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**Tactile coding  
"Where" and "What" in the Whisker Sensory System.**

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# **“Where” and “What” in the Whisker Sensory System**

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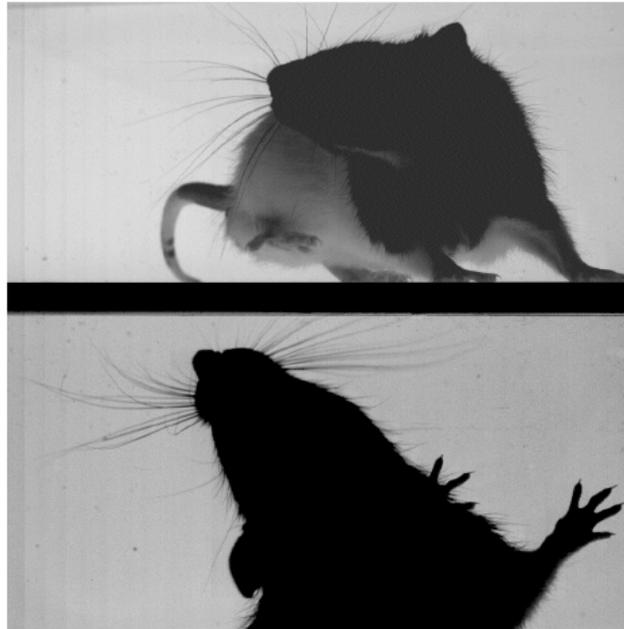
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## Preface

**How does the brain construct a representation of the surrounding world by the sense of touch? In the visual system, different neuronal pathways are specialized for the processing of information about the spatial coordinates of objects as opposed to their identity – in shorthand, “where” and “what”. Rats and other nocturnal animals seek out and palpate objects with their whiskers to build up a neuronal representation of “where” and “what”. Here, we review behavioral studies of tactile discrimination and discuss new findings about the underlying neuronal representations. We show that the identity and spatial coordinates of contacted objects can be decoded only through integration of self-generated signals commanding whisker motion.**

## Introduction

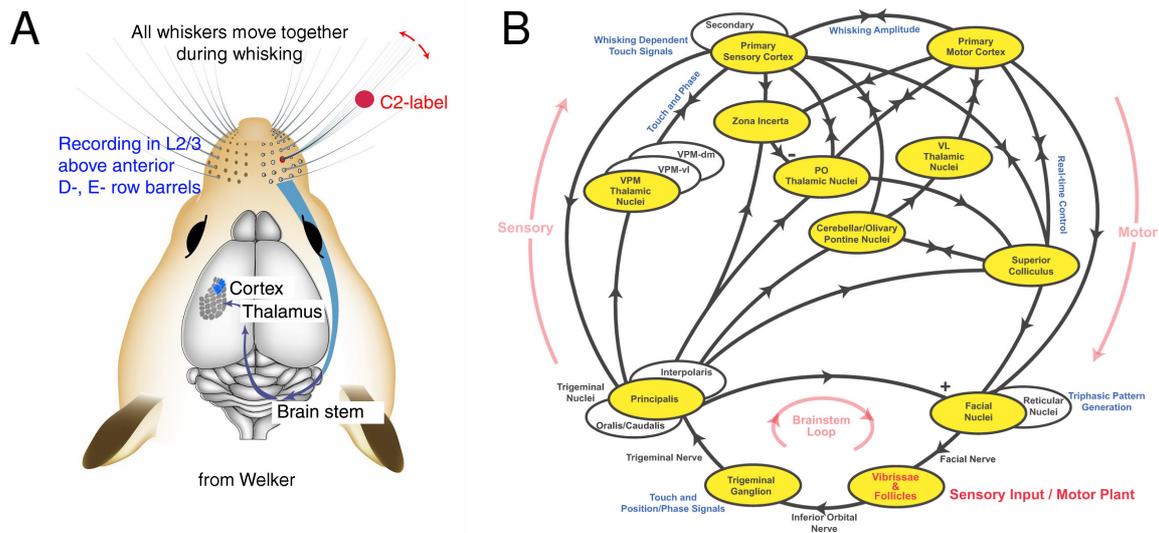
The classic study of Vincent (1912) illustrated that rats’ abilities to navigate through a raised labyrinth depended on whisker usage. Along with olfaction (Bhalli), whisker touch represents the major channel used by rodents to collect information from the nearby environment. They use their facial vibrissae – the “whiskers” – to recognize the positions of floors, walls, and objects, particularly in dark surroundings (Figure 1). Once they encounter an object, they use their whiskers to collect additional information about its features – such as its size and shape (Brecht) and surface texture (Carvell and Simons, Guic-Robles, Prigg, von Heimendahl). All of these feats are accomplished through an active process called “whisking”: sweeping of the whiskers forward and backward to encounter objects and palpate them (Berg and Kleinfeld; Kleinfeld et al.), usually in conjunction with movement of the head (Prescott, Hartmann).



