervate each whisker's follicle (Clarke and Bowsher, 1962; Dörfel, 1985). The central branch enters the brain stem to form synapses in the trigeminal nuclei (Clarke and Bowsher, 1962; Torvik, 1956). The trigeminal nuclei convey afferent vibrissal information to the thalamus via parallel pathways which then continue to the somatosensory cortex (Deschênes et al., 2005). Somatosensory cortex, defined as the area receiving direct input from the ascending somatosensory pathway, consists of a primary field (SI) and a secondary field (SII).

The primary field, SI, has been studied intensively in rats and mice. In this area, macrovibrissae have a distinct representation. Both histological (Woolsey and van der Loos, 1970) and electrophysiological (Welker and Woolsey, 1974) studies demonstrated a one-to-one correspondence between macrovibrissae and *barrels* – distinct clusters of neurons in SI. Hence, the whisker-receiving area of SI is often called *barrel cortex*. In addition to the wealth of knowledge provided to developmental neurobiology (Andres and Van der Loos, 1985), the elegant topography of the sensory pathway offers a great convenience to behavioral neurophysiology: by simultaneous recording of barrel cortical activity and video-monitoring of the whiskers, it is possible to directly correlate the motion of an identified whisker with the firing of the cortical neurons that receive input from that whisker. Later sections will illustrate some of the conclusions available from such correlations.

3.3. Connections of barrel cortex

Among the major subcortical targets of the somatosensory cortex is the striatum, which contains anatomical and functional maps of the whiskers (Alloway et al., 2000; Wright et al., 2001). Other descending projections target the same thalamic structures which provide sensory input (Chmielowska et al., 1989).

SI and SII send and receive dense reciprocal connections (Carvell and Simons, 1987; Kim and Ebner, 1999). It is an open question as to whether SI and SII in rodents function in a hierarchical manner as is believed to be the case in primates (Pons et al., 1992) or operate in parallel on different sorts of somatosensory information. The functional properties of the secondary field, SII, have been examined rarely, and only in anesthetized animals (Carvell and Simons, 1986; Kwegyir-Afful and Keller, 2004).

4. Behavioral measures of tactile sensation

The principal function of the nervous system is to generate behavior. Indeed, one might argue that it is the *only* function of the nervous system inasmuch as the taking of actions in accordance with changing demands of the environment allows the organism to survive and reproduce. Over the last decades, new methods have been developed for the characterization of neuronal activity at the level of single cells and neuronal ensembles. More recently, neuroscience has, in a way, returned to its roots by exercising a careful attention to animal behavior (an approach that was employed long before cellular and molecular methods existed). A particularly exciting strategy is to connect the two methods, that is, to relate a detailed and quantitative characterization of animal behavior to the underlying cellular and molecular mechanisms at work in the brain. The efficiency and the accuracy of expert sensory systems provide a good setting for such investigations.

How does the brain use information collected by sensory systems to make decisions and select the appropriate action? We describe two methods for quantifying under controlled laboratory conditions how precisely a rat can distinguish between discrete sensory stimuli.

4.1. Quantification of behavioral performance: go: no-go discrimination task

In this procedure rats can be alternately exposed to two points on a stimulus dimension, one of which (denoted S+) signals that the animal's response will produce a valuable outcome (e.g., a sweet taste) while the other (denoted S−) signals that a response will produce a negative outcome (e.g., a bitter taste; see Fig. 3A). Rats easily solve such problems: they quickly come to respond in the presence of S+ and refrain from responding in the presence of S−. However, the simplicity of the procedure masks the complexity of the computations required. The solution requires subjects to parse the environment into those aspects which are relevant (the stimulus dimension) and those which are irrelevant (for example, common background cues), in essence, distinguishing salient from non-salient cues. They must discriminate between the two points on the relevant dimension with respect to their positive (S+) and negative (S−) consequences, attributing appropriate motivational significance to each cue. Variations of this basic discrimination procedure can be used to study the accuracy with which an animal can select and use sensory cues to optimize the outcome.

4.2. Quantification of behavioral performance: two-alternative forced-choice design

In a go: no-go design like that outlined above, on every trial the animal chooses between licking the reward spout (go response) or refraining from doing so (no-go response) based on its allocation of the stimulus to the category S+ versus S−. A different form of experiment entails discrimination between pairs of stimuli arranged into a two-alternative forced-choice design so that, on every trial, the animal chooses between two available responses (Fig. 3B). For example, the S+ and S− stimulus may be presented simultaneously on the left and right side of the rat with the position occupied by each changing from trial to trial. The rat samples both stimuli and turns toward the reward spout on the same side as the S+. In this case, the rat may receive a reward on every trial, provided it selects the correct reward spout.

Requiring the animal to explicitly discriminate between two stimuli provides two key advantages over a go: no-go paradigm. First, it avoids the stimulus generalization problem that is inherent to the go: no-go paradigm. If the animal recognizes the S+ as the rewarded stimulus, it may generalize its positive response to S−

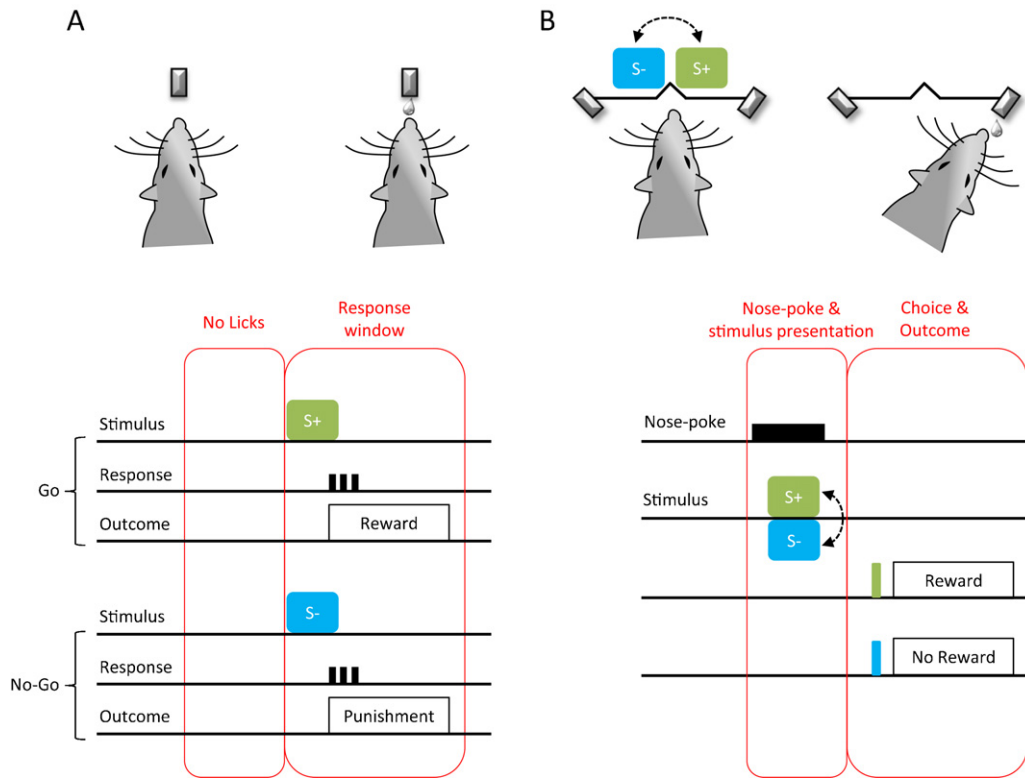


Fig. 3. (A) An example of a go: no-go design also known as the “licking suppression” paradigm. The rat is required to refrain from licking for a specific period of time (no licking) after which the stimulus is presented. The rat is then given a response window during which it decides whether to lick the spout or to suppress licking. The rat is normally head-fixed. Licks that are generated in response to the stimulus designated as S+ are rewarded whereas licks to S- are unrewarded (or punished either by bitter taste, by a loud sound, by a shock, or by further delaying the next stimulus presentation with a time-out penalty). (B) Two-alternative forced-choice paradigm. The rat initiates a trial by a nose poke. After a delay period the rat receives two simultaneous stimuli on its left and right whisker pads. One of the two stimuli is designated as S+ and the other as S-. The rat is required to explicitly make a discrimination and to identify the S+ and turn toward the corresponding drinking spout. Correct choices are rewarded.

stimuli that it can in fact recognize as distinct from the S+. How “broadly” the rat will generalize from S+ depends on its criterion for “sameness”, its motivation, the value of the reward and other factors which the experimenter cannot measure. To further complicate matters, the criterion (degree of generalization) may shift across a test session, for example as the rat approaches satiety. All of these factors confound the experimenter’s estimate of the animal’s capacity to discriminate S+ from S-. In contrast, in the two-alternative forced-choice design the rat does not judge a single stimulus as S+ (or close enough to S+ to warrant the same reaction); rather, it must identify which of two stimuli is the S+. The complication of the threshold for “sameness” is no longer at play.

