

'Where' and 'what' in the whisker sensorimotor system

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Abstract | In the visual system of primates, different neuronal pathways are specialized for processing information about the spatial coordinates of objects and their identity — that is, 'where' and 'what'. By contrast, rats and other nocturnal animals build up a neuronal representation of 'where' and 'what' by seeking out and palpating objects with their whiskers. We present recent evidence about how the brain constructs a representation of the surrounding world through whisker-mediated sense of touch. While considerable knowledge exists about the representation of the physical properties of stimuli — like texture, shape and position — we know little about how the brain represents their meaning. Future research may elucidate this and show how the transformation of one representation to another is achieved.

Surface texture

Texture relates to the surface pattern of objects. Roughness is one of the attributes of texture. The roughness of an irregular sandpaper-like surface texture is quantified by its grain size; the larger the grains, the coarser the texture.

The classic study by Vincent¹ illustrated that a rat's ability to navigate through a raised labyrinth depends on the use of its whiskers. Whisker touch represents the major channel through which rodents collect information from the nearby environment. They use their whiskers — also called facial vibrissae — to recognize the positions of floors, walls and objects, particularly in dark surroundings. Once they encounter an object they collect additional information about its features, such as its size and shape² and surface texture^{3–6}, through an active process called 'whisking': a sweeping motion of the whiskers forwards and backwards to encounter objects and palpate them^{7,8}, usually in conjunction with movement of the head^{9,10} (see [Supplementary information S1 \(movie\)](#)).

Since neurophysiologists and anatomists began to focus on the rodent whisker system in the 1970's, great strides have been made in unravelling the neuronal pathways that transmit information from the whiskers to the sensory cortex^{11–13}. However, the sensory stimuli that were used to probe the system have usually been stereotypical whisker deflections, chosen for their simplicity and ease of presentation. The past few years have seen the initial attempts to understand how the sensory system represents features of the surrounding world that are selected by the animal rather than by the researcher. How is contact with an object transduced into neuronal spike trains? How do these spike trains represent the things that are encountered by the whiskers? This shift in research strategies means that it is critical to summarize what is known and what needs to be better understood. Coding of the direction

and frequency of whisker movement has been recently reviewed¹². Here, we discuss behavioural and electrophysiological studies of tactile discrimination, focusing on how rodents use their whiskers to collect two general types of knowledge about the world: first, the location of objects in the environment, relative to the animal's head ('where'), and second, the properties and identity of objects ('what'). We suggest that 'where' and 'what' can be decoded only through integration of self-generated whisker-motion signals. Finally, we indicate future directions of research that seem likely to be productive.

Organization of the whisker sensory system

The structure that anchors a whisker to the skin is called follicle. It gives tactile sensitivity and motion to the whisker, which is itself inert material. Each follicle is innervated by the peripheral branches of about 200 cells of the trigeminal ganglion¹⁴, whose nerve endings convert mechanical energy into action potentials (FIG. 1a). These afferent signals travel past the cell bodies in the trigeminal ganglion and continue along the central branch to form synapses in the trigeminal nuclei of the brainstem^{15,16}. The trigeminal nuclei convey afferent vibrissal information to the thalamus via parallel pathways (BOX 1) that then continue to the barrel field of the somatosensory cortex¹⁷.

The large whiskers on each side of a rat's snout (also called macrovibrissae) are arranged in a grid made up of 5 rows, designated A to E, and several numbered arcs, so that an individual whisker can be identified by its row

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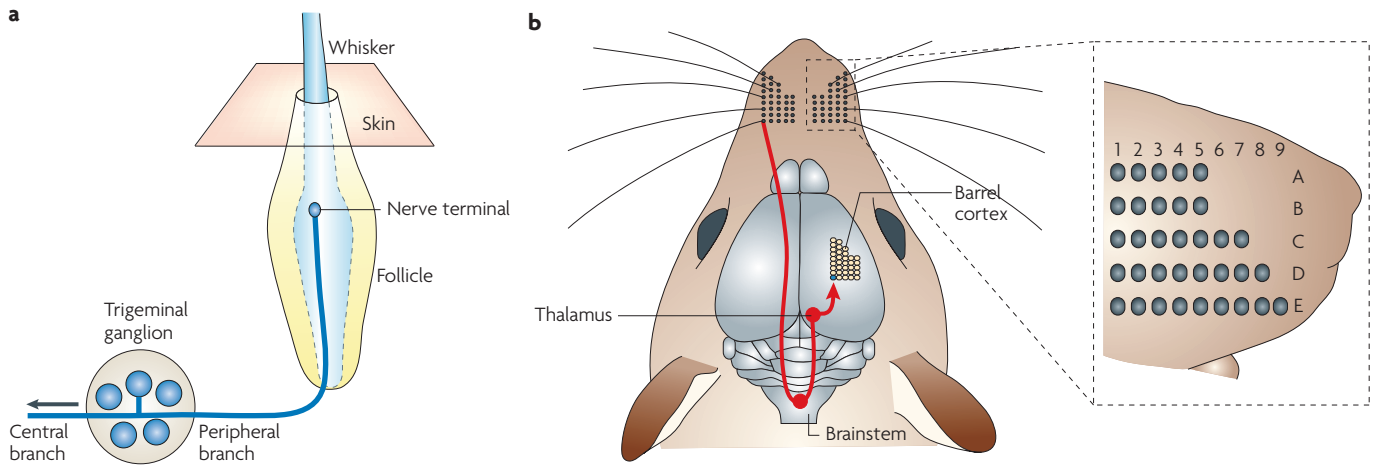


Figure 1 | Layout of the whisker sensory pathway. **a** | In each whisker follicle, mechanoreceptors respond specifically to rotation of the follicle by its muscles or to deflection of the whisker shaft by external contacts, both of which encode information about the direction, velocity and duration of displacements and torques. **a** | Schematic illustration of a mechanoreceptor terminal. Afferent sensory fibres travel together in the infra-orbital branch of the trigeminal nerve to the cell bodies, which are located in the trigeminal ganglion that lies just outside the brainstem. The central branch of the ganglion cell projects toward the trigeminal complex in the thalamus (arrow). **b** | 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 (see inset). After a synapse in the brainstem, axons of the second-order neurons cross the midline and travel to the thalamic somatosensory nuclei; thalamic neurons project to the barrels in the primary somatosensory cortex.

and arc coordinates (for example, C3). This whisker array is identical in all rats (FIG. 1b). The layout of the barrels in the somatosensory cortex replicates the layout of the whiskers on the snout¹⁸. The clear anatomical maps at each level of the ascending pathway have long suggested a 'whisker-to-barrel' connection. Even though neurons in the barrel cortex possess a receptive field that extends to several whiskers, it is usually clear — both in anaesthetized and in awake animals — that a single, topographically appropriate whisker exercises the strongest influence on a neuron's firing (reviewed in REFS 12, 19).