**Figure 1. Collection of information about surrounding objects through the whiskers**

By head and body movement, combined with whisking motion, the rat positions its sensory apparatus in the optimal location for exploration and object identification. Here, the rat is filmed from two views as it explores a transparent glass wall. From Mitchison et al. (2007).

Since neurophysiologists and anatomists began to focus on the rodent whisker system in the 1970's, great strides have been made in unraveling the functional circuitry of the relevant pathways (Figure 2). In the last few years efforts have been directed towards the natural, ecological functioning of the whiskers. How is contact with an object transduced into neuronal spike trains? How do these spike trains represent the things encountered by the whiskers? Taking the lead from visual system organization, we consider two general kinds of knowledge about the world – (i) the location of objects in the environment, in head-centered coordinates, and (ii) the properties and identity of objects. Finally, we will indicate future directions that seem likely to be profitable.



**Figure 2. Organization of the sensorimotor system**

(A) Layout of whisker sensory pathway. In rats the vibrissae form a two-dimensional grid of five rows on each side of the snout, each row containing five to nine whiskers ranging between 15 and 50 mm in length. In each whisker's follicle, several populations of mechanoreceptors respond to rotation of the follicle by its muscles and deflection of the whisker shaft by external contacts, encoding information about the direction, velocity, and duration of displacements and torques. The mechanoreceptor cell bodies are located in the trigeminal ganglion and the first synapse is located in the trigeminal complex. The axons of the second-order neurons cross the midline and travel to the thalamic somatosensory nuclei; thalamic neurons project to the "barrels" of primary somatosensory cortex. Modified from E. Welker.

(B) Anatomy of nested loops in the whisker system. The proposed connectional scheme is distilled from a large number of studies to illustrate a roadmap of the flow of neuronal signals. As an active sensing system, stations involved in processing of whisker sensory signals are also strongly connected with those involved in controlling head, body and whisker motion. Broadly speaking, the ascending sensory pathways are depicted on the left and the descending motor pathways on the right. The inner most loop provides on-line positive feedback and involves only brainstem structures (Nguyen and Kleinfeld). This is enveloped by loops at the cerebellar, midbrain and ultimately thalamocortical level (Kleinfeld et al., 1999; Kleinfeld 2007). Additional pathways through the basal ganglia are not shown. Abbreviations: VPM-ventroposterior medial; vl-ventrolateral; PO-posterior; VL-ventrolateral.

## “Where” in the Whisker Sensory System

Rats and mice use their whiskers to detect the presence and location of objects when moving through an environment (Brecht). For example, in the dark they can learn to “gap-cross” – to perch at the edge of a raised platform and use their whiskers to localize a second platform before crossing for a reward (Hutson and Masterton, 1986; others). In a

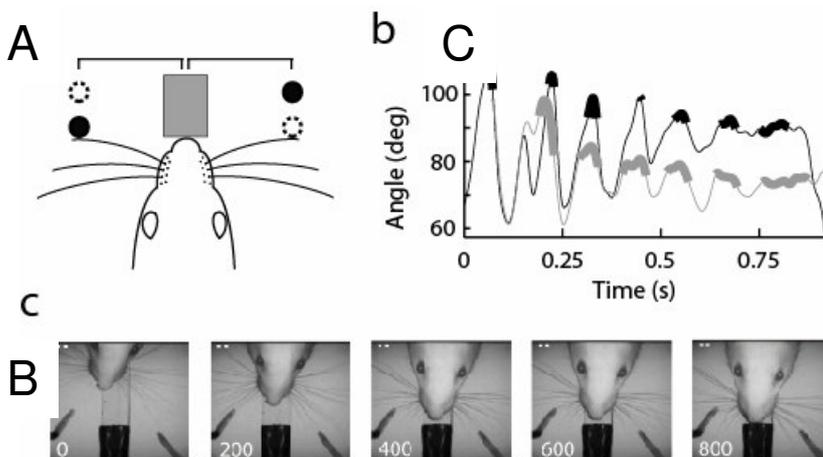
similar test, when rats are placed on a raised platform with a glass floor below, they whisk against the glass surface before stepping down; they use visual information to detect the floor only if the whiskers are cut (Schiffman et al., 1970). Studies of how rats use their whiskers to determine the configuration of objects in the environment are summarized in the next section.