The second advantage is that the two-alternative forced-choice design requires the rat to treat stimuli as events in external space. Recall, from the discussion of Whitfield (1979), that decorticate cats can suppress licking (no-go) when an acoustic stimulus changes location in space, but the same cats cannot be trained to move towards stimuli in space. Closer to the present focus on tactile perception, Hutson and Masterton (1986) demonstrated that after ablation of barrel cortex rats could suppress licking when the frequency of whisker air-puff changed, but could not be trained to jump onto a reward-platform which they localized using their whiskers. We suggest that rats may be able to perform go: no-go (or lick: no-lick) tasks in the absence of cortex based on the direct transfer of information from subcortical centers to motor networks, but interacting with the environment when cued by stimuli, as in the two-alternative forced-choice design, is more likely to involve a contribution of the cortex. Behaviors which require the animal to interact with surrounding space are ideal for probing the unique functions of cortical sensory processing. A further

advantage of the two-alternative forced-choice paradigm is that it is more likely to involve sensory decisions in the context of a goal-directed action. This is in contrast with the more habitual nature of a licking response that is expected to involve reflexive behaviors that are therefore more prone to impulsivity.

5. Modes of operation

5.1. Active sensing

Active sensing systems are purposive and information-seeking (Prescott et al., 2011). Active sensing entails control of the sensor apparatus, in whatever manner best suits the task, so as to maximize information gain. Although the concept of sensor apparatus control applies to all modalities, it is perhaps most evident in the modality of touch.

A discussion of human tactile perception is beyond the scope of this article, but it is interesting to note some features that distinguish hand-mediated from whisker-mediated tactile perception, as well as features in common. Humans (and other primates) grasp and manipulate objects with their hands whereas rodents do not grasp or manipulate objects with their whiskers. (However, tactile information collected through the whiskers may be a precursor to grasping with the paw or mouth.) Moreover, human haptic perception relies to a great extent on proprioceptive signals from the joints and tendons. Proprioceptive signals of this sort are not present in the whisker follicles.

Common to human and rat tactile perception, we argue, is variation in the mode of operation according to the ongoing task. Humans adopt a broad range of sensorimotor strategies to collect information through the hands. These many regimes of acquisition

are collectively referred to as “haptic exploration” (Lederman and Klatzky, 1987). They range from following edges, palpating surfaces to detect texture and softness, and resting the fingertips on an object to detect vibration or motion (Jones and Lederman, 2006).

The rat whisker-mediated sensory system is also a prominent case of active sensing inasmuch as the rat precisely controls its whiskers. Self-generated whisker motion is critical for wall following (Jenks et al., 2010), distance estimation (Harris et al., 1999), and identifying properties such as texture (Diamond et al., 2008a), shape and size (Brecht et al., 1997; Harvey et al., 2001). As a rat or mouse feels its way through the world, it senses its own whisking (Ganguly and Kleinfeld, 2004). From the relationship between the whisking cycle and the contact signal (Curtis and Kleinfeld, 2009) the animal localizes objects with millimeter-precision (Knutsen et al., 2006). The extraordinary sensitivity of receptors in the follicle allows the rat to detect tiny whisker deflections (Adibi and Arabzadeh, 2011; Stüttgen and Schwarz, 2008).

5.2. Generative and receptive modes

Rather than review each of these, we wish to simplify the full complement of sensory capacities by arguing that whisker-mediated perception can arise through two general modes of operation: (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. The animal *causes* the percept by its own motion. We will focus on the discrimination of texture as a condition in which rats generate neuronal sensory representations through their own whisker motion. In the receptive mode, rats immobilize their whiskers to optimize the collection of signals from an object that is moving by its own power. We will focus on the discrimination of vibrations applied to the whiskers by external devices as an operation in the receptive mode.

We shall raise a number of questions. How do rats approach the object to be identified? How do the whiskers transduce object properties? How is a continuous stimulus dimension partitioned into behaviorally relevant categories and how are such categories encoded in memory? We first describe behavioral paradigms that allow quantification of performance for both generative and receptive modes of operation of the whisker sensory system. Next, we will outline the neuronal processing properties that underlie these behaviors. Finally, we propose a model for how an intrinsic stimulus representation is modified by discrimination learning to generate behaviorally relevant categories to guide action.

6. Receptor to decision in the generative mode

The generative mode of sensing in humans was described by the philosopher Merleau-Ponty:

[...] the knowing touch projects us outside our body through movement. [...] There are tactile phenomena, alleged tactile qualities, like roughness and smoothness, which disappear completely if the exploratory movement is eliminated. Movement and time are not only an objective condition of knowing touch, but a phenomenal component of tactile data. They bring about the patterning of tactile phenomena, just as light shows up the configuration of a visible surface. (Merleau-Ponty, 1945) (p. 367 of translation by Colin Smith.)

Rats, in the generative mode, sweep their whiskers forwards and backwards at a frequency of about 10 Hz, describing elegant arcs (Berg and Kleinfeld, 2003; Brecht et al., 1997; Carvell and

Simons, 1990; Hill et al., 2008; Perkon et al., 2011; Zuo et al., 2011). The rhythmic sweeping action is called “whisking” and an individual cycle is called a “whisk.” Whisking is the starting point for the perception of texture, as described in the following sections.

6.1. Generative mode: perceptual capacities and characteristics of the behavior

The perception of surface texture is critical to rodent behavior, for example in the selection of nesting materials (Rhodes and Richmond, 1985). A number of tasks have been devised to test texture perception. For example, when rats (in the dark) face two platforms with different textures at the entryway, they can learn to identify the reward-associated texture and jump to the correct platform. In tasks like this, rats learn to extract the identity of a texture based on one to three touches per whisker and display accurate judgments of a texture within 100 ms of initial whisker contact (von Heimendahl et al., 2007). Rats show high discriminative capacities when they are trained to compare two spatial densities of grooves on a surface (Carvell and Simons, 1990). More recently, Morita and colleagues (Morita et al., 2011) trained rats to discriminate between sandpapers of various degrees of roughness. Using their whiskers, rats could successfully discriminate two sandpapers with a difference in mean grit size of just 100 versus 82 μm . The accuracy of their judgments (Morita et al., 2011), combined with the speed of decision making (von Heimendahl et al., 2007) indicates a high level of efficiency. How does the brain accomplish whisker-mediated texture discrimination?

For an efficient decoding of the sensory signal arising in the generative mode, the sensory system must integrate “knowledge” of motor output in order to correctly interpret incoming information. Just as the brain would not be able to estimate the weight of an object we are lifting without taking into account the motor signals that produce muscle contraction, the afferent signal from a whisker cannot be optimally decoded without information about the whisker movement that generated the tactile signal. How does the sensory system obtain knowledge of the executed movement? There are two possibilities. First, sensory pathways might receive copies of the motor signal from the brainstem, zona incerta, the cerebellum and the motor cortices (Ahrens and Kleinfeld, 2004; Veinante and Deschenes, 2003). Second, the sensory pathway itself might carry afferent signals about whisking (Yu et al., 2006). Whichever of the two mechanisms is at play (or, more likely, some combination), all available anatomical and physiological evidence indicates that the barrel cortex is a direct participant in the motor network.

To identify surface texture rats make a sequence of brief contacts with their whiskers (von Heimendahl et al., 2007). Consistent with its fine motor control, whisking has been shown to be tuned to task requirements (Berg and Kleinfeld, 2003; Carvell and Simons, 1990; Harvey et al., 2001). Performance in a texture discrimination task was found to be positively correlated with the frequency bandwidth and the duration of whisking (Carvell and Simons, 1995). The use of high-speed video cameras has allowed whisker kinematics to be studied at higher temporal and spatial resolutions as whiskers come in contact with textures in an awake behaving rat. A recent study found evidence for the use of an adaptive motor strategy in the whisker system. In a two alternative forced-choice paradigm, rats were trained to classify surfaces based on the specific distancing of their grooves. When they were subjected to the clipping of the whiskers, leaving about 5 per side as compared to the normal complement of more than 30 per side, their behavior changed in ways that appear consistent with an optimization of motor output to compensate for lost information. The rats increased the total contact time, per trial, of the remaining whiskers. These results lead to the intriguing notion that the rats

use an information-seeking ‘cognitive’ motor strategy, instead of a rigid motor program (Zuo et al., 2011).