'Where' in the whisker sensory system

Many nocturnal animals (and some diurnal ones), including numerous rodent and insectivore species, use their whiskers to detect the presence and location of objects when moving through an environment. For example, in the dark, rats can learn to 'gap-cross', that is, to perch at the edge of a raised platform and use their whiskers to localize a second platform before crossing the gap to retrieve a reward on the second platform^{20,21}. In a similar test, when rats are placed on a platform that is elevated above a glass floor, they whisk against the glass surface before stepping down; they use visual information to detect the floor only if their whiskers are cut²². Studies of how rats use their whiskers to determine the configuration of objects in the environment are summarized in the next section.

Behavioural measures of object localization. The position of an object in head-centered coordinates (that is, relative to an animal's head) can be defined along three axes: the medio-lateral (radial) axis, the rostral-caudal (horizontal) axis and the dorso-ventral (vertical) axis. A number of behavioural studies have established that rats use their whiskers to perceive space in each of these dimensions.

The ability to determine object location in the radial dimension was tested in experiments in which rats had to classify the width of an alleyway as either 'wide' or 'narrow' (REF. 23). The rats were trained to align their head between two equidistant walls and to palpate them using only their macrovibrissae. By gradually decreasing the difference between 'wide' and 'narrow' across training sessions, rats learned to distinguish between aperture widths that varied by as little as 3 mm. Active whisking was not observed during the behaviour, and paralysis of the whisker pad by bilateral transections of the facial nerves did not reduce the success rates. Instead of whisking, rats brought their whiskers into contact with the alleyway walls through a combination of head and body movements. Although each whisker encodes radial distance independently, multiple whiskers appear to act together: removal of increasing numbers of whiskers resulted in a progressive impairment of performance until chance performance was reached when only a single whisker was left intact on either side of the snout. These results show that rats integrate signals about contact from many whiskers to obtain accurate readings of radial distance.

A follow-up study²⁴ showed that rats were capable of comparing the relative bilateral radial offset between the alleyway walls by successfully discriminating the walls as either 'equidistant' or 'non-equidistant'. Again, in this task the rats did not show any active whisking while palpating the walls. The difference between near and far, on each side, was 11 mm.

A behavioural paradigm (FIG. 2) was recently developed to study object localization in the horizontal dimension²⁵. A vertical pole was placed on each side of the rats' snout at different horizontal positions, with the posterior pole in a fixed reference location. The rats had to detect whether

Macrovisbrissae
Long (3–40 mm), sparsely spaced (2 per cm²) whiskers located on the middle and posterior part of a rat's snout. They are ordered in a regular, geometric grid and exhibit prominent forward and backward whisking motion.

Barrel
A set of neurons in the somatosensory cortex. Each barrel is responsible for processing the input from one whisker.

the left or the right pole was at the horizontal reference location, and then orient towards a liquid-dispensing spout on that side. Through successive stages of training, rats learned to position their snout against a central

nose-poke, so that only the macrovibrissae were in contact with the poles. Most rats were able to discriminate the location of the reference pole even when the horizontal offset of the distractor pole was as small as 1.5 mm, or

Box 1 | Parallel pathways to the cortex

Neurons of the trigeminal ganglion (TG) send a peripheral branch to the skin and a central branch into the trigeminal nuclei (TN) of the brainstem. Afferent signals travel past the cell bodies in the TG and continue along the central branch to form synapses in the TN. Multiple afferent pathways originate from these nuclei, some of them forming sensorimotor loops below the cortical level¹¹. Three afferent pathways eventually reach cortical levels (see panel a).

Lemniscal pathway (red). Neurons in the principal TN are clustered into 'barrelettes'. The axons of these second-order neurons cross the midline and travel, via the lemniscal pathway, to the 'barreloids' of the dorsomedial section of the ventral posterior medial nucleus (VPMdm) of the thalamus. Both barrelettes and barreloids are sets of modules arranged as a topographic projection of the whiskers themselves; neurons in a given module respond principally to the somatotopically connected whisker.

The axons of VPMdm neurons project to the primary somatosensory cortex (S1), where they terminate in 'barrels', dense clusters of small neurons in layer IV^{18,66,67}.

Extralemniscal pathway (blue). Neurons in the caudal part of the interpolar TN are also clustered into whisker-related barrelettes. They project to the ventrolateral domain of the VPM (VPMvl), where neurons are clustered into the 'tails' of the VPMdm barreloids^{68,69}. The axons of VPMvl neurons project to the septa between the barrels of S1 and to the secondary somatosensory cortex (S2)⁶⁸.

Paralemniscal pathway (green).

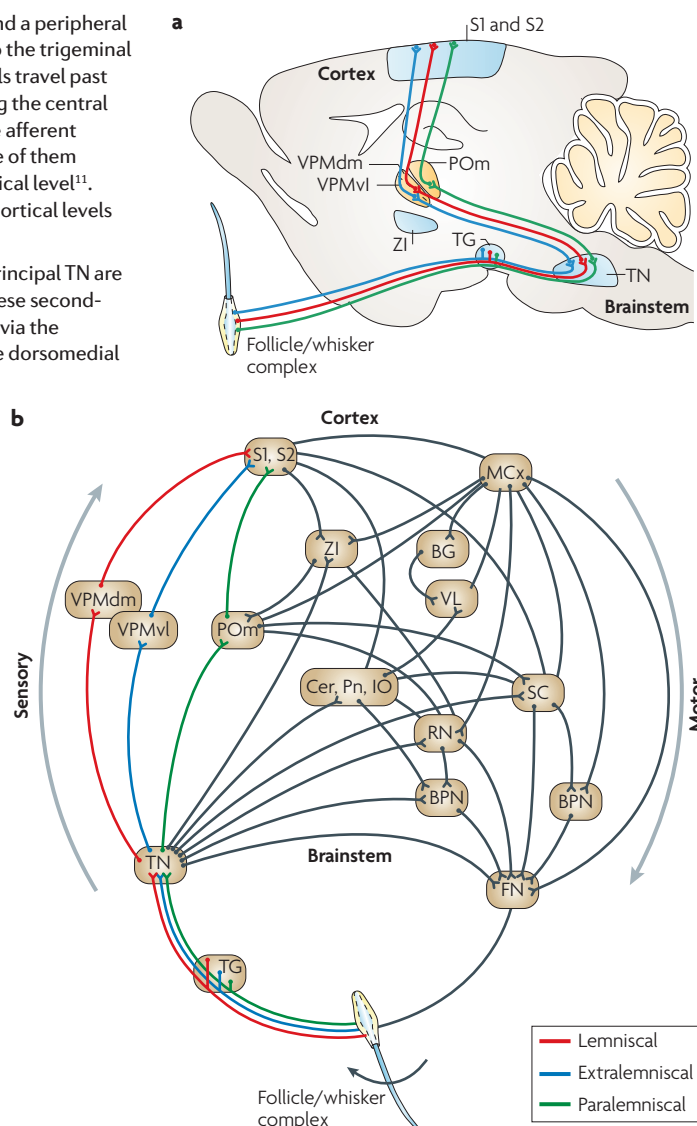
Neurons in the rostral part of the interpolar TN are not spatially clustered. They project, among other targets, to the medial sector of the posterior nucleus (POm)^{68,69} and to the zona incerta (ZI)⁷⁰. The axons of POm neurons project to targets immediately ventral to the barrels, in layer 5a of S1 (REFS 71–73), S2 (REFS 68,74,75) and to the primary motor cortex (MCx)⁷⁶. Contrary to the lemniscal pathway, the paralemniscal pathway is not spatially-specific and seems to integrate multiple-whisker information^{77,78}.

