

# Orthogonal coding of object location

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**It has been argued whether internal representations are encoded using a universal ('the neural code') or multiple codes. Here, we review a series of experiments that demonstrate that tactile encoding of object location via whisking employs an orthogonal, triple-code scheme. Rats, and other rodents, actively move the whiskers back and forth to localize and identify objects. Neural recordings from primary sensory afferents, along with behavioral observations, demonstrate that vertical coordinates of contacted objects are encoded by the identity of activated afferents, horizontal coordinates by the timing of activation and radial coordinates by the intensity of activation. Because these codes are mutually independent, the three-dimensional location of an object could, in principle, be encoded by individual afferents during single whisker-object contacts. One advantage of such a same-neuron-different-codes scheme over the traditionally assumed same-code-different-neurons scheme is a reduction of code ambiguity that, in turn, simplifies decoding circuits.**

## Introduction

Twenty years ago, the question 'what is the neural code?' was frequently heard in the corridors of neuroscience departments. Unlike the genetic code, which maps specific tri-nucleotide sequences to specific amino acids, no single neural variable has been found that consistently maps specific activity patterns to specific internal representations. Moreover, research conducted during the past twenty years indicates that the aforementioned question is ill-posed because well-posed coding questions should specify the external coded quality, the encoding system and the neuronal level in that system.

Neural codes for specific qualities, systems and levels range from the simple to the complex. In some cases, the presence of action potentials unequivocally signals a specific stimulus, such as a noxious one. More typically, however, action potentials additionally encode the intensity, timing or spatial characteristics of a stimulus. In principle, different attributes of external objects can be encoded, at each neuronal level of a given sensory system, by different neurons using the same code, by the same neurons using different codes or by different neurons using different codes.

Here, we review recent advances in understanding how primary afferents of the rodent vibrissal (whisker) system encode the three-dimensional location of objects. Sensory information from a single whisker enters the nervous system via 200–400 afferents that are activated when

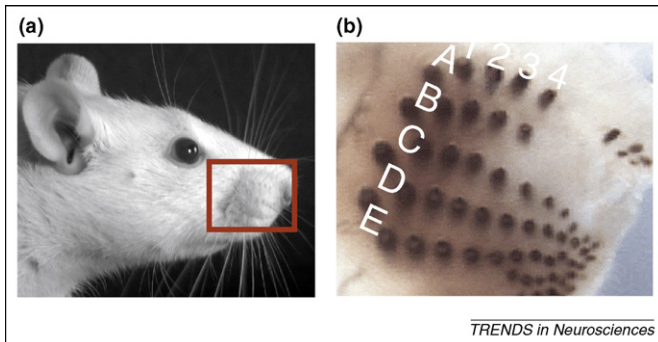
the whisker is actively moved or contacts an object. After contact, the whisker bends and vibrates [1], activating mechanoreceptors within the whisker follicle [2]. By recording the activation of individual primary afferents when the whisker is moved in a controlled but naturalistic manner in anesthetized rats, and monitoring whisker movements and performance of rats during localization of objects, we have begun to understand the principles of neural coding in the vibrissal system. Here, we review evidence that primary afferents of the vibrissal system employ an orthogonal coding scheme to represent the location of objects.

## Principles of encoding object location

Rats possess a specialized system for active touch. The mystacial pad contains ~35 large whiskers (vibrissae) arranged in five rows and seven columns (Figure 1). One salient function of the whiskers is object localization. By sweeping their whiskers back and forth at rates of 5–20 Hz, rats efficiently scan the environment and localize objects within a few whisking cycles [3–5]. The location of an object, or whisker, can be represented in several coordinate systems. Here, we primarily refer to head- and whisker-related Cartesian or spherical coordinates (Box 1). Cartesian coordinates are specified by three spatially orthogonal axes: the (i) rostrocaudal (horizontal), (ii) dorsoventral (vertical) and (iii) mediolateral (radial) axes. Spherical object coordinates are specified in terms of azimuth, elevation and radial distance. Transformations between these coordinate frames are straightforward (Box 1) and we discuss encoding in both in parallel.

In principle, the coordinate of an object along each axis could be represented by different neural codes, each belonging to a different encoding domain. Four such domains are space, intensity, time and posture. Spatial encoding is based on the distribution of activated sensory neurons, intensity coding on the amount of sensory activation, temporal coding on the timing of activation, and posture coding on whisker posture during contact. Additionally, different combinations, or derivatives, of these variables could encode object location.