6.2. Whisker kinematics

Since whisker motion is the starting point for any tactile capacity, a critical step is to understand how motion represents the contacted surface. During lateral motion along textured surfaces, surface features such as groove depth or grain size, and the spacing between them, would be expected to modulate the movement profile. Can one identify the contacted surface based on the observation of the movement profile? The whisker-texture contact profile was firstly characterized at high temporal and spatial resolutions in anesthetized preparation using electrical stimulation of the facial nerve – *electrical whisking* (Arabzadeh et al., 2005). Various textures were then placed in contact with the whisker to generate a *texture library* – a collection of movement profiles at the base of the whisker for hundreds of sweeps over each texture. Dissection of the kinetic profiles revealed that as a whisker palpates a texture, its movement transiently changes with every contact and release from surface grains – the characteristic high-velocity, high-acceleration event that arises from the whisker-grain interaction is also known as a *stick-slip* event. Each texture resulted in a unique “kinetic signature” defined by the number and the profile of the high-velocity events (Arabzadeh et al., 2005). Further experiments recorded whisker motion in awake rats as they whisked against sandpapers of different grain size and confirmed that the rate and magnitude of kinetic events varied systematically with sandpaper textures (Wolfe et al., 2008) as well as grooved surfaces (Zuo et al., 2011). The whisker movement profiles obtained during awake active whisking against sandpapers were remarkably similar to those collected during electrical whisking (Diamond et al., 2008a). Fig. 4 shows an example of a slip movement as the whisker springs loose in posterior direction after it is released from a groove during a texture classification task (Zuo et al., 2011).

6.3. Neuronal responses to texture-induced whisker motion

The next step was to verify whether whisker motion profiles unique to each texture – the “kinetic signatures” of surfaces – produce reliable and systematically distinct neuronal responses. For this hypothesis to be viable, the kinetic signatures must fulfill two criteria: (i) they must evoke neuronal activity that carries information about texture and (ii) the neuronal responses must be available in the time interval during which the behavioral

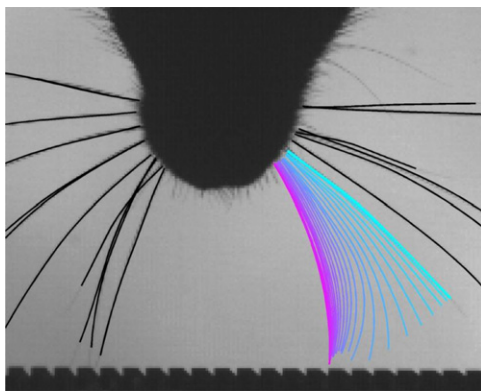


Fig. 4. Frame-to-frame tracking of whisker position as it gets stuck in a groove and is subsequently released at high velocity. Whisker C4 is traced in color over sequential 1 ms steps. Whisker kinematic events like this provide input to sensory receptors that allow the brain to identify the texture.

discrimination is performed and must directly influence the animal's choices (Diamond et al., 2008b).

Recording neuronal response to various textured stimuli in an anesthetized preparation confirmed the first criterion. The *texture library* was replayed to the base of the whiskers of anesthetized rats while neuronal responses were obtained at two levels of the pathway. Responses of the first-order neurons of the trigeminal ganglion and those of barrel cortex showed a reliable encoding of the kinetic signature – at every stage, individual neurons as well as neuronal ensembles were effectively driven by the high-velocity whisker movements and thus replicated the kinetic signature in their response profile (Arabzadeh et al., 2005). Lottem and Azouz (2008) induced electrical whisking in anesthetized rats and concurrently recorded from trigeminal ganglion neurons. Again, despite the high variability in whisking parameters, different textures were translated into distinct movement profiles and resulted in distinct neuronal responses in the first-order neurons.

Testing the second criterion requires measurements in behaving animals. Simultaneous recording of cortical neuronal activity from rats performing texture discrimination tasks confirmed the predictions of the anesthetized studies (Jadhav et al., 2009; von Heimendahl et al., 2007). Alignment of high energy stick-slip events with neuronal responding in barrel cortex revealed a transient increase in firing rate and firing synchrony on surfaces (Jadhav et al., 2009).

Currently two biologically plausible coding mechanisms have been identified, the “temporal integration” and the “temporal pattern” hypotheses. According to the first hypothesis, the brain encodes texture by a single quantity of spikes (total number of spikes, or else spikes per unit of time) accumulated across a whisk. In short, when the texture-specific kinetic signature causes high energy (i.e., high velocity and acceleration) movements to reach the receptors in the follicle, high firing rates are evoked; lower energy movement elicits lower firing rate. According to the second hypothesis, textures are encoded in the temporal sequence of high energy events within the kinetic signature. For example, one texture may evoke a kinetic signature with regularly timed stick-slip events, and a second texture may evoke a signature with alternating long and short intervals. The temporal pattern of kinetic events is captured in the neuronal firing pattern (Arabzadeh et al., 2006), and if the readout mechanism can decode firing patterns, then the animal would possess a much higher capacity for representing textures than if it used only the firing rate decoding mechanism.

6.4. Decoding – trial to trial read out of the neuronal signal

Decoding refers to the process by which a “downstream” neuronal population extracts information contained in the firing of an “upstream” neuronal population. Although the investigator can never specify decoding mechanisms with certainty, hypotheses can be tested by determining whether a proposed mechanism is consistent with the animal's behavior. More specifically, if the information extracted through a candidate decoding mechanism can explain the trial by trial variation in an animal's percept (measured by its behavioral choice) then that mechanism gains validity as a potential decoding principle. The perception of surface texture depends upon cortical processing (Guic-Robles et al., 1992). For this reason, we look to cortex for the representation of texture best correlated with the animal's explicit judgment of the stimulus. How are spike trains in the sensory system “read out” to support a behavioral discrimination between textures? In a texture discrimination paradigm, rats were trained to perch at the edge of a platform to touch a textured plate with their whiskers, and then to indicate their discrimination of the texture's identity by turning either left or right to collect a water reward (von Heimendahl et al.,

2007). On correct trials when rats accurately identified the stimulus, 75 ms before the rat made its choice, the average firing rate of the cortical neurons varied according to the contacted texture. It was higher for rough textures and lower for smooth textures. For trials of incorrect discrimination, at 75 ms before the rat made its choice, the firing-rate code was reversed; it was lower for rough textures and higher for smooth textures. Thus when the barrel cortex neurons carried the “right” signal the rat was likely to make a correct choice, decoding the signal to mean surface was ‘rough’, and when they carried the “wrong” signal it was likely to make an incorrect choice, decoding the signal to mean the surface was ‘rough’, when it was actually ‘smooth’. Therefore in each trial the rat made its decision based on the magnitude of whisker evoked activity in the barrel cortex. Mutual information analysis revealed that the temporal pattern of spikes can provide extra information to the brain above and beyond what is available in spike counts (Arabzadeh et al., 2006). However, it is not clear whether this extra information can be read out by the brain and thus can contribute to behavior. The authors are currently examining larger data sets to determine whether there is texture information present in the temporal firing patterns of cortical populations and whether that information is decoded, e.g., whether the temporal pattern information present correlates with the animal's choice.

6.5. Object invariance

In the real world, incoming sensory data are never identical in two encounters with the same object. For instance, observations of behavior reveal high levels of variability in the way rats sample surface textures from one trial to another. This includes variability in the angle of approach, the distance from snout to texture, the amplitude, frequency, and speed of whisker motion as well as variability in the number of whiskers that come into contact with the surface (Zuo et al., 2011). Trial to trial differences in the way whiskers engage a surface may cause spike patterns to vary, making the precise temporal code less robust than a spike count code. Yet, when the position or angle of a textured plate is changed, a trained rat correctly identifies the texture on its first encounter (unpublished observations). In spite of such trial to trial variability rats achieve high levels of performance. How do cortical neurons attain texture invariance? Currently little is known about how the neuronal kinetic signatures survive trial to trial variability and give rise to texture invariance.