Recently, a fourth pathway, ascending from the principal TN through the 'heads' of the barreloids in the VPMdm, has been reported⁷⁹. The cortical targets of this pathway have not yet been determined.

The functions of the different pathways have not yet been directly tested and hypotheses vary across research groups. In our view, the response selectivity during artificial whisking suggest that paralemniscal neurons in the POm convey information about whisking kinematics, extralemniscal neurons in the VPMvl convey contact timing, and lemniscal neurons in the VPMdm convey detailed whisking and touch information^{78,80–82}.

The pathways are part of a complex network of sensorimotor vibrissal loops (panel b), which ascend through the pathways discussed above and then descend back to the whiskers through motor pathways (not discussed in this Review).

Additional abbreviations: BG, basal ganglia; BPN, brainstem premotor nuclei (arbitrarily divided to two oval circles); Cer, cerebellum; FN, facial nucleus; IO, inferior olive; Pn, pontine nuclei; RN, red nucleus; SC, superior colliculus; VL, ventrolateral thalamic nucleus. Connections indicated by lines without a synapse-like ending are reciprocal.



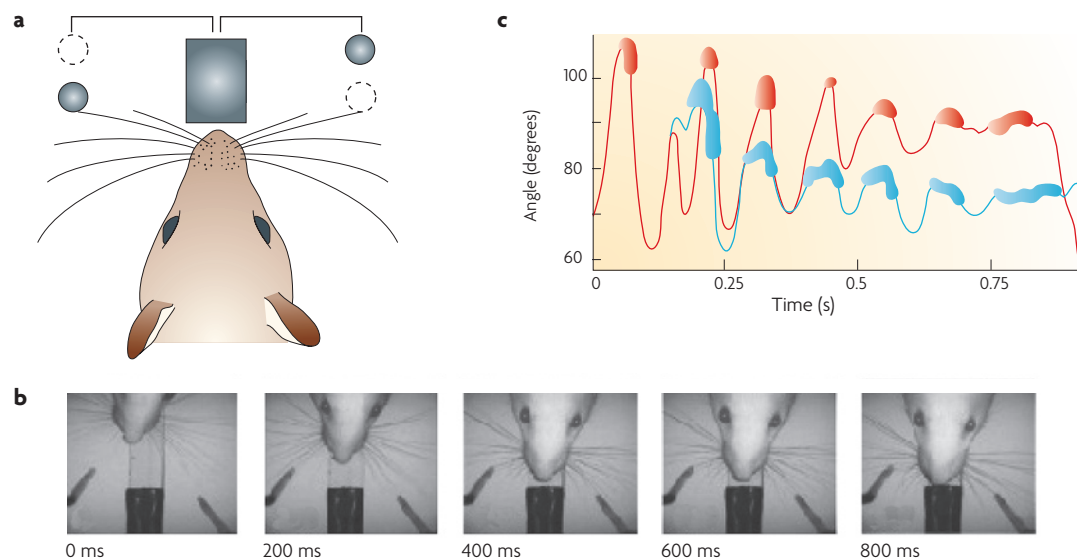


Figure 2 | Bilateral comparison of horizontal object localization. **a** | Rats were trained to align their head with a nose-poke. Vertical rods were placed on both sides of the head (circles) and the rats discriminated their relative rostro-caudal positions. Grey circles indicate the position of the rods in trials in which the left rod is placed posterior to the right rod. Dashed circles indicate the position of the rods in trials in which the right rod is placed posterior to the left rod. **b** | Typical head and whisker movements during a horizontal object-localization task. Under infrared light (in which rats cannot see), the rat aligns its head to the nose-poke 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. During this period, it swept its whiskers back and forth in a rhythmic manner to contact the poles. The red line indicates the angle of the right C2 whisker and the blue line indicates the angle of the left C2 whisker. Contact between whisker and object is indicated by the thicker areas on the lines. Figure modified, with permission, from REF. 25 © 2006 Society for Neuroscience.

6° of whisker sweep. Some rats performed well when the difference between the reference and distractor poles was only 0.24 mm, or 1°. Sensorimotor function in this task differed from that in the radial object-localization task in two ways. First, sensing horizontal spatial offsets required whisking: rats actively moved their whiskers back and forth 3–6 times per trial (with a trial lasting approximately 500 msec). When whisking motion was abolished by bilateral transection of the motor nerves, performance accuracy dropped to chance level. Second, partial whisker removal did not impair accuracy; rats performed equally well, or better, with just a single, intact left and right whisker. Interestingly, although rats were allowed to move their head and body, better performance in the horizontal object-localization task was correlated with fewer (and smaller) head-movements, suggesting that head-stabilization is part of the sensory-motor horizontal localization strategy.

The above tasks involve comparing the positions of two objects relative to each other. Other whisker-dependent tasks require the rat to know the position of an object relative to the animal itself. When a rat measures the location of a platform across a gap using a single whisker^{20,26}, it probably does so by sensing the whisker-object contact point in head-centred coordinates. This capacity was investigated in psychophysical experiments in which rats had to detect, with a single whisker, the angular position of one pole relative to their face (FIG. 3). The rats performed this task with an angular resolution equal to or better than 15° (REF. 27). Because

the rats were trained to suppress head-movements, the only way that they could contact the object was through whisker movements. Thus, for both types of horizontal localization task — comparing the relative locations of two objects and finding the absolute location of an object in space, respectively — the animal uses reference signals about vibrissa position^{28,29}. Further work is required to understand the nature of such reference signals and how they are exploited in different tasks.

Independently of the nature of the reference signal, it is clear that for relative sensing (FIG. 2; also see REF. 30) active-touch produces hyperacuity. Hyperacuity can also be found in vision³¹: when comparing the locations of two concurrently present objects, acuity reaches ~1° with vibrissal touch and ~3 arcseconds with human vision. These levels of acuity are well beyond the spatial resolution of the receptors (whisker follicles and photoreceptors) themselves. By contrast, when localizing objects in body or head-centred frameworks (FIG. 3), acuity is lower (less than 15° with vibrissal localization, ~1° with human vision).

Neuronal encoding of object location. What signals do neurons along the trigeminal pathway carry about object position? Although it is important that this question be investigated in awake behaving animals, a good starting point is to measure the activity of sensory receptor neurons during whisker motion that is induced artificially by electrical stimulation of the facial motor nerve in anaesthetized animals^{29,32}. In such experiments,

Hyperacuity

Sensory acuity that exceeds the spatial resolution of the sensor. Vibrissal hyperacuity is the ability to resolve spatial offsets that are smaller than the inter-vibrissal spacing.

Sensory receptor neuron

Neuron that converts a physical stimulus into electric impulses. In the whisker system, the cells of the trigeminal ganglion act as sensory receptor neurons.