### Behavioral measures of object localization

Object position in head-centered coordinates can be defined in three dimensions; i) the medio-lateral axis (termed radial), ii) the rostro-caudal axis (horizontal), and iii) the dorso-ventral axis (vertical). We begin by presenting studies that have quantified the sensitivity of rats to object location. Then we discuss the neuronal coding of object coordinates.

As a test of the ability to measure space in the radial dimension, rats were trained to classify as “wide” or “narrow” the distance between two walls, one on the left and one on the right of the snout (Krupa et al, 2001; Schuler et al, 2002). Rats performed this task correctly for distance differences down to 3 mm, and did so without whisking – indeed, transection of the facial nerve (thus paralyzing the whisker pad musculature) did not impair performance. Removal of progressively larger numbers of whiskers led to a progressive impairment until chance performance was reached once a single whisker was left intact on either side of the snout. These results show that rats integrate signals about whisker contact across the two sides of the snout to obtain accurate readings of radial distance.

As a test of the ability to measure space in the horizontal dimension, rats were trained to compare the relative forward-backward positions of two vertical poles positioned on opposite sides of the snout (Figure 3). Horizontal localization performance typically reached 1.5 mm, or 6° of whisker rotation, and at best 0.24 mm, or 1° (Knutsen et al, 2006). In two key ways, sensory-motor function in this task differed from the radial task. First, rats produced 3-6 whisking cycles per trial and after motor nerve lesion accuracy dropped to chance. Second, accuracy was not impaired by partial whisker removal; rats performed equally well with just a single left and right whisker intact.



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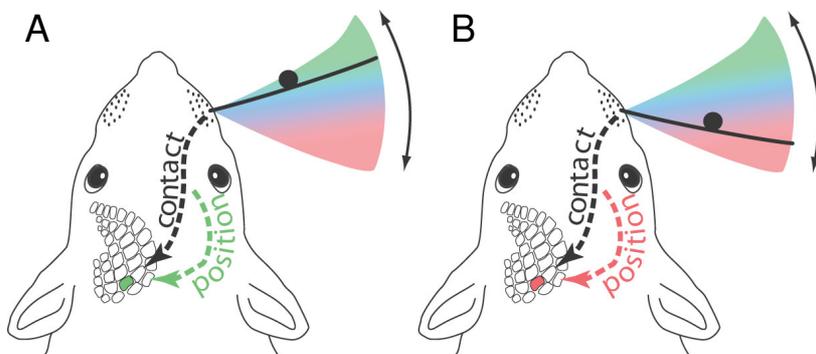
### Figure 3. Bilateral comparison of horizontal object localization

(A) Rats were trained to align their head with a nosepoke. Vertical rods were placed on both sides of the head (circles) and the rats discriminated their relative rostro-caudal positions. Black circles: trial in which left is posterior to right. Dashed circles: trial in which right is posterior to left.

(B) Typical head and whisker movements during a horizontal localization task. Under infrared light, the rat aligns its head to the nosepoke and uses its whiskers to contact and determine the relative horizontal locations of the two vertical poles.

(C) Whisker movements during one trial. The rat entered the discrimination area at time 0 and exited after about 1 sec. In the intervening period, it swept its whiskers back and forth in a rhythmic manner to contact the poles. Black line is the angle of the right C2 whisker, and the grey line of left C2 whisker. Whisker-object contact is indicated by a thicker line. From Knudsen et al.

The above tasks involve integrating or comparing the relative positions of two objects, but tasks like gap-crossing (Hutson and Masterton, 1986) require the rat to know the *absolute* position of the object-whisker contact point. In an absolute-position task, rats were able to measure the horizontal location of one pole with a single whisker (Figure 4) at an angular resolution equal to or better than  $15^\circ$  (Mehta et al, 2007).



### Figure 4. Absolute horizontal object localization

(A) Unlike comparative localization, absolute localization requires confluence of a contact signal (black dashed line) with a signal related to self-generated whisking, shown here schematically as the multi-colored fan. Whisking signal (green dashed line leading to contralateral barrel cortex) reports the whisker in the anterior position at the instant of object contact.

(B) Whisking signal (salmon-colored dashed line) reports the whisker in the posterior position at the instant of object contact.