However, one line of evidence comes from a close analysis of the *texture library* and the neuronal activity recorded across the

pathway when a component of the library was replayed to the whiskers (Arabzadeh et al., 2005). The library consisted of kinetic data collected for hundreds of sweeps over various textures. This allowed us to remove trial to trial variability in a subset of trials: a specific movement profile was selected from the library and presented repeatedly. While first-order responses were exquisitely reliable, cortical responses showed significant variations across these repeated trials. Because of the precise temporal alignment of spikes to the high-velocity events, the first-order neuron response was nearly identical on each trial – across 100 stimulus presentations spike times corresponding to a specific high-velocity event had a standard deviation of about 0.1 ms or less. Individual sweeps over the same texture thus resulted in distinct response profiles in the first-order neuron. While cortical neurons were highly informative about texture identity, they did not differentiate between multiple sweeps over the same texture; the cortical response to a repeated replay was similar to their response to one hundred unique sweeps over the same texture.

The mechanisms underlying invariant perception of textures are yet to be investigated in behaving rats. The study will require direct correlations between various aspects of neuronal activity and the rats' response.

7. Receptor to decision in the receptive mode

If we need to check whether our computer has been turned off, we would likely place our fingertips lightly on the case to feel for vibrations produced by the fan. It is unlikely we would palpate the surface and sweep our fingertips along it, as we would do for a texture judgment (Gamzu and Ahissar, 2001). Such active motion can confound the skin vibration emanating from the computer fan with the skin vibration produced by motion along surface features. Thus, we (primates) adjust our hand and finger motor output according to what information we need to extract about the objects around us.

It is difficult to quantify rodents' use of their whiskers in natural, out-of-laboratory settings. But even in the absence of objective data it seems reasonable to assume that some forms of perception rely on blocking motor output to keep the whiskers immobile, much the same as we block hand motion. For example, how do rats perceive the passage of a large predator above their burrow? We speculate that they place their whiskers in contact with the walls and floor, with negligible whisking output, to “listen” for vibrations (see Fig. 5).



Fig. 5. The receptive mode. As a predator approaches the rat's hiding place, the vibration signal might be transferred to the whiskers through their contact with the walls and floor of the burrow. Changes in vibration intensity over short time intervals would provide important information about the speed and direction of the predator. Drawing by Marco Gigante.

It is tempting to name the state of the sensory system characterized by exploratory whisking as “active” and the state of quiet immobility as “passive” (Kleinfeld et al., 2006), but we suggest that this nomenclature is misleading in its implication that the nervous system itself becomes passive in the immobile state, waiting to be subjected to unknown events. Behavioral work (see below) indicates that the animal is highly “active” even when it places and holds its whiskers in contact with a moving stimulus. For this reason we refer to the “quiet” whisker and brain state as the “receptive mode” rather than the passive mode.

We can further develop the illustration of the rat feeling for ground vibrations in the receptive mode. If the burrow’s walls tremble, is the predator approaching (increasing vibration intensity) or moving away (decreasing vibration intensity)? Changes and differences in vibration intensity seem ecologically relevant. In the sections below, we describe two behaviors, and possible neuronal correlates, that arise from judgments of whisker vibration intensity.

7.1. Perceiving a sinusoidal vibration: behavioral capacities

Rats were trained in a behavioral paradigm (Fig. 6) involving discrimination of vibrotactile stimuli (Adibi et al., 2012). Rats started each trial by a nose-poke into the stimulus aperture where whiskers came in contact with two mesh plates. After a random delay period (during which rats were required to sustain the nose-poke position) two vibration stimuli were presented simultaneously on the right and the left mesh plates. To receive a reward, rats had to turn towards the side with the higher intensity vibration (i.e., the stimulus designated as S+). What features do rats use to compare the intensity of two vibrations? Which features of whisker motion does the sensory system extract to construct percepts? We addressed this question by training rats to make discriminations between sinusoidal vibrations that differed in amplitude (A) or frequency (f) or both. One set of rats learned to reliably identify which of two vibrations had higher frequency (f_1 versus f_2) when amplitudes were equal. Another set of rats learned to reliably identify which of two vibrations had higher amplitude (A_1 versus A_2) when frequencies were equal. While these results indicate that both elemental features contribute to the rats’ sensation, a further test found that the capacity to discriminate A and f was reduced to chance when the difference in one feature was counterbalanced by the difference in the other feature: rats could not discriminate amplitude or frequency whenever $A_1 f_1 = A_2 f_2$. Fig. 7A shows a summary of the behavioral results. Thus, vibrations

were sensed as the product Af rather than as separable elemental features, A and f . The product Af is proportional to a physical entity, the mean speed. Analysis of performance revealed that rats extracted more information about differences in Af than predicted by the sum of the information in elemental differences. These behavioral experiments support the predictions of earlier physiological studies by demonstrating that rats are “blind” to the elemental features present in a sinusoidal whisker vibration; instead, they perceive a composite feature, the speed of whisker motion.

7.2. Perceiving a noisy vibration: behavioral capacities

We recently devised a second task to measure the capacity of rats to perceive differences in vibration intensity (Fassihi et al., 2012). Rather than comparing two stimuli applied simultaneously to their left- and right-side whiskers, the rats compare two stimuli delivered sequentially. At the outset, they are trained to position their snout in a nose hole such that their head is stationary and their right-side whiskers are firmly in contact with a plate that delivers motion along the anterior–posterior axis. Instead of a perfectly repeating sinusoid (Adibi et al., 2012), the stimulus is a sequence of position values drawn from a Gaussian distribution with standard deviation denoted σ . The first stimulus is called “base” (defined by σ_1) and the second stimulus “comparison” (defined by σ_2). In the standard protocol, the duration of base and comparison stimuli both are 400 ms. By considering trials with σ_1 fixed while σ_2 spans a range of values, psychometric curves can be constructed. Performance is above 75% correct when the stimulus intensity difference index defined as the absolute value of $(\sigma_1 - \sigma_2)/(\sigma_1 + \sigma_2)$, is larger than 0.1. The discriminative capacity of rats in this task is equivalent to that of human subjects who receive the same stimulus set on their fingertip (Fassihi et al., 2012).

It has been debated how sensory systems accumulate stimulus information over time; it has been suggested that the maximum time across which whisker motion could be integrated to lead to a behavioral choice may be as low as 25 ms (Stüttgen and Schwarz, 2010). To investigate this, we varied the duration of the comparison stimulus: 200, 400, or 600 ms. The rats’ performance improved for longer comparison stimuli, suggesting that for stimuli with a probabilistic structure, evidence can be accumulated over time.

The task described above is appealing not only because it will allow insights into how “noisy”, unpredictable stimuli are encoded

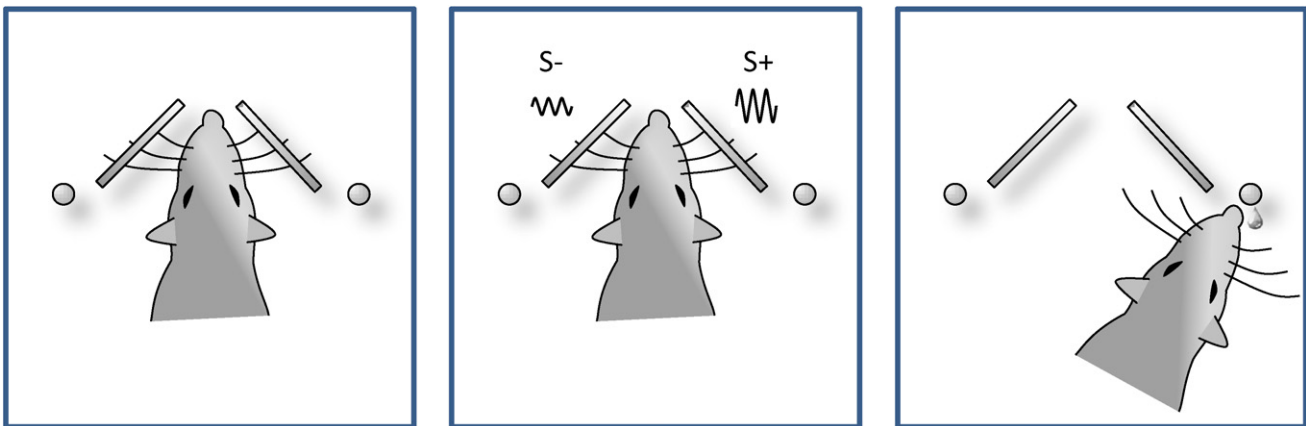


Fig. 6. Schematic representation of the vibrotactile discrimination task [from Adibi et al., 2012]. The rat initiated each trial by a nose-poke into the stimulus aperture while touching the two mesh plates with its whiskers (left panel). After a random delay period during which nose-poke was continually maintained, the stimuli were presented simultaneously on the left and right mesh (middle panel). Having identified the plate vibrating with S+ the rat made a behavioral choice by turning towards the corresponding drinking spouts (circles) and receive a reward (right panel).