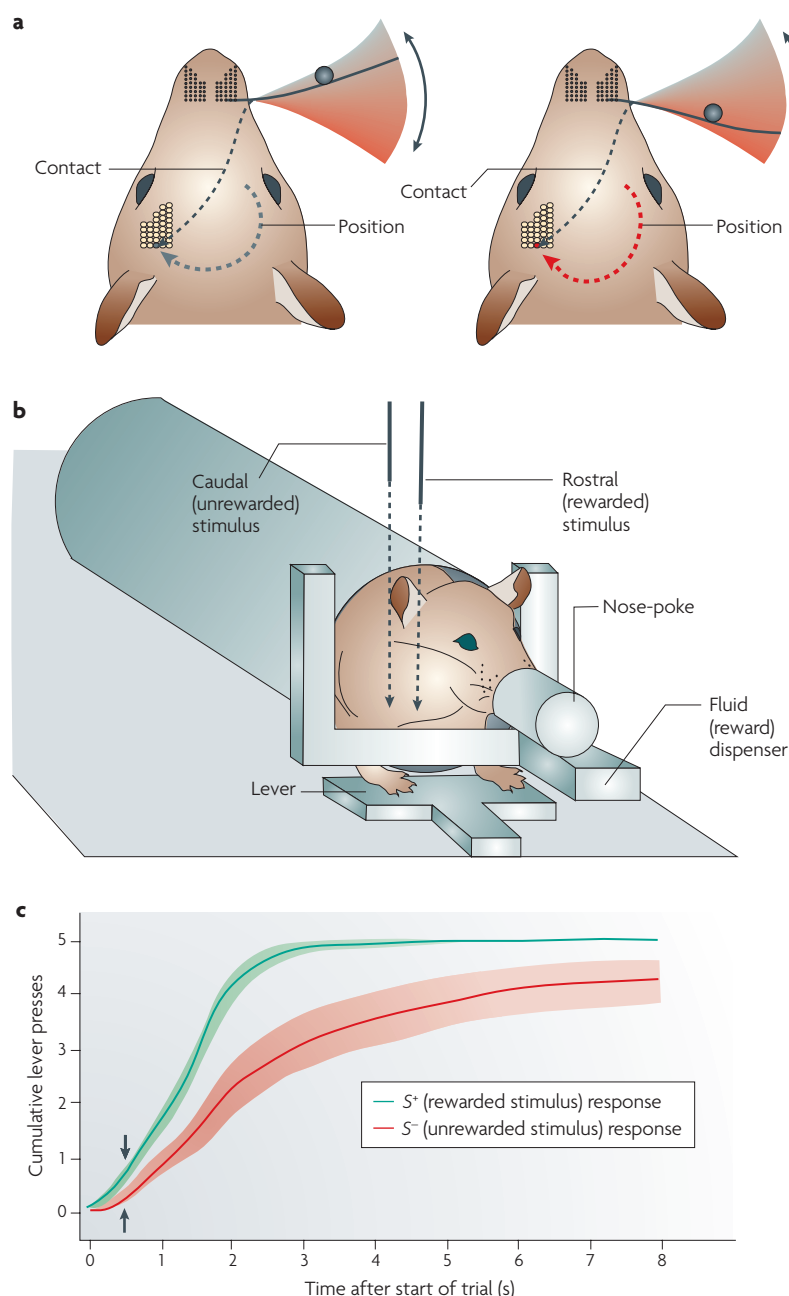


Figure 3 | Absolute horizontal object localization. a | The absolute localization of a vertical rod (filled grey circle) requires the confluence of a contact signal (black dashed line) with a signal related to self-generated whisking, shown here schematically as a graded-colour fan. In the left panel, the whisking signal (indicated by the grey dashed arrow pointing to the contralateral barrel cortex) conveys that the whisker is in the anterior position at the instant of object contact. In the right panel, the whisking signal (red dashed arrow) conveys that the whisker is in the posterior position at the instant of object contact. **b** | Apparatus for testing of absolute horizontal object localization. Trials start when an animal interrupts the nose-poke sensor, causing either the rostral or caudal rod to descend into the vibrissa field. The stimuli are positioned through a circular guide that is fixed relative to the nose-poke. Lever presses in response to the S^+ stimulus, either rostral or caudal for a given animal, were rewarded with a drop of water in the fluid dispenser. **c** | Temporal profile of cumulative lever press counts for one session, averaged separately over S^+ (green line) and S^- (red line) trials. Differences in the counts of lever pressing indicate that the animal recognized the position of the rod. The curves give the mean \pm 2 SEM cumulative lever press counts for S^+ trials (green) and S^- trials (red). The arrows at 0.5 s mark the time point after which curves are non-overlapping. Figure modified from REF. 27.

neuronal responses have been measured during two conditions, namely when the whisker moved in the air without touching anything and with a vertical pole (extending the entire height of the whisker array) positioned at different locations in the path of the moving whiskers. In these conditions, three functional classes of primary sensory neuron were detected: first, 'whisking cells', which fired during whisking *per se*, regardless of whether the whiskers touched anything; second, 'touch cells', which fired upon contact, sustained pressure or detachment, but not to whisking alone; and third, 'whisking/touch cells', which fired during both types of event.

The nature of afferent signals in the awake rat is less clear. By recording neuronal activity in the trigeminal ganglion of freely moving rats and comparing epochs of massive vibrissal touch (which caused gross bending of whiskers to less than half of their length) to epochs without touch, a wide distribution of selectivity was noted, from neurons that responded mostly to whisking to those that responded mostly to touch³³. Whether a stronger selectivity exists in the awake rat among individual afferents and during epochs of light touch is not yet known.

However, assuming that the neuronal responses to whisking and touch that are observed during artificial whisking can be verified in awake animals, object position could be encoded as follows: radial location could be encoded by firing rate and/or by spike count. As a whisker sweeps forward, object contact would be reported by touch cells and whisking/touch cells. The majority of these cells show an increase in firing rate as the radial distance of the object from the whisker base decreases³². This could result from the progressively greater force applied to receptors in the whisker follicle as the radial distance between object and whisker decreases³⁴, because less energy goes into bending the whiskers when the thicker, proximal part of the whisker shaft contacts the object.

Horizontal location could be encoded through the same contact signal, but by spike timing rather than spike count. As a whisker contacts an object progressively later in a whisk cycle the farther the object is positioned forward, the onset time of the contact signal correlates with the horizontal coordinate. However, this form of temporal code can only be decoded if there is a reference signal that encodes the spatial location of the whisker over time (FIGS 2,3). In that case, the reference signal can be compared with the contact signal to extract object position^{29,35}. The spiking activity of whisking cells located in the trigeminal ganglion²⁹ could provide such a reference signal, as these cells transmit information about the angular phase and position of the whiskers. Experiments in awake behaving rats have shown that this whisking signal is conserved all the way to the barrel cortex²⁸. So, neurons that receive both phase-specific whisking signals and touch signals could decode horizontal object position by detecting the concurrence of the two types of signal. From studies in anaesthetized rats, it is known that whisking signals and touch signals are still separate at the level of the

thalamus³⁶. In the barrel cortex, whisking and touch separation is less distinct³⁷, although cortical activity has been shown to be modulated by whisking and touch at both the single-cell^{6,28,37–40} and population levels^{41–43}. Recent findings suggest that whisking and touch signals converge on single cortical neurons whose firing reports the horizontal coordinate of a touched object relative to the face (discussed in REF. 44). Their output depends on a nonlinear interaction between whisking and touch signals: whisking strongly modulates the response of these neurons to touch, possibly through shunting inhibition or a functionally equivalent gating mechanism.