## Neuronal encoding of object position

What signals do neurons carry about object position? A good place to begin is the activity of sensory receptor neurons during whisker motion. Artificial whisking was induced in anesthetized animals by electrical stimulation of the facial motor nerve, and three functional classes of primary sensory neurons were detected: (i) “whisking cells” responded to whisking with or without contact; (ii) “touch cells” responded to either contact, sustained pressure, or detach, but not to whisking alone; (iii) “whisking/touch cells” responded to both sorts of events (Szwed et al., 2003, 2006). This trio of primary sensory neuron types could encode object position as follows.

As a whisker sweeps forward, object contact is reported by touch and whisking/touch cells. Because the fan swept out during a whisk is co-planar with the whisker row (Fig. 2A), vertical location could be based on an “identity code”: the mere presence of a touch response reports contact with an object at the elevation of the active neuron’s receptive

field. However, an identity code could not function for radial and horizontal position. When a sweeping whisker contacts a vertical pole, the majority of touch-sensitive sensory neurons show an increase in firing rate as radial distance decreases (Szwed et al., 2006). This could result from the progressively greater force applied to receptors in the follicle. Thus, rate-coding is the best candidate for radial position.

The same contact signal must also underlie horizontal location, but it can be decoded only if there exists a *reference signal* reporting whisker angle at the instant of contact (Figure 3). The “whisking” signals found in primary neurons may be the origin of this reference. The integration site of touch and whisking reference signals is currently unknown; they seem to be separate at the level of the thalamus (Yu et al., 2006). At the level of barrel cortex, some neurons carry clear contact signals (Crochet and Petersen 2006; Hentschke et al.; Derdikman et al., 2006; von Heimendahl et al.); other neurons show whisk-related firing rate modulation, such that the rate for different neurons peaks at different phases in the whisk cycle (Fee et al., 1998). Preliminary data show combination of touch and whisking reference signals in cortex: firing rate codes contact relative to the phase of the whisk cycle (Curtis and Kleinfeld, SFN abstract 2006).

The way in which rats use their whiskers is consistent with the notion that the different spatial dimensions are encoded by the elementary neuronal variables outlined above and that there are separate coding mechanisms for horizontal and radial discrimination. On one hand, during horizontal localization: (i) rats actively whisk when performing accurate horizontal discrimination, (ii) accuracy correlates with whisking power, (iii) whisking paralysis induced by motor nerve lesions leads to chance-performance, and (iv) rats continue to perform the task at high acuity with a single intact whisker (Knutzen et al., 2006). All of this suggests that encoding of horizontal location depends on a whisking signal.

On the other hand, during radial localization (i) rats suppress whisking when assessing radial distances, (ii) whisking paralysis does not impair performance, (iii) accuracy depends on the number of intact contacting whiskers (Krupa et al., 2001). These observations suggest that encoding of radial location depends *not* on a whisking signal but on contact-evoked firing rate; the less reliable radial signal on a cell-to-cell basis (Szwed et al., 2006) can be easily integrated across whiskers by convergence. Still, demonstrating the operation of these neuronal codes in awake, behaving rats remains a challenge.

## **“What” in the Whisker Sensory System**

Rats make behavioral choices according to the *identity* of objects palpated by their whiskers. The accuracy of such judgments (approaching or exceeding the performance of primates) combined with the minimal elapsed time between first contact and behavioral action (as little as 100 ms) indicates that whisker-mediated object identification is highly specialized and enormously efficient; as such, the underlying neuronal mechanisms can provide crucial knowledge to neuroscientists investigating other sensory modalities and to roboticists developing biologically-inspired artificial tactile systems.