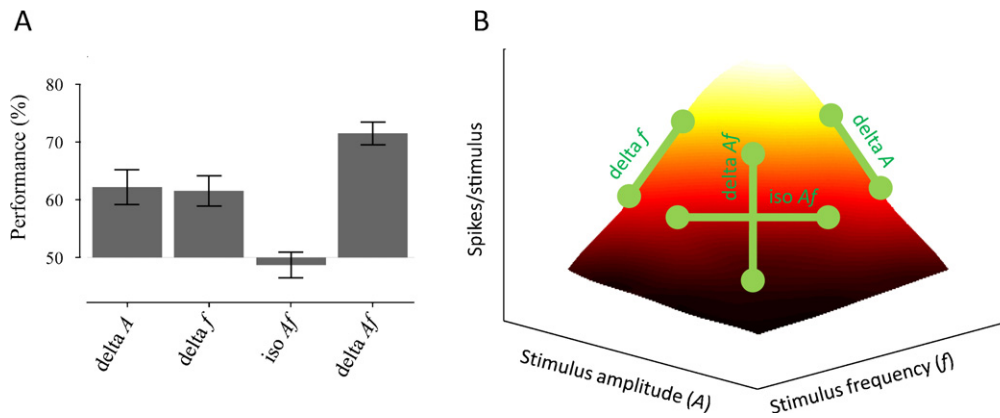


Fig. 7. (A) Behavioral performances across various stimulus dimensions [from Adibi et al., 2012]. Rats could discriminate between stimuli with pure differences in amplitude (delta A) or frequency (delta f). Performance was highest when changes in amplitude and frequency were combined in the same direction (delta Af). When changes in amplitude and frequency were combined in the opposite direction (iso Af) the resulting vibrations were indiscriminable. (B) Response magnitude function of a typical barrel cortex neuron to sinusoidal vibration stimuli [from Arabzadeh et al., 2003, 2004]. The four types of discrimination, as defined in A, are illustrated by green lines.

in the sensory system, but also because it is constructed in such a way as to force the rat to retain information about the “base” stimulus in working memory. Although rodents can perform spatial alternation and odor or object-guided delayed match-to-sample, there is no study showing working memory for stimuli distributed along a sensory continuum. The main result to date is that performance remains high across all delays up to 4 s, the longest tested (Fassihi et al., 2012).

7.3. Neuronal responses to whisker motion in the receptive mode

The outcome of the behavioral study on perception of sinusoidal vibrations is consistent with neuronal responses to the same stimuli. In earlier studies, we analyzed the cortical neuronal activity evoked by sinusoidal vibrations of the whisker shaft of anesthetized rats. We systematically varied vibration amplitude (A) and frequency (f) while making extracellular recordings from barrel cortex neurons to construct the neuronal response functions (Arabzadeh et al., 2003, 2004). The results demonstrated that single neurons and cortical ensembles reliably encode the product Af by their firing rate: increases in Af were accompanied by increases in firing rate. Methods of mutual information quantified the signal carried by barrel cortex neurons about the two elemental features A and f separately and their potential joint encoding. Neurons were found to reduce the dimensionality of the stimulus from two features (A, f) to a single feature, the product Af (Arabzadeh et al., 2003, 2004) (Fig. 7B). Furthermore, the nature of this code was highly efficient for a population – because different neurons encoded stimuli in the same manner, information loss was negligible even when the activity of separate neuronal clusters was pooled.

Importantly, the two elemental features A and f could not be decoded separately: any given firing rate could result from an infinite number of individual A and f values provided that they formed, together, a single value of Af . Thus, in summary, the failure of neuronal populations to distinguish between the two elemental features seems to be the clearest explanation for the failure of behaving rats to distinguish between these same two elemental features.

Experiments using aperiodic, unpredictable stimuli provide predictions for how sensory cortical neurons may encode the stimuli used in the “noise” comparison task. Neurons in barrel cortex are more responsive to noisy stimuli than regular, periodic stimuli (Lak et al., 2008, 2010; Maravall et al., 2007; Petersen et al., 2009). A preliminary analysis of neuronal activity from anesthetized rats provides support for a simple model where (i) both firing

rate and spike count are correlated with the stimulus position standard deviation σ and (ii) differences in both firing rate and spike count could be decoded to allow comparison of the base and comparison stimuli (Fassihi et al., 2012). The change in performance as a function of variable stimulus duration suggests that firing rate is a better candidate than spike count as the decoded feature.

8. Beyond sensory cortex

In visual perception, object identification is believed to emerge in the “ventral” processing pathway that travels within the inferotemporal lobe, passing from primary visual cortex to the hippocampus (Devlin and Price, 2007). The study of sensory processing in rats beyond the primary cortical fields is in its infancy. We wish to present hypotheses and predictions, as well as some preliminary findings. Our thinking is motivated by investigations of visual object perception; for this reason, we suppose that processing of tactile information generates the animal’s knowledge of the object that it is contacting through stages of transformation from primary sensory cortex to hippocampus.

8.1. Pathways for intracortical processing

As in the primate visual system, anatomical evidence in rats suggests that somatosensory information reaches the hippocampus. Fig. 8 gives a schematic view of the intracortical pathways and the key areas involved. We will focus on the dual routes by which tactile information from somatosensory cortex (SI plus SII) reaches the entorhinal cortex and, from there, hippocampus (Burwell and Amaral, 1998; Swanson, 1981).

Route I. Sensory cortex projects in the anterior direction directly to the dorsal part of medial prefrontal cortex (FC) – SI sparsely and SII more densely. This part of medial prefrontal cortex is believed to be an analogue of the dorsolateral prefrontal cortex of primates. Prefrontal areas, in turn, project to the lateral entorhinal area and directly to hippocampus.

Route II. Sensory cortex also projects to perirhinal cortex (PER). The target region consists of the upper bank of the rhinal sulcus (homolog of Brodmann area 36 in primates) and the lower bank of the rhinal sulcus (homolog of area 35). Perirhinal cortex projects to the entorhinal cortex (ERH). Entorhinal cortex receives input from all intracortical sensory processing streams and is the gateway to the hippocampus proper. Medial entorhinal area is mostly supplied via the postrhinal cortex

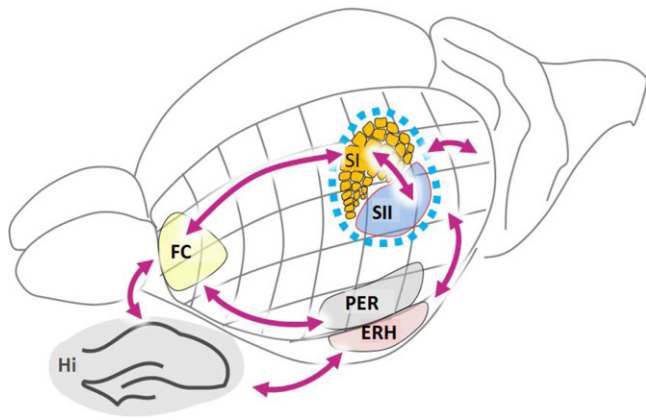


Fig. 8. Intra-cortical streams flowing from the vibrissal somatosensory cortex consisting of a primary (SI) and a secondary field (SII) with reciprocal connections. Hippocampus (Hi), buried below the surface, is uncovered and moved for this illustration. PER, perirhinal cortex; ERH, entorhinal cortex; FC represents the dorsal part of the medial prefrontal cortex.

and is the established seat of grid cells (Hafting et al., 2005). In contrast, lateral entorhinal area receives a stronger input from perirhinal cortex (and direct, but weaker, inputs from SI and SII) and is likely to be the relay stage for tactile inputs to the hippocampus.

Does tactile information indeed reach the hippocampus, and, if so, in what form? In rats, the best-described property of hippocampal cells is the place field (O'Keefe, 1976) but evidence is accumulating that neurons also encode events or objects in conjunction with space (Fortin et al., 2004). This evidence for a more general function makes rat hippocampus analogous to human hippocampus, where neurons are active during storage and recall of recent episodes (Gelbard-Sagiv et al., 2008).

8.2. Representation of touch at the end of the sensory pathway

We recently designed an experiment to determine whether texture is encoded in the hippocampus (Itskov et al., 2011). The critical step was to increase the number of stimuli from two textures, with a single texture associated with each action of the rat (turn left versus turn right) to four textures. Since now two different textures were associated with the same reward location and action, any difference in activity must reflect the coding of touch rather than some aspect of explicit behavior (Fig. 9). In this way our experiments were able to tease out the stimulus representation in hippocampus without spatial or behavioral confounds. We found that 18% of neurons sampled in CA1 region of hippocampus discriminated between two textures associated with the same action. Because the texture pair was presented in the same location and the rat moved through space in the identical way in response to contact, the result shows an explicit hippocampal representation of touch, beyond that of space. We interpret these findings as an indication that the hippocampus has the function of forming episodes composed of the relationship between tactile experience and its spatial context.