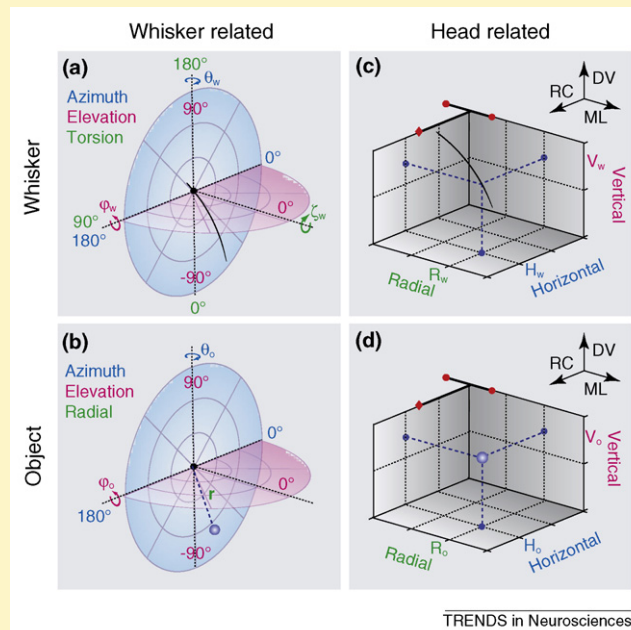
The simplest implementation of a spatial code is coding by neuron identity, known as a 'labeled-line' scheme, in which every neuron is associated with one sensory event. During object localization, labeled-line coding assumes that a specific cell is exclusively activated when an object is contacted at a particular location. Because primary sensory neurons are connected to only one whisker, these cells do encode the identities of the whiskers that contact an object. Thus, if the identity of contacting whiskers relates to object location, primary neurons will encode



**Figure 1.** (a) The whiskers of the rat mystacial pad (red rectangle) are organized in (b) five rows (A–E) and four or more arcs [38]. Four stragglers appear to the left of the letters.

### Box 1. Coordinates of whisker orientation and object location

Several body parts are involved in positioning the whiskers in space, including the body, head, mystacial pad and the whiskers' follicles. Each of these can be rotated or translated by a specific set of muscles and according to a specific frame of coordinates. Transformations between one coordinate frame to another are required when external objects, localized by one system (e.g. whisker), are approached by another system (e.g. mouth). **Figure 1** describes coordinates of whiskers and external objects in two coordinate frames: whisker related and head related.



**Figure 1.** (a) Whisker coordinates in a spherical, whisker-related reference frame. The orientation of a whisker in space can be described relative to its virtual pivot point (black dot at the origin) by the spherical coordinates azimuth  $\theta$  (magenta), elevation  $\varphi$  (green) and torsional angle  $\zeta$  (blue) [15]. (b) Object coordinates in a whisker-related reference frame. The position of an external object (purple ball) can also be described in spherical whisker-related coordinates, but with the radial distance from the pivot point replacing torsional angle. (c–d) Whisker and object coordinates in a Cartesian, head-related reference frame. The position of any point along the whisker shaft (c), or that of an object (d), can be described relative to the head, indicated here by the position of the eyes (red dots) and nose (red diamond) and by its horizontal (rostro-caudal; H), vertical (dorso-ventral; V) and radial (medio-lateral; R) coordinates. Subscripts denote whether the angles or positions refer to whisker (w) or object (o) coordinates.