### **Judgement of shape**

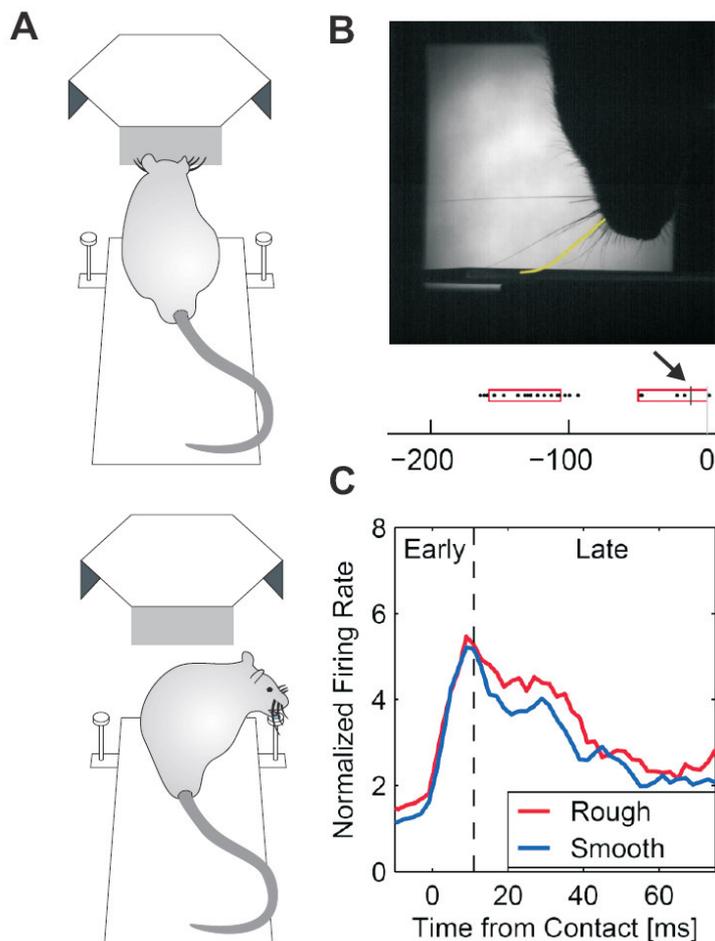
Shape can be an enormously important clue as to the identity of an object. To determine whether the whisker sensory system can support shape discrimination, rats were trained in the dark to judge the form of small (<1 cm) cookies distributed about a table in front of them (Brecht). All the cookies possessing one shape contained quinine, a bitter, odorless substance aversive to rats. A single cookie, with a different shape, was free of quinine and therefore edible. Rats learned to identify the untainted cookie by quickly palpating each candidate with the small whiskers around the nose and mouth (the so-called “microvibrissae”). Unfortunately, high-speed video was not available to document whisker motion.

It is likely that rats use the longer and more widely spaced posterior whiskers (“macrovibrissae”) to judge the form of objects too large to be spanned by the grid of microvibrissae. Though there are as yet no observations of whisker dynamics during shape judgement, a sound hypothesis was put forward recently based on an artificial whisker apparatus (Hartmann et al., *Nature*). The bending of a whisker-like fiber varied as it was swept along a surface – the fiber straightened slightly when it extended into cavities and curved as it passed over protuberances. The torque acting on the fiber was read off from a strain gauge at the base and, after many sweeps, a good approximation of shape features could be reconstructed. If the whisker follicle contains sensory receptors to encode torque, the analogous strategy could be the starting point for shape recognition.

### **Behavioral measures of texture**

Texture is another physical property likely to be a reliable clue to the identity of an object. Rats and mice palpate surfaces with their whiskers, giving rise to fast and accurate texture discrimination. To document the behavior, the animal is presented on each trial with one of two possible surfaces and receives a reward upon making a choice indicating correct recognition of the texture (Carvell and Simons, Guic-Robles). In one experiment where rats learned to discriminate reliably a smooth from a rough surface having shallow (30  $\mu\text{m}$ ) grooves spaced at 90  $\mu\text{m}$  intervals, it was proposed that the capacity of the rodent whisker system to distinguish texture is comparable to that of primates using their fingertips.

In a recent study, rats were trained to perch at the edge of an elevated platform, extending their whiskers across a gap to touch a textured plate mounted on a second platform. After identifying the texture present on that trial – either smooth or rough – the rat had to withdraw and turn to a water spout. The texture identity indicated whether a left or right turn was correct (Figure 5A). As it probed the texture, whisker motion was filmed with high-speed cameras (Figure 5B). On a typical trial, one whisker made 1–3 touches of 24–62 ms duration each before the rat made its choice, summing to a total touch time per whisker of 88–224 ms; the time from first whisker contact to the choice action was 98–330 ms (interquartile ranges). None of these contact parameters differed according to the texture presented to the animals, suggesting that motor output was not modulated by the encountered texture.



**Figure 5. Texture discrimination task**

(A) Upper panel: rat extends to touch the texture (gray rectangle) with its whiskers. Lower panel: having identified the texture, the rat turns to the drinking spout on the right to receive a water reward.

(B) Captured by high-speed film under IR light, the rat touches textured plate with whisker C2 colored yellow). Below, barrel C2 spike train recorded on this trial. Red boxes are touch times and the arrow points to the time at which the image was captured. 0 ms is the moment of rat withdrawal.