As we conduct new experiments, our working hypothesis is that along the stream of cortical areas neurons will show a progressive shift in the nature of information carried, from physical features ("what is the motion of the whiskers?") to the meaning of the sensation ("what are the whiskers touching?"). Texture properties will be represented in SI as a continuum: neuronal firing rate encode the physical properties of the contacted surface such as groove density. In later stages of processing, we expect to find two classes of neurons, those with positive and those with negative slopes. We speculate that the formation of dual populations beyond somatosensory cortex is a generalization of the finding in primates that SII neurons exhibit both positive and negative slopes for increasing vibrotactile frequency (Romo and de Lafuente, 2012).

An appealing notion is that perception is achieved by the abstraction of stimuli from a continuum, allowing physically similar events to take on very different meanings. Stimuli acquire

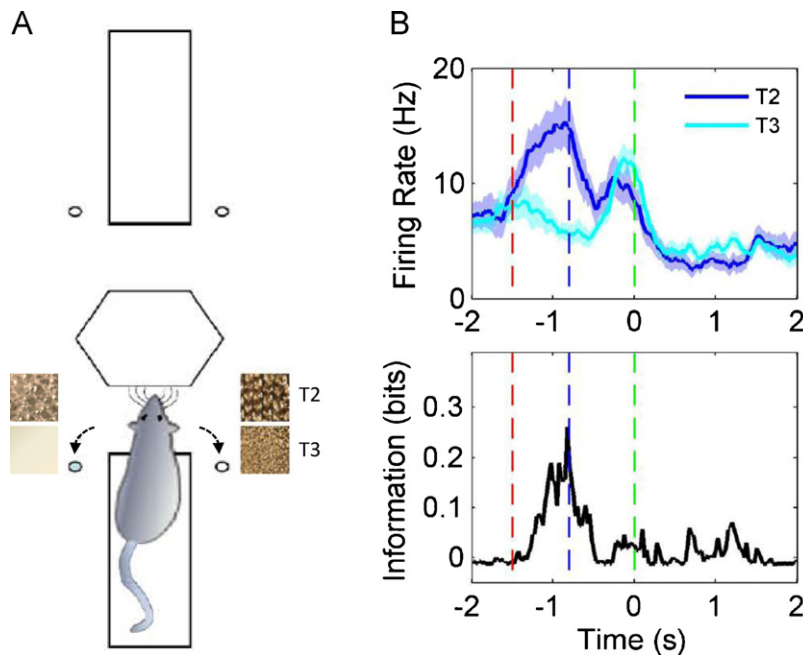


Fig. 9. (A) Behavioral paradigm from (Itskov et al., 2011). On each trial the rat approached the center of the platform to touch a textured plate with its whiskers. Four textures were used (T1 to T4). The rat then discriminated the surface of the plate and, according to its identity, turned left or right to obtain a reward. (B) Top panel: firing of this CA1 neuron distinguished between T2 and T3, associated with the same action. Neuronal activity averaged across trials (s.e.m. in shading) aligned to reward collection (0 s). The vertical dashed lines indicate the beginning of the touch (red), turn (blue) and the reward (green) phase of the behavior. Lower panel illustrates how the texture information that is carried in the response of this neuron rises during the touch phase.

“labels” or “tokens” as they are processed along intracortical streams. In our study, the neuronal representation of textures in the hippocampus had no relation to the graded responses found in SI: any given neuron could give its maximum response for any of the textured stimuli, not necessarily the roughest one (Itskov et al., 2011). It is clear that the responses were no longer a “sensory code” but a representation of discrete objects.

8.3. Challenges

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)? The words of Whitfield are (again) well composed:

“When we hear the sound of a bell, we know perfectly well, as men have known from antiquity, that in no way does the vibrating bell itself enter the nervous system. Yet we become aware of the ringing bell as an external object, and not as a series of sense data. Nevertheless, the sound enters the ear only as a set of aerial vibrations, and it is only this information that the sensory transducers have to work on. It is the transformation between the two representations that is the essence of our problem.” (p.130)

To make Whitfield’s idea more explicit, consider that all the “raw data” that sensory receptors collect from the outside world are present in the peripheral sensory system. At the entry regions to the cerebral cortex – the sensory cortical areas – neuronal activity constitutes a rich and diversified representation of the physical events impinging on the receptors. While the specific operations carried out on sensory signals once they reach the neocortex depend on the sensory modality (and even within the acoustic modality, words are processed differently than music (Peretz, 2006)), one general answer holds up for any input – intracortical processing serves to integrate, elaborate, and distribute elemental sensory signals in such a way that those signals gain new meaning through learning or, if familiar, can be interpreted by linkage with stored knowledge. In short, the transformations within cortex serve to construct perception – the abstraction of stimuli from a continuum, allowing physically similar events to take on very different meanings. Stimuli acquire “labels” or “tokens” as they are processed along intracortical streams. Thus, when we take a fruit in hand, we feel its texture and recognize a peach; we do not (unless asked to do so) perceive the pattern of activation of the receptors in our skin.

Work done since Whitfield’s 1979 review indicates that, beyond attributing meaning to sensory data, an additional and related function of cortex is to compare current stimuli to those stored in memory. This function comes into play whether the stimuli are real-world things, like the peach that is being palpated, or are simpler sensory data like a computer-controlled skin vibration. Both cases require access to stored information – the memory of what a peach feels like, or the memory of what the vibration delivered a few seconds earlier felt like. Such stored representations appear to reside in cortex. Romo and de Lafuente (2012) emphasize the memory operations of primate cortex, and we expect that in the whisker-mediated working memory task, analogous operations will also be discovered in the rat cortical processing streams. A further step in cortical processing is to partition a continuous stimulus dimension into behaviourally relevant categories and to assign predictive values to stimulus categories based on their associative strength within an environment and the uncertainty with which they predict rewards. It is safe to say that the whisker sensory system promises fertile ground for the continuing study of the transformation from receptor to decision.

Acknowledgments

This work was supported by the Human Frontier Science Program (contract RG0041/2009-C), the European Research Council, the European Union (contract BIOTACT-21590 and CORONET), the Compagnia San Paolo, the Australian Research Council Discovery Project DP0987133 and Australian National Health & Medical Research Council Project Grant 1028670.