Encoding of vertical location has not yet been examined in combined physiological–behavioural studies, but a simple and plausible hypothesis can be formulated. Because the whisk trajectory of a single whisker is coplanar with a whole row of whiskers, vertical location could be based on an ‘identity code’: the mere presence of a touch response in a neuron that is related to a specific whisker, located anywhere along the trigeminal pathway, could report contact with an object at the elevation of that whisker.

An interesting feature of the proposed encoding schemes is that they can coexist in the activity pattern of the primary sensory neurons. The way in which rats use their whiskers is consistent with this suggestion. For example, when determining an object’s horizontal location, rats actively whisk and their performance accuracy correlates with the energy put into whisking; whisking paralysis induced by motor nerve lesion annuls performance and rats continue to perform the task at high accuracy with only a single intact whisker on each side^{25,27}. These behavioural findings suggest that the encoding of horizontal location depends on kinetic information that is fully available from individual whiskers. This is in agreement with a coding scheme that involves temporal comparison between a touch signal and a reference whisking signal; the same data argue against either spatial-coding or rate-coding schemes. By contrast, when determining an object’s radial location, rats suppress whisking; whisking paralysis does not impair performance and accuracy depends on the number of intact whiskers²³. These observations indicate that radial location encoding is independent of whisking-related signals but seems to be based on contact-evoked firing rates of primary sensory touch neurons. The single-cell strength of the signal for radial location is weak, with just a subset of cells reliably reporting radial location differences equivalent to 30% of the whisker length³². This low encoding resolution explains why rats require large numbers of whiskers: the overall signal strength can be improved by pooling the signals from multiple touch cells that are associated with the set of contacting whiskers.

Thus, single-cell recordings in anaesthetized rats and psychometric and motor constraints observed in behaving rats are consistent with a space–time–rate triple-coding encoding scheme of object location. Demonstrating the operation of this encoding scheme in awake, behaving rats at the neuronal level remains a challenge.

‘What’ in the whisker sensory system

It is natural for whisking animals to make behavioural choices according to the identity of the objects palpated by their whiskers. For example, under laboratory conditions, when rats are faced with two platforms, each covered with a different texture, they can easily learn to identify the reward-associated texture and jump onto the correct platform^{3–6}. In tasks such as this, the high accuracy of the rats’ judgments, combined with the short amount of time between first whisker contact with the platforms and the onset of the behavioural action (as little as 100 ms), indicates that whisker-mediated object identification is enormously efficient; as such, the neuronal mechanisms underlying this capacity can provide crucial knowledge to neuroscientists investigating other sensory modalities and to the field of biomimetics, which aims to develop biologically-inspired artificial tactile systems.

Judgment of shape. Shape is an important clue about the identity of an object. In an experiment that set out to determine whether the whisker sensory system can support shape discrimination, rats were trained in the dark to judge the shape of small (less than 1 cm) cookies that were distributed on a table in front of them². All but one of the cookies possessed the same shape and contained caffeine, a bitter but odourless substance that is aversive to rats. One cookie had a different shape and did not contain caffeine and was therefore edible. Rats learned to identify the untainted cookie by quickly palpating each cookie with the small whiskers around the nose and mouth (the so-called microvibrissae). At the time of this groundbreaking study, high-speed video was not available to document whisking, but whisking as a means of reconstructing shape has been documented more recently by observation of the Etruscan shrew (FIG. 4a) through high-speed video in the dark⁴⁵. This animal, the smallest terrestrial mammal, identifies prey (crickets) and selects its bite location possibly after a single whisk on the potential target. Shape cues, such as the cricket’s legs, guide the behaviour (FIG. 4b,c).

It is likely that rats use their longer and more widely spaced posterior whiskers (macrovibrissae) to judge the form of objects that are too large to be spanned by the grid of microvibrissae. Though there are as yet no observations of whisker dynamics during shape judgement, it was recently proposed that whiskers have a role in this process. The hypothesis was based on data obtained from an artificial whisker apparatus³⁴ in which the bending of a whisker-like fibre varied as it was swept along a surface — the fibre straightened slightly when it extended into cavities and curved as it passed over protuberances. The torque acting on the fibre was read off from a strain gauge at the base of the fibre and, after many sweeps, a good approximation of shape features could be reconstructed. Because it is likely that the whisker follicle contains sensory receptors to encode torque, the analogous strategy could be the starting point for shape recognition.

Temporal code

A coding scheme where not only the rate of action potentials is informative, but also their firing pattern. Two stimuli which evoke the same firing rate may be discriminated if they evoke unique firing patterns.

Spatial-coding

A coding scheme where the position of the active neuron carries critical information. For example, if C3 neurons fire, the stimulus location is specified as being in the trajectory of the C3 whisker. This type of coding is sometimes called ‘identity coding’.

Rate-coding

A coding scheme where a stimulus’ quality, such as its intensity, is transmitted by the quantity of spikes emitted per unit of time.

Microvibrissae

Short (few mm), densely spaced (87 per cm²) whiskers located on the anterior part of a rat’s snout. They are not ordered in a regular grid and exhibit little or no whisking motion.