(C) Dynamics of neuronal response during whisker contact. From high-speed film, 1210 whisker contacts with the textured plates were documented simultaneous with recordings of barrel cortex neuronal activity. The instant of whisker contact set to 0 ms. For both textures, firing rate rose rapidly immediately following contact (4-11 ms). Subsequently, the magnitude of response separated according to texture, yielding significantly higher firing rate for rough (red) than smooth (smooth).

### Neuronal encoding of texture

Although barrel cortex is known to be an essential processing step in texture judgment (Guic-Robles), the underlying neuronal representation has been difficult to uncover (Prigg). A first step came from experiments using artificial whisking (evoked by electrical stimulus of the whisking motor nerve) in anesthetized rats (Arabzadeh et al.). Movement of a whisker across a given texture gave rise to a vibration at the whisker base with a “kinetic signature” characteristic of the contacted surface. Textures of differing coarseness induced kinetic signatures distinguished by total energy; in the trigeminal ganglion and barrel cortex, the energy of whisker vibration was translated into the neuronal firing rate.

The hypotheses gained from studying anesthetized rats were tested in awake rats carrying out texture discriminations (Figure 5A), when stimuli were not imposed on the receptors but were generated by the animal through its own motor program. To look for the central representation of texture, spikes recorded from barrel cortex neurons were aligned to the instant of whisker contact with the plate, judged from high-speed films (Figure 5B). Separating the responses into two separate traces corresponding to average rough and smooth touches (Fig. 5C), there was no texture-related difference during the initial, sharply rising response phase (4–11 ms, marked “early” in Fig. 6C). Shortly thereafter, a greater firing rate for rough touches (red trace) compared to smooth touches (blue trace) became evident (11 ms–end), thereby confirming firing rate as the fundamental coding mechanism. Activity during the last 75 ms before the animal’s choice transmitted the most informative signal; in this window, neuronal clusters carried, on average, 0.03 bits of information about the stimulus on trials in which the rat’s behavioral response was correct.

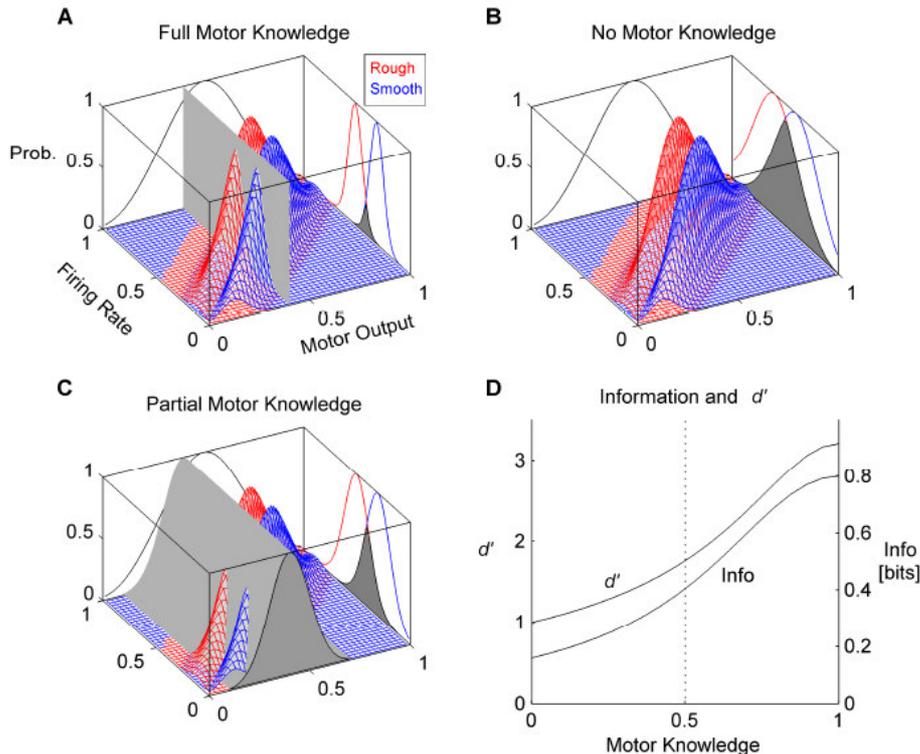
Analysis of trial-to-trial variability is a powerful approach for learning how cortical activity guides behavior (Newsome, Romo). In the texture discrimination task, examination of the responses in trials when the rat misidentified the texture revealed that, in contrast to correct trials, neuronal firing rate was higher for smooth than for rough. Analysis of high-speed films suggested that the inappropriate signal on incorrect trials was due, at least in part, to non-optimal whisker contact. Thus, for the selected task, barrel cortex firing rate on each trial leads directly to the animal’s judgement of texture.