References

- Adibi, M., Arabzadeh, E., 2011. A comparison of neuronal and behavioral detection and discrimination performances in rat whisker system. *Journal of Neurophysiology* 105, 356–365.
- Adibi, M., Diamond, M.E., Arabzadeh, E., 2012. Behavioral study of whisker-mediated vibration sensation in rats. *Proceedings of the National Academy of Sciences of the United States of America* 109, 971–976.
- Ahrens, K.F., Kleinfeld, D., 2004. Current flow in vibrissa motor cortex can phase-lock with exploratory rhythmic whisking in rat. *Journal of Neurophysiology* 92, 1700–1707.
- Alloway, K.D., Mutch, J.J., Hoffer, Z.S., Hoover, J.E., 2000. Overlapping corticostriatal projections from the rodent vibrissal representations in primary and secondary somatosensory cortex. *Journal of Comparative Neurology* 428, 51–67.
- Andres, F.L., Van der Loos, H., 1985. From sensory periphery to cortex: the architecture of the barrelfield as modified by various early manipulations of the mouse whiskerpad. *Anatomy and Embryology* 172, 11–20.
- Arabzadeh, E., Panzeri, S., Diamond, M.E., 2004. Whisker vibration information carried by rat barrel cortex neurons. *Journal of Neuroscience* 24, 6011–6020.
- Arabzadeh, E., Panzeri, S., Diamond, M.E., 2006. Deciphering the spike train of a sensory neuron: counts and temporal patterns in the rat whisker pathway. *Journal of Neuroscience* 26, 9216–9226.
- Arabzadeh, E., Petersen, R.S., Diamond, M.E., 2003. Encoding of whisker vibration by rat barrel cortex neurons: implications for texture discrimination. *Journal of Neuroscience* 23, 9146–9154.
- Arabzadeh, E., Zorzin, E., Diamond, M.E., 2005. Neuronal encoding of texture in the whisker sensory pathway. *PLoS Biology* 3, e17.
- Berg, R.W., Kleinfeld, D., 2003. Rhythmic whisking by rat: retraction as well as protraction of the vibrissae is under active muscular control. *Journal of Neurophysiology* 89, 104–117.
- Birdwell, J.A., Solomon, J.H., Thajchayapong, M., Taylor, M.A., Cheely, M., Towal, R.B., Conradt, J., Hartmann, M.J., 2007. Biomechanical models for radial distance determination by the rat vibrissal system. *Journal of Neurophysiology* 98, 2439–2455.
- Brecht, M., Preilowski, B., Merzenich, M.M., 1997. Functional architecture of the mystacial vibrissae. *Behavioural Brain Research* 84, 81–97.
- Burwell, R.D., Amaral, D.G., 1998. Cortical afferents of the perirhinal, postrhinal, and entorhinal cortices of the rat. *Journal of Comparative Neurology* 398, 179–205.
- Carvell, G.E., Simons, D.J., 1986. Somatotopic organization of the second somatosensory area (SII) in the cerebral cortex of the mouse. *Somatosensory Research* 3, 213–237.
- Carvell, G.E., Simons, D.J., 1987. Thalamic and corticocortical connections of the second somatic sensory area of the mouse. *Journal of Comparative Neurology* 265, 409–427.
- Carvell, G.E., Simons, D.J., 1990. Biometric analyses of vibrissal tactile discrimination in the rat. *Journal of Neuroscience* 10, 2638–2648.
- Carvell, G.E., Simons, D.J., 1995. Task- and subject-related differences in sensorimotor behavior during active touch. *Somatosensory and Motor Research* 12, 1–9.
- Chmielowska, J., Carvell, G.E., Simons, D.J., 1989. Spatial organization of thalamo-cortical and corticothalamic projection systems in the rat Sml barrel cortex. *Journal of Comparative Neurology* 285, 325–338.
- Clarke, W., Bowsher, D., 1962. Terminal distribution of primary afferent trigeminal fibers in the rat. *Experimental Neurology* 6, 372–383.
- Curtis, J.C., Kleinfeld, D., 2009. Phase-to-rate transformations encode touch in cortical neurons of a scanning sensorimotor system. *Nature Neuroscience* 12, 492–501.
- Deschênes, M., Timofeeva, E., Lavallée, P., Dufresne, C., 2005. The vibrissal system as a model of thalamic operations. *Progress in Brain Research* 149, 31–40.
- Devlin, J.T., Price, C.J., 2007. Perirhinal contributions to human visual perception. *Current Biology* 17, 1484–1488.
- Diamond, M.E., 2010. Texture sensation through the fingertips and the whiskers. *Current Opinion in Neurobiology* 20, 319–327.
- Diamond, M.E., von Heimendahl, M., Arabzadeh, E., 2008a. Whisker-mediated texture discrimination. *PLoS Biology* 6, e220.
- Diamond, M.E., von Heimendahl, M., Itskov, P., Arabzadeh, E., 2008b. Response to: Ritt et al., “embodied information processing: vibrissa mechanics and texture features shape micromotions in actively sensing rats” *Neuron* 57, 599–613 *Neuron* 60, 743–744; author reply 745–747.
- Diamond, M.E., von Heimendahl, M., Knutsen, P.M., Kleinfeld, D., Ahissar, E., 2008c. Where and what in the whisker sensorimotor system. *Nature Reviews Neuroscience* 9, 601–612.
- Dörfel, J., 1985. The innervation of the mystacial region of the white mouse: a topographical study. *Journal of Anatomy* 142, 173–184.
- Ebara, S., Kumamoto, K., Matsuura, T., Mazurkiewicz, J.E., Rice, F.L., 2002. Similarities and differences in the innervation of mystacial vibrissal follicle-sinus