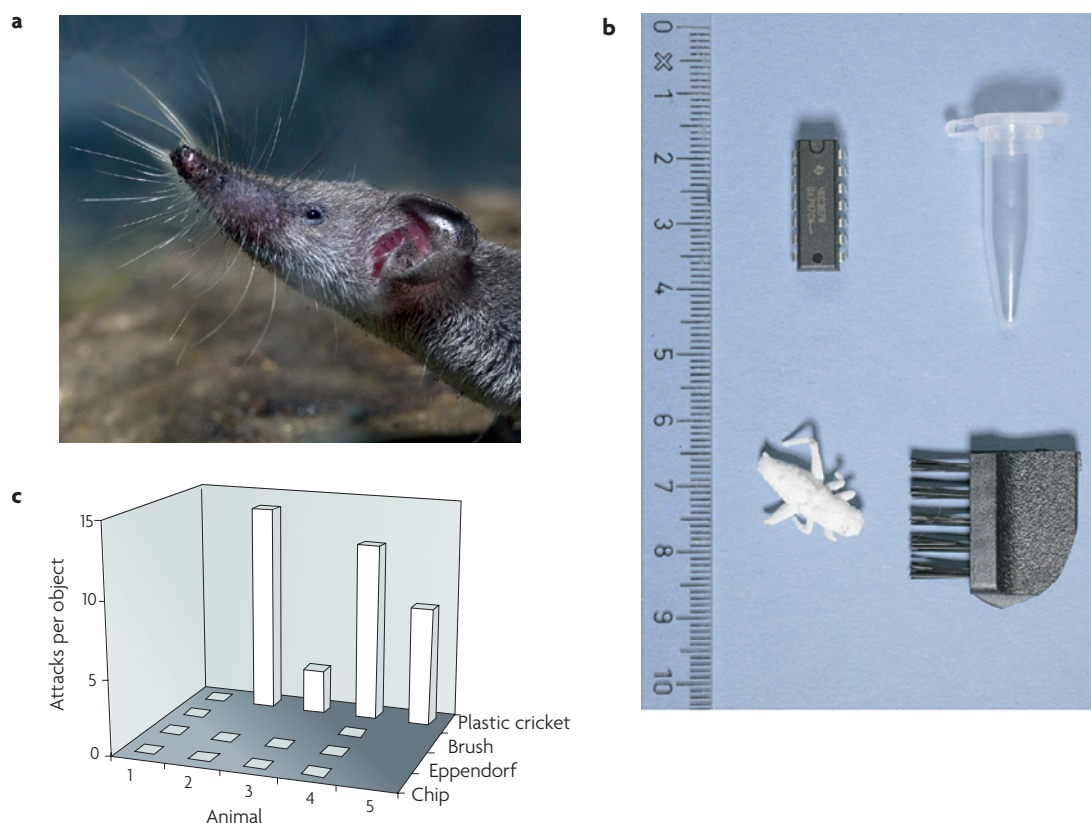


Figure 4 | Object recognition by shape. **a** | Whisker-laden snout of the Etruscan shrew. **b** | Objects placed in an arena near a hungry shrew. The arena was lit only with infrared light, in which the animal cannot see. One object was shaped like a cricket, the preferred prey of the shrew. **c** | Shrews attacked plastic crickets, but not other objects, after palpating them with their whiskers, indicating that shape is both necessary and sufficient to trigger an attack. Animal number 1 failed to attack the plastic cricket, which had lost some of its shape cues in previous encounters; the same animal did, however, attack newly made plastic crickets in a later stage (data not shown). Panel **a** © Dietmar Nill/linea images. Panel **b** and **c** were modified, with permission, from REF. 45 © (2006) National Academy of Sciences.

Judgement of texture. Texture is another physical property that can be a reliable clue about the identity of an object. For example, the walls and floors that rodents contact as they navigate, and the materials they use in nest building⁴⁶, are all characterized by small-scale surface features. One way to test texture discrimination is to train an animal to associate each of two textures with a specific action^{3,4}. This approach has shown that rats can learn to associate one of the textures with a reward and by whisker palpation can reliably discriminate a smooth surface from a rough surface containing shallow (30 μm) grooves that are spaced at 90 μm intervals³. It has been proposed that the capacity of the rodent whisker system to distinguish texture is comparable to that of fingertips in primates^{47,48}, though direct comparisons do not yet exist.

In a recent study⁶, 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. In each trial, the rat had to identify the texture — either smooth or rough — and then withdraw and turn to a water spout to receive a reward. The texture indicated whether the reward would be presented to the left or right of the rat (FIG. 5a). As the rat probed

the texture, whisker motion was filmed with high-speed cameras (FIG. 5b). Texture identification was efficient and accurate. On a typical trial, an individual 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 contacted texture.

Neuronal encoding of texture. Although the barrel cortex is known to be essential for the discrimination of texture⁴, the neuronal representation of texture has been difficult to uncover⁵. A first clue came from experiments in which the whiskers of anaesthetized rats were made to move by electrical stimulation of the motor fibres that innervate the whisker muscles⁴⁹. Movement of a whisker across a given texture gave rise to a vibration at the whisker base with a kinetic signature that was characteristic of the contacted surface and that was defined by the temporal profile and temporal integral of whisker velocity^{49,50}. With these texture-induced vibrations

Kinetic signature

The temporal profile of a whisker's movement as it slides across a texture. It is characteristic of the texture, modulated by sliding speed and whisker length (among other factors), and appears to be quite robust.

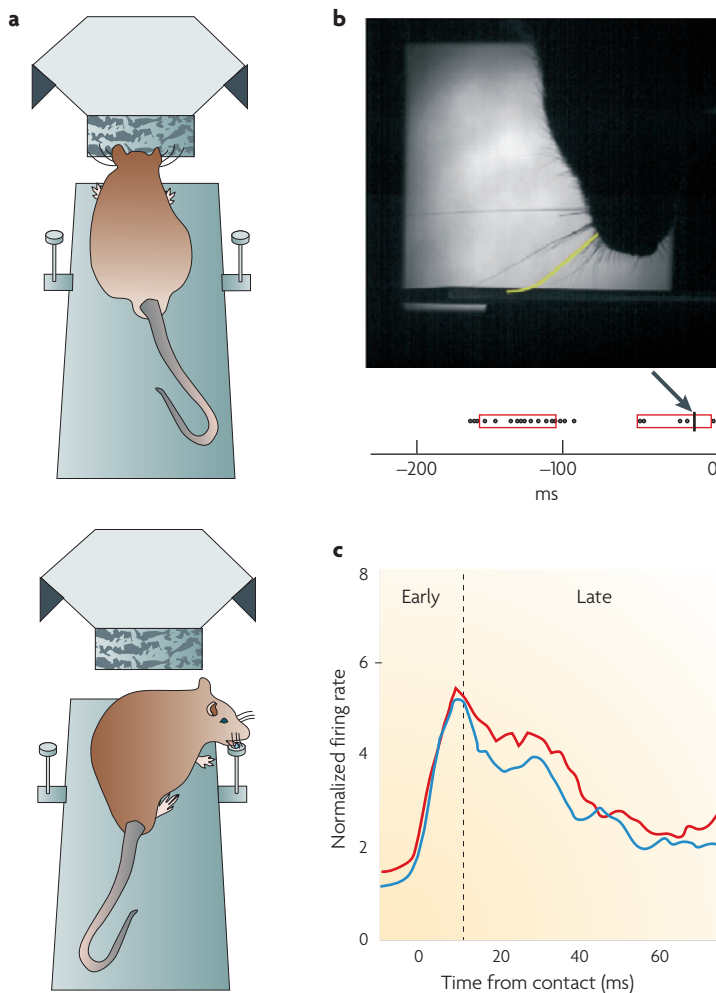


Figure 5 | Texture discrimination task. **a** | Upper panel: the rat extends to touch the texture (textured rectangle) with its whiskers. Lower panel: having identified the texture, the rat turns to the drinking spout on the right to receive a water reward. **b** | Captured by a high-speed camera under infrared light, the rat touches the textured plate with whisker C2 (yellow). Below the film frame, the spike train recorded from barrel C2 on this trial is shown. The red boxes indicate the touch times and the arrow points to the time at which the image was captured. 0 ms is the moment the rat withdrew from the plate. **c** | Dynamics of the neuronal response during whisker contact. Whisker contacts with the textured plates were documented from high-speed films simultaneously with recordings of neuronal activity in the barrel cortex. The instant of whisker contact was set at 0 ms. For both textures, the firing rate increased rapidly immediately after contact (4–11 ms, ‘early’). Subsequently (‘late’), the response patterns separated according to texture: a significantly higher firing rate was found for rough (red) compared with smooth (blue) textures. Figure modified from REF. 6.