## Sensory motor integration

In rats, as in humans (Gamzu), tactile exploration entails the interplay of motor output and sensory input: the large facial vibrissae sweep forwards and backwards in a “whisking” motion whose spatio-temporal set points and trajectories are determined by the motor system. Perturbation of the whisking motion, by a contacted object, gives rise to sensory signals carrying information about the object. Just as we could not estimate the weight of an object we are lifting without taking into account motor signals that encode muscle contraction, it is certain that a whisker sensory signal cannot be optimally decoded without information about the active movement that induced the signal. Figure 2B highlighted three of the loops whereby the sensory pathway can receive motor copies – through the brain stem, the cerebellum, and the motor cortex (Kleinfeld, Ebner, Ahrens, Brecht, Hentschke, Berg).

While all motor variation appear as noise to an experimenter who studies the dependence of sensory signals on a stimulus, this need not be the case for the animal. During texture discrimination, for example, if the rat can access information about its distance from the plate and its self-generated whisking motion, it may be able to compensate for the variability. It is worth exploring in detail how such a motor efferent copy can optimize the decoding of sensory signals. Figure 6 presents a numerical model of barrel cortex neuronal activity underlying a texture discrimination task. The model’s output is a probability distribution of firing rates on a given trial, determined by (a) the motor output (e.g., whisking strength) on that trial, and (b) the contacted surface, rough or smooth. Motor output is normally distributed around 0.5, ranging from 0 to 1 (see black curve in the motor-probability plane, back wall in fig. 14A). The evoked firing rate for both textures varies linearly with motor output (i.e., we assume that more spikes are evoked by a strong than by a weak whisk), but for any given motor value the barrel cortex response is likely to be greater for a rough than a smooth contact.

Suppose the “decoder” of sensory signals receives and exploits a precise copy of the motor output provided by the motor system. With the elimination of uncertainty along the motor dimension, the sensory response on any given trial is predicted by a “slice” through the two distributions (Fig. 6A). The resulting distributions, for a motor output of 0.4, are shown projected onto the probability - firing rate plane (right wall in panel A). The sharp separation between the rough and smooth response distributions enables highly efficient decoding. With the parameters chosen—for illustrative purposes—in the model, and provided that the decoder has exact knowledge of the motor output on every trial,  $d' = 3.20$  and the information carried by firing rate in each trial is 0.80 bits.



**Figure 6. Use of motor knowledge to discriminate sensory inputs**

Panels (A–C): Joint probability distribution of firing rate and motor output, for rough (red) and smooth (blue) texture. (A) For a precisely known motor output (vertical slice), the firing rate distributions are given by the conditional distributions, shown projected on the right wall. (B) If motor output is unknown, firing rate is distributed following the marginal distributions, shown on the right wall. Note the much greater variance and overlap. (C) If motor output is known with some gaussian uncertainty, firing rate is distributed following a weighted average of conditional distributions, visualized here by an intersection with a gaussian. The resulting distributions have an intermediate degree of overlap. (D)  $d'$  and information of firing rate about texture as a function of motor knowledge. A value of 0 corresponds to no motor knowledge (like in B), 1 is full knowledge (like in A), and 0.5 corresponds to the level of partial knowledge shown in (C).

Thus, with complete motor knowledge, the discriminability is as good as though the system were passively receiving a stimulus. Under these conditions, purely sensory noise (the variances of the projected distributions in panel A) reflects the fact that even with repetitions of the identical whisker kinetic pattern, neuronal responses are non-identical across trials (Arabzadeh et al., 2005).

If no knowledge of the motor output is available (Fig. 6B), the sensory response on any given trial must be decoded using the rough and smooth response distributions including full motor variability, shown projected onto the probability–firing rate plane. When we analyze neuronal responses in an awake, behaving rat with no independent signal from the motor system, our decoding algorithms operate in this manner. As shown in Figure 5C, neurons in barrel cortex have a slightly (10%) higher mean firing rate when the whisker touches a rough surface versus a smooth surface when all trials are considered together with no distinction according to motor output. With the selected parameters of the model,  $d' = 1$  and the information is 0.16 bits.