- complexes in the rat and cat: a confocal microscopic study. *Journal of Comparative Neurology* 449, 103–119.
- Fasshih, A., Akrami, A., Esmaili, V., Diamond, M.E., 2012. Sensation of a – noisy whisker vibration in rats: psychometric and neurometric analysis. *Cosyne Abstracts 2012*, Salt Lake City USA.
- Fortin, N.J., Wright, S.P., Eichenbaum, H., 2004. Recollection-like memory retrieval in rats is dependent on the hippocampus. *Nature* 431, 188–191.
- Gamzu, E., Ahissar, E., 2001. Importance of temporal cues for tactile spatial-frequency discrimination. *Journal of Neuroscience* 21, 7416–7427.
- Ganguly, K., Kleinfeld, D., 2004. Goal-directed whisking increases phase-locking between vibrissa movement and electrical activity in primary sensory cortex in rat. *Proceedings of the National Academy of Sciences of the United States of America* 101, 12348–12353.
- Gelbard-Sagiv, H., Mukamel, R., Harel, M., Malach, R., Fried, I., 2008. Internally generated reactivation of single neurons in human hippocampus during free recall. *Science* 322, 96–101.
- Guic-Robles, E., Jenkins, W.M., Bravo, H., 1992. Vibrissal roughness discrimination is barrelcortex-dependent. *Behavioural Brain Research* 48, 145–152.
- Hafting, T., Fyhn, M., Molden, S., Moser, M.B., Moser, E.I., 2005. Microstructure of a spatial map in the entorhinal cortex. *Nature* 436, 801–806.
- Harris, J.A., Petersen, R.S., Diamond, M.E., 1999. Distribution of tactile learning and its neural basis. *Proceedings of the National Academy of Sciences of the United States of America* 96, 7587–7591.
- Harvey, M., Bermejo, R., Zeigler, H.P., 2001. Discriminative whisking in the head-fixed rat: optoelectronic monitoring during tactile detection and discrimination tasks. *Somatosensory and Motor Research* 18, 211.
- Hill, D.N., Bermejo, R., Zeigler, H.P., Kleinfeld, D., 2008. Biomechanics of the vibrissa motor plant in rat: rhythmic whisking consists of triphasic neuromuscular activity. *Journal of Neuroscience* 28, 3438–3455.
- Hutson, K.A., Masterton, R.B., 1986. The sensory contribution of a single vibrissa's cortical barrel. *Journal of Neurophysiology* 56, 1196–1223.
- Itskov, P.M., Vinnik, E., Diamond, M.E., 2011. Hippocampal representation of touch-guided behavior in rats: persistent and independent traces of stimulus and reward location. *PLoS ONE* 6, e16462.
- Jadhav, S.P., Wolfe, J., Feldman, D.E., 2009. Sparse temporal coding of elementary tactile features during active whisker sensation. *Nature Neuroscience* 12, 792–800.
- Jenks, R.A., Vaziri, A., Bolori, A.R., Stanley, G.B., 2010. Self-motion and the shaping of sensory signals. *Journal of Neurophysiology* 103, 2195–2207.
- Jones, L.A., Lederman, S.J., 2006. *Human Hand Function*. Oxford University Press, USA.
- Jones, L.M., Lee, S., Trageser, J.C., Simons, D.J., Keller, A., 2004. Precise temporal responses in whisker trigeminal neurons. *Journal of Neurophysiology* 92, 665–668.
- Kepecs, A., Uchida, N., Zariwala, H.A., Mainen, Z.F., 2008. Neural correlates, computation and behavioural impact of decision confidence. *Nature* 455, 227–231.
- Kim, U., Ebner, F.F., 1999. Barrels and septa: separate circuits in rat barrels field cortex. *Journal of Comparative Neurology* 408, 489–505.
- Kleinfeld, D., Ahissar, E., Diamond, M.E., 2006. Active sensation: insights from the rodent vibrissa sensorimotor system. *Current Opinion in Neurobiology* 16, 435–444.
- Knutsen, P.M., Pietr, M., Ahissar, E., 2006. Haptic object localization in the vibrissal system: behavior and performance. *Journal of Neuroscience* 26, 8451–8464.
- Kouh, M., Poggio, T., 2008. A canonical neural circuit for cortical nonlinear operations. *Neural Computation* 20, 1427–1451.
- Kwegyir-Afful, E.E., Keller, A., 2004. Response properties of whisker-related neurons in rat second somatosensory cortex. *Journal of Neurophysiology* 92, 2083–2092.
- Lak, A., Arabzadeh, E., Diamond, M.E., 2008. Enhanced response of neurons in rat somatosensory cortex to stimuli containing temporal noise. *Cerebral Cortex* 18, 1085–1093.
- Lak, A., Arabzadeh, E., Harris, J., Diamond, M., 2010. Correlated physiological and perceptual effects of noise in a tactile stimulus. *Proceedings of the National Academy of Sciences of the United States of America* 107, 7981–7986.
- Lavan, D., McDonald, J.S., Westbrook, R.F., Arabzadeh, E., 2011. Behavioural correlate of choice confidence in a discrete trial paradigm. *PLoS ONE* 6, e26863.
- Lederman, S.J., Klatzky, R.L., 1987. Hand movements: a window into haptic object recognition. *Cognitive Psychology* 19, 342–368.
- Lichtenstein, S.H., Carvell, G.E., Simons, D.J., 1990. Responses of rat trigeminal ganglion neurons to movements of vibrissae in different directions. *Somatosensory and Motor Research* 7, 47–65.
- Lottem, E., Azouz, R., 2008. Dynamic translation of surface coarseness into whisker vibrations. *Journal of Neurophysiology* 100, 2852.
- Lottem, E., Azouz, R., 2011. A unifying framework underlying mechanotransduction in the somatosensory system. *Journal of Neuroscience* 31, 8520–8532.
- Maravall, M., Petersen, R.S., Fairhall, A.L., Arabzadeh, E., Diamond, M.E., 2007. Shifts in coding properties and maintenance of information transmission during adaptation in barrel cortex. *PLoS Biology* 5, e19.
- Merleau-Ponty, M., 1945. *Phénoménologie de la perception*. Gallimard, Paris.
- Mitchinson, B., Arabzadeh, E., Diamond, M.E., Prescott, T.J., 2008. Spike-timing in primary sensory neurons: a model of somatosensory transduction in the rat. *Biological Cybernetics* 98, 185–194.
- Mitchinson, B., Gurney, K.N., Redgrave, P., Melhuish, C., Pipe, A.G., Pearson, M., Gilhespy, I., Prescott, T.J., 2004. Empirically inspired simulated electro-mechanical model of the rat mystacial follicle-sinus complex. *Proceedings of the Royal Society B: Biological Sciences* 271, 2509–2516.
- Morita, T., Kang, H., Wolfe, J., Jadhav, S.P., Feldman, D.E., 2011. Psychometric curve and behavioral strategies for whisker-based texture discrimination in rats. *PLoS ONE* 6, e20437.
- Munk, H., 1881. *Ueber die Functionen der Grosshirnrinde; gesammelte Mittheilungen aus den Jahren 1877–80*. Hirschwald, Berlin.
- Murphy, R.A., Mondragon, E., Murphy, V.A., 2008. Rule learning by rats. *Science* 319, 1849–1851.
- Neff, W.D., Diamond, I.T., 1958. The neural basis of auditory discrimination. In: Harlow, H.F., Woolsey, C.N. (Eds.), *Biological and Biochemical Bases of Behavior*. University of Wisconsin Press, Madison, pp. 101–126.
- Nicholls, J.G., Martin, A.R., Fuchs, P.A., Brown, D.A., Diamond, M.E., Weisblat, D.A., 2012. *From Neuron to Brain*. Sinauer, Sunderland, MA.
- O'Keefe, J., 1976. Place units in the hippocampus of the freely moving rat. *Experimental Neurology* 51, 78–109.
- Peretz, I., 2006. The nature of music from a biological perspective. *Cognition* 100, 1–32.
- Perkon, I., Kosir, A., Itskov, P.M., Tasic, J.F., Diamond, M.E., 2011. Unsupervised quantification of whisking and head movement in freely moving rodents. *Journal of Neurophysiology* 105, 1950–1962.
- Petersen, R.S., Panzeri, S., Maravall, M., 2009. Neural coding and contextual influences in the whisker system. *Biological Cybernetics* 100, 427–446.
- Pons, T.P., Garraghty, P.E., Mishkin, M., 1992. Serial and parallel processing of tactual information in somatosensory cortex of rhesus monkeys. *Journal of Neurophysiology* 68, 518–527.
- Prescott, T.J., Diamond, M.E., Wing, A.M., 2011. Active touch sensing: an introduction to the theme issue. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 366, 2989–2995.
- Rhodes, D.H., Richmond, M.E., 1985. Influence of soil texture, moisture and temperature on nest-site selection and burrowing by the pine vole, *Microtus pineorum*. *American Midland Naturalist* 102–108.
- Rice, F.L., Mance, A., Munger, B.L., 1986. A comparative light microscopic analysis of the sensory innervation of the mystacial pad. I. Innervation of vibrissal follicle-sinus complexes. *Journal of Comparative Neurology* 252, 154–174.
- Romo, R., de Lafuente, V., 2012. Conversion of sensory signals into perceptual decisions. *Progress in Neurobiology*, <http://dx.doi.org/10.1016/j.pneurobio.2012.03.007> in press.
- Shoykhet, M., Doherty, D., Simons, D.J., 2000. Coding of deflection velocity and amplitude by whisker primary afferent neurons: implications for higher level processing. *Somatosensory and Motor Research* 17, 171–180.
- Stüttgen, M.C., Schwarz, C., 2008. Psychophysical and neurometric detection performance under stimulus uncertainty. *Nature Neuroscience* 11, 1091–1099.
- Stüttgen, M.C., Schwarz, C., 2010. Integration of vibrotactile signals for whisker-related perception in rats is governed by short time constants: comparison of neurometric and psychometric detection performance. *Journal of Neuroscience* 30, 2060–2069.
- Swanson, L.W., 1981. A direct projection from Ammon's horn to prefrontal cortex in the rat. *Brain Research* 217, 150–154.
- Tafazolli, S., Di Filippo, A., Zoccolan, D., 2012. Transformation-tolerant object recognition in rats revealed by visual priming. *Journal of Neuroscience* 32, 21–34.
- Thorpe, S.J., Fize, D., Marlot, C., 1996. Speed of processing in the human visual system. *Nature* 381, 520–522.
- Torvik, A., 1956. Afferent connections to the sensory trigeminal nuclei, the nucleus of the solitary tract and adjacent structures; an experimental study in the rat. *Journal of Comparative Neurology* 106, 51–141.
- Veinante, P., Deschenes, M., 2003. Single-cell study of motor cortex projections to the barrel field in rats. *Journal of Comparative Neurology* 464, 98–103.
- Vincent, S., 1912. *The Functions of the Vibrissae in the Behavior of the White Rat*. University of Chicago.
- Voges, D., Carl, K., Klauer, G.J., Uhlig, R., Schilling, C., Behn, C., Witte, H., 2012. Structural characterisation of the whisker system of the rat. *IEEE Sensors Journal* 12, 332–339.
- von Heimendahl, M., Itskov, P.M., Arabzadeh, E., Diamond, M.E., 2007. Neuronal activity in rat barrel cortex underlying texture discrimination. *PLoS Biology* 5, e305.
- Welker, C., Woolsey, T.A., 1974. Structure of layer IV in the somatosensory neocortex of the rat: description and comparison with the mouse. *Journal of Comparative Neurology* 158, 437–453.
- Whitfield, I.C., 1979. The object of the sensory cortex. *Brain, Behavior and Evolution* 16, 129–154.
- Williams, C.M., Kramer, E.M., 2010. The advantages of a tapered whisker. *PLoS ONE* 5, e8806.
- Wolfe, J., Hill, D.N., Pahlavan, S., Drew, P.J., Kleinfeld, D., Feldman, D.E., 2008. Texture coding in the rat whisker system: slip-stick versus differential resonance. *PLoS Biology* 6, e215.
- Woolsey, T.A., van der Loos, H., 1970. The structural organization of layer IV in the somatosensory region (SI) of mouse cerebral cortex. The description of a cortical field composed of discrete cytoarchitectonic units. *Brain Research* 17, 205–242.
- Wright, A.K., Ramanathan, S., Arbuthnott, G.W., 2001. Identification of the source of the bilateral projection system from cortex to somatosensory neostriatum and an exploration of its physiological actions. *Neuroscience* 103, 87–96.
- Yamane, Y., Carlson, E.T., Bowman, K.C., Wang, Z., Connor, C.E., 2008. A neural code for three-dimensional object shape in macaque inferotemporal cortex. *Nature Neuroscience* 11, 1352–1360.
- Yu, C., Derdikman, D., Haidarliu, S., Ahissar, E., 2006. Parallel thalamic pathways for whisking and touch signals in the rat. *PLoS Biology* 4, e124.
- Zoccolan, D., Oertel, N., DiCarlo, J.J., Cox, D.D., 2009. A rodent model for the study of invariant visual object recognition. *Proceedings of the National Academy of Sciences of the United States of America* 106, 8748–8753.
- Zuo, Y., Perkon, I., Diamond, M.E., 2011. Whisking and whisker kinematics during a texture classification task. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* 366, 3058–3069.