Principal whisker
The whisker that upon stimulation evokes the strongest response in a given sensory neuron.

presented as stimuli, the responses of sensory receptors and neurons in the whisker area of the cortex were recorded. This uncovered two potential coding mechanisms by which texture might be represented: textures with similar overall coarseness were discriminable by distinctive, temporally precise firing patterns, whereas textures of significantly different coarseness were distinguished by firing rate — rough textures evoked more spikes than smooth textures⁵¹.

In awake, freely behaving rats, stimuli are generated by the animal through its own whisker motor programme. To test whether the results from the studies in

anaesthetized rats described above are applicable to awake behaving rats, animals were trained to perform texture discriminations while neuronal activity (single- or multi-units) in the barrel cortex was measured⁶. The specific aim of this experiment was to verify the prediction that roughness was encoded by the firing rate of barrel cortex neurons⁴⁹. Based on the well-known connection between one cortical barrel and its topographically matched whisker (reviewed in REF. 12), spikes could be aligned to the moment of contact of the principal whisker with a textured surface, as judged from high-speed films (FIG. 5b). The responses were then divided into two separate traces that corresponded to whisker contacts with rough and smooth textures, respectively (red and blue trace in FIG. 5c); during the initial, sharply rising response phase (4–11 ms, marked ‘early’ in FIG. 5c), there were no significant texture-related differences in neuronal firing. However, in the second phase, neurons showed a greater firing rate in response to their whiskers’ touching rough surfaces (red trace) compared with smooth ones (blue trace). This result suggests that the firing rate might be the fundamental coding mechanism for texture. However, this conclusion rests on the assumption that a rat can decode neuronal activity in precise temporal alignment with individual whisker contacts. Thus, in a second analysis no precise knowledge of whisker contact times was assumed: neuronal activity was measured before the rat made a behavioural choice, that is, before the moment when it stopped examining the texture. Neuronal activity during the last 75 ms before the animal made a choice transmitted the most informative signal; in this window, neuronal clusters carried, on average, 0.02 bits of information about the stimulus.

Analysis of trial-to-trial variability of the posited neuronal coding feature is a powerful approach for learning how cortical activity guides behaviour⁵². In the texture discrimination task, an examination of the neuronal responses in trials in which the rat misidentified the texture revealed that, in contrast to correct trials, neuronal firing rates were higher in response to contact with smooth rather than rough textures. An analysis of high-speed films suggested that in incorrect trials the inappropriate signal was due, at least in part, to non-optimal whisker contact. These experiments clearly point to the firing rate of barrel-cortex neurons in each trial as the critical neuronal feature underlying the animal’s judgement of texture. However, the features of whisker motion that encode texture during active stimulus discrimination are currently subject of debate^{53–55}.

Sensorimotor integration

In the sense of touch, it is the motion of the sensory receptors themselves that leads to an afferent signal — whether these receptors are in our fingertips sliding along a surface⁵⁶ or in a rat’s whisker follicles as it palpates an object. Thus, tactile exploration entails the interplay between motor output and sensory input. Just as we 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

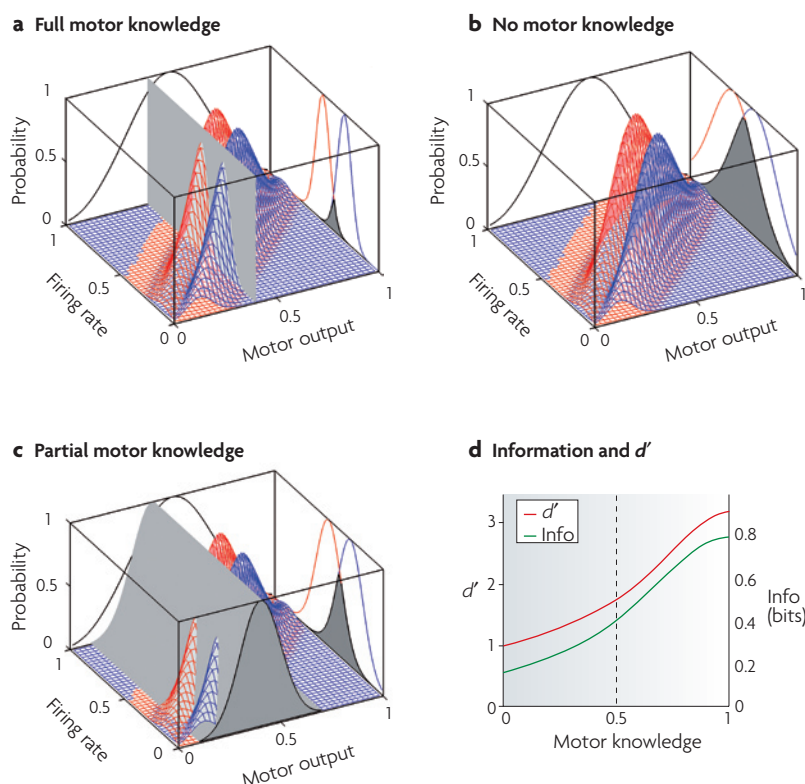


Figure 6 | The role of motor signals in decoding sensory inputs. Illustration of a model of active sensorimotor integration for an animal that has to discriminate between two objects according to the size of the neuronal response that is evoked by whisker contact with the objects. The model assumes, first, that the greater the difference in spike counts that are associated with two stimuli, the more reliable the resulting discrimination; and, second, that for contact with a given object, a stronger motor output leads to a higher firing rate. In panels **a–c**, the z-axis depicts the probability distributions for firing rate (x-axis) and motor output (y-axis) for rough (red) and smooth (blue) textures. **a** | For a precisely known motor output (vertical slice), the firing-rate distributions are given by the conditional distributions, which are projected on the right wall of the graph. **b** | If the motor output is unknown, the firing rate is distributed following the marginal distributions, shown on the right wall. Note the much greater variance and overlap. **c** | If the motor output is known with some Gaussian uncertainty, the firing rate is distributed following a weighted average of conditional distributions, visualized here by an intersection with a Gaussian distribution. The resulting firing-rate distributions, projected on the right wall, have an intermediate degree of overlap. **d** | d' and information (Info) of firing rate about texture is shown as a function of motor knowledge. A value of 0 corresponds to no motor knowledge (as in part **b**), 1 is full knowledge (as in part **a**) and 0.5 corresponds to the level of partial knowledge (shown in part **c**).

information about the movement that generated the tactile signal to begin with. In the whisker sensorimotor system, the perturbation of the whisker movements that result from contact with an object gives rise to sensory signals that carry information about the object. In earlier sections, we reviewed evidence that rats localize objects by combining contact-evoked afferent signals with self-generated motion signals. Here, we present a simple model of active sensorimotor integration where the animal must discriminate between two objects according to the size of the neuronal responses that are evoked by whisker contact with the objects. It is based on two biologically plausible assumptions. First, the greater the difference in spike counts that are associated with two stimuli, the more reliable the resulting discrimination.

d'
(d prime). A measure of the discriminability of two stimuli. If the stimuli differ with respect to some quantity, d' is defined as the difference between the means divided by the standard deviations.