Texture decoding with an intermediate degree of motor knowledge is illustrated in panel C. This would apply if, for instance, barrel cortex receives information about whisking strength from motor cortex, but this motor copy does not perfectly correspond to real whisker motion because motor cortex output passes through many centers before reaching the vibrissal muscles.

Imperfect integration of the motor signal could result in additional loss of precision. As a result, the expected sensory response corresponds to a gaussian-shaped section slice through the two parallel elevations (panel C). The resulting response distributions are again projected onto the probability–firing rate plane. In our model,  $d' = 1.76$  and the information is 0.41 bits. Panel D show how  $d'$  and information about texture increase as the decoder is given progressively greater knowledge about the whisking signal that evoked the sensory response.

Because “active sensing” is general to most modalities (Ahissar), understanding how the sensory systems utilize knowledge of motor output to build up representations of objects is a major challenge.

## **Future directions**

Along with continuing work on fundamental physiological mechanisms of the sensory system (Brecht, Helmchen, etc.), three problems strike us as particularly important in understanding how the brain of actively whisking animals builds up a representation of the surrounding world.

First is to characterize precisely how the state of the whisker is reported by neuronal activity in behaving animals. The problem is complicated by the “high-dimensionality” of whisker state – the number of candidate mechanical parameters (position, velocity, speed, acceleration, torque etc.) is very large. Different neurons may encode different features. Although there has been progress in quantifying which elements of naturalistic whisker motion evoke spikes in anesthetized animals (Szwed 2003, Arabzadeh 2005), it has proven difficult to acquire a large enough number of spikes in awake rats concurrent with accurate monitoring of the whiskers. Once an adequate data set is acquired, the optimal analysis would be by reverse correlation to obtain an unbiased characterization of the sensory filter that neurons adopt, at processing levels from the trigeminal ganglion to barrel cortex, while the animal explores its environment. Neuroscientists have not yet identified, in a rigorous, quantitative manner, what features of the environment are reported by neurons of

any sensory modality in an awake, freely moving mammal. It is a realistic goal in the whisker sensory system.

Second is to elucidate the transformation of neuronal representations from stages where they encode physical signals to stages where they encode things that are meaningful to the animal. What matters to the survival of a rat, after all, is not only the capacity of its neurons to encode whisker kinetics, but also to represent the identity of the object that induced the kinetics – trap or cheese? It has been argued convincingly that this transformation is a primary function of cortical processing (Whitfield, 1976). The work reviewed here has begun to shed light on how cortical neurons represent the location and characteristic features of a contacted object. It will be exciting to build on this, proceeding from the study of how the brain encodes elemental properties to how it encodes the higher-level, more abstract *meaning* of a stimulus – its category, its value, and the action which must be taken.

As a third and related issue, we pose the question of whether the animal acquires the identity of the things it touches (“what”) and the spatial coordinates of the things it touches (“where”) through separate cortical processing streams. In visual cortical processing, both the dorsal “where” processing stream and the ventral “what” processing stream utilize elemental information (from primary visual cortex) about the orientation, size, and shape of objects, and about their spatial relations. The two streams, however, deal with the available visual information in different ways: The ventral stream transforms visual information into perceptual representations that embody the identifying features of objects, whereas the dorsal stream transforms visual information into representations of the configuration of objects within egocentric frames of reference, thereby mediating goal-directed acts.

Likewise, in whisker-mediated touch the same information supports knowledge of object identity and spatial coordinates. Suppose a rat learns that food is located behind a sphere but not behind a cube. Discrimination between the two objects derives from the horizontal, radial and vertical location of contact during the whisk: thus, spatial coordinates translate to an object's identity as sphere or cube. Yet the same coordinates instruct the animal's pathway around the object to the food.

Inferotemporal (IT) neurons can show a response to the identity of a face invariant with respect to position or viewing angle of the face (citation). By analogy, within “what” and “where” processing streams in touch, neuronal response during extraction of features of one type will be invariant to changes in features of the other type. Our prediction is that in barrel cortex neurons will be found to encode mainly the elemental physical signals evoked by object contact. In a higher-order station along the “what” pathway (perhaps located ventral to barrel cortex), neurons might encode “cube” or “sphere” independently of their spatial coordinates; in a higher-order station along the “where” pathway (perhaps located posterior to barrel cortex), neurons might encode “move to the left” or “move to the right” independently of the object identity. Both such streams would be constituents in the general transformation of neuronal representations from stages where they encode physical signals to stages where they encode things that are meaningful to the animal.