Second, for contact with a given object, a stronger motor output (where strength refers to a combination of motor variables — for example, the amplitude and speed of a whisk) leads to a higher firing rate.

To examine the role of self-induced motion in object coding, we will consider the discrimination of surface texture (FIG. 6). According to evidence presented in the section on neuronal encoding of texture (FIG. 5), contact with a rough surface produces, on average, a higher firing rate than contact with a smooth surface. Accordingly, in FIG. 6 the two textures are associated with the high-firing rate distribution (red) and the low-firing rate distribution (blue), respectively. However, a greater number of spikes is evoked by a strong whisking movement than by a weak one. Thus, the red and blue response probability distributions predict progressively higher firing rates as the strength of motor output goes from 0 to 1.

Let us assume an ideal 'decoder' of sensory signals that has perfect knowledge of the motor output. This would eliminate any uncertainty along the motor dimension, and the firing rate on any given trial would then be predicted by a 'slice' through the red and blue surfaces (FIG. 6a). The sharp separation between the rough and smooth response distributions enables efficient decoding. With the parameters chosen in the model, and provided that the decoder has exact knowledge of the motor output in every trial, $d' = 3.20$ and the information that is carried by the firing rate in each trial is 0.80 bits. One 'bit' corresponds to complete knowledge of the motor output in a task with two possible outcomes; a value of 0.8 bits means that the firing rate allows a correct inference of texture in 97% of trials. With complete motor knowledge, the intrinsic response variance is the only remaining source of uncertainty. This variance is reflected by the fact that even when an immobile animal passively receives repeated stimuli of an identical texture, neuronal responses differ across trials⁴⁹ due to the noise that is generated along the afferent pathway and to fluctuations in the excitability of the receiving cortical population^{57,40}.

If no knowledge of the motor output is available (FIG. 6b), the sensory response in any given trial must be decoded using the rough and smooth response distributions encompassing the full motor range; these are shown projected on the right wall of the graph. When neuronal responses from an awake, behaving rat are analysed with no independent signal from the motor system, the experimenter's decoding algorithms operate in this manner; this is the situation in the experiment depicted in FIG. 5. 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 (FIG. 6c) would occur in situations in which the barrel cortex receives information about whisking strength, but in which the received motor signal does not exactly match the actual whisker motion and/or cannot be perfectly integrated into the sensory system. In this case, the expected sensory response corresponds to a Gaussian-shaped slice through the two parallel elevations (FIG. 6c). The resulting response distributions are again projected on the right wall. In our model, $d' = 1.76$ and the information is 0.41 bits.

As the decoder has access to progressively greater knowledge about the whisking signal that evoked the sensory response, both d' and information (bits) about the texture increase (FIG. 6d). The model makes a precise prediction: as soon as we are able to measure a rat's motor output, either by tracking the whiskers or by electromyography, we will be able to explain much of the trial-to-trial variation in the contact-evoked firing rate. Once we compensate for the variation created by the motor output, only the variation that is associated with the stimulus remains. This signal would be expected to give a much better read-out of the contacted object than the 'motor-ignorant' signal that has been analysed previously⁶. Although here the model was applied to texture discrimination, the main idea can be applied to any two distributions. For example, a high firing rate could encode contact with a pole or wall that is positioned close to the snout and a low firing rate could encode contact with an object that is located farther away from the snout (small and large radial distance, respectively).

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^{7,11,39,58,59}. Second, the sensory pathway itself might carry afferent signals about whisker motion through the whisking cells described above^{29,36}. In general, anatomical and physiological evidence^{60,61} indicates that the barrel cortex is a direct participant in the motor network (BOX 1).

Future directions

Along with continuing work on the fundamental mechanisms of synaptic integration (reviewed in REFS 12,13), three problems strike us as particularly important in understanding how the brain of actively whisking animals builds up a representation of the surrounding world.

The first problem is the characterization of how whisker dynamics are reported by neuronal activity in behaving animals. This problem is complex owing to the large number of mechanical parameters that define the state of the whisker (such as position, velocity, speed, acceleration and torque, all in three dimensions) and that could, potentially, be encoded by neurons. Different neurons might encode different features. Although there has been progress in quantifying which elements of natural whisker motion evoke spikes in the sensory pathways of anesthetized animals^{29,49,62}, it has proven difficult to record a large enough number of spikes in awake rats and at the same time accurately monitor the whiskers. Neuroscientists have not yet identified in a rigorous, quantitative manner which features of the environment are reported by neurons of any sensory modality in an awake, freely moving mammal, but this is a realistic goal for researchers of the whisker sensory system.

As a second problem, we pose the question of whether the animal forms explicit representations of the identity of the things it touches ('what') and of the spatial coordinates of these things ('where') through separate cortical processing streams. In visual cortical processing, both the dorsal 'where' processing stream and the ventral 'what' processing

stream use elemental information from the primary visual cortex about the orientation, size and shape of objects, and about their spatial relations. However, the two streams 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 — many inferotemporal neurons respond to the identity of a face even if the visual field position or viewing angle of the face is altered⁶³. In parallel, the dorsal stream transforms visual information into representations of the configuration of objects within egocentric frames of reference, thereby mediating goal-directed acts⁶⁴. 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 a sphere or cube. Yet the same coordinates translate to object location and thereby instruct the animal's quickest pathway around the object to the food. By analogy with vision, within 'what' and 'where' processing streams in touch, the neuronal response to features of one type will not be affected by changes in features of the other type. Our prediction is that in stations along the 'what' pathway, neurons will be found to encode 'cube' or 'sphere' independently of the objects' spatial coordinates, whereas in stations along the 'where' pathway, neurons might encode 'move left' or 'move right' independently of the object's identity. Both streams would contribute to the general transformation of neuronal representations from stages at which they encode physical signals to stages at which they encode the identity of an object and the actions required by the presence of that object. Where in the whisker system such separation begins is an open question¹⁹. Emergence of functional streams from higher-order cortical processing is one possibility, but an alternative possibility needs to be considered: the richly varying assortment of receptors in the follicle make it a possible starting place for separate functional streams. Some receptor types may generate signals that are crucial for one functional stream but not the other.

The third problem, which is inseparable from the first two, is to elucidate how neuronal representations are transformed from stages at which they encode physical signals to stages at which they encode things that are meaningful to the animal. What matters to the survival of a rodent, after all, is not only the capacity of its neurons to encode whisker kinetics, but also the ability to determine the identity of the object that induced the kinetics — mouse trap or cheese? It has been argued convincingly that this transformation is a primary function of cortical processing⁶⁵. 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 that must be taken.

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Recording of electrical activity
generated by the muscle.

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FURTHER INFORMATION

Mathew Diamond's homepage: www.sissa.it/cns/tactile

SUPPLEMENTARY INFORMATION

See online article: [S1](#) (movie)

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CORRIGENDUM

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