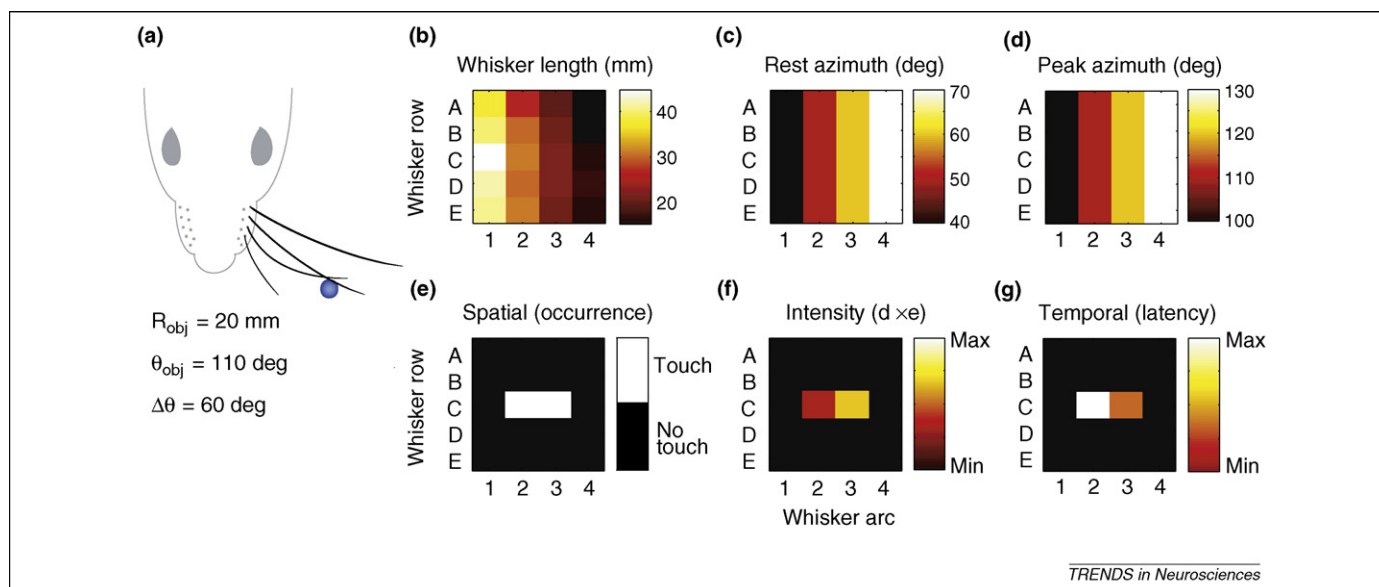
location by labeled lines. This is illustrated in **Figure 2**, which demonstrates different encoding schemes when a realistically sized whisker array protracts from a typical resting angle and encounters a small object at the height of row C. When all whiskers synchronously protract, only whiskers in the row at the same elevation as the object can contact the object. The resulting identities of contacting whiskers, thus, reliably encode the elevation of the object (**Figure 2e**). Additional information about the position of an object can be derived from the intensity of sensory activation. In its simplest form, the intensity code is again a labeled-line, binary code; afferents fire if, and only if, contact intensity (velocity change or bending) passes a certain threshold. More likely, however, is that afferents respond with a rate function; higher contact intensity result in more spikes being emitted by the afferents [6]. Coding of object position by intensity is illustrated in **Figure 2f**, in which sensory activation is assumed to be proportional to the degree of protraction upon contact. In this scenario, the azimuth of the least-protracted contacting whisker (C2) is closest to the azimuth of the object owing to bending of the other contacting whiskers with greater azimuths. Thus, the order of sensory-activation magnitude can map space and action onto different activity levels; the further protracted the whiskers or the closer the object along the horizontal axis, the more intense the sensory activation will be.

Spatial and intensity codes are limited in how accurately they can represent object location because these are discrete codes; spatial codes are carried by individual primary afferents, of which there is a finite number, and intensity codes by discrete spike events. The resolution of such codes can be extended by interpolating across space and intensity (e.g. between activity levels of neighboring whiskers) or by integrating the activity of many afferents. Temporal codes, however, are measured along a continuum and, thus, have potentially higher resolution. Indeed, temporal codes encode stimuli with sub-millisecond precision along the trigeminal pathway [7–9]. Because the whiskers move, the timing of whisker–object contacts and, thus, the timing of afferent activation encodes object position (**Figure 2g**). Relative to other reference events (such as the position signal in **Figure 2d**, internally generated or mechanoreceptor derived) these temporal events encode the coordinate of the object along the movement axis.

The intensity and temporal codes in **Figure 2** depend on motor variables. Motor or proprioceptive signals that indicate whisker posture (e.g. azimuth; **Figure 2d**) can also encode object location when taking into account contact timing and whisker morphology.

### Response characteristics of primary vibrissal afferents

The vibrissal system is composed of many nested motor-sensory loops [10]. This architecture enables rats to dynamically control whisker movement [4,11–16], which rats exploit when performing different tasks [3,5,17]. Although beneficial for the rat, such dynamic control renders successive contacts different from each other [4], which prevents systematic investigation of sensory signals during object localization. To systematically study sensory signals



**Figure 2.** Object location in a head-centered reference frame represented through different encoding schemes. (a) During a typical whisking cycle, the whisker field protracts synchronously, here represented by four whiskers in row C. (b) The length distribution of whiskers drops approximately linear along arcs [39]. (c) In this illustration, all whiskers were assumed to protract 60 degrees (deg) azimuthally from different rest angles to the most protracted positions in (d). (e–g) The effects of contact with a point object for individual whiskers were simulated for different encoding schemes during peak protraction. The object was positioned at a radial coordinate ( $R_{obj}$ ) of 20 mm, 110 deg azimuth and at the vertical level of whisker row C. (e) Coding by identity: during maximal protraction of the whole whisker field, only whiskers C2 and C3 contacted the object. (f) Coding by intensity: the intensity of the contact was estimated by multiplying the identity matrix in (e) by the whisker position matrix in (d). (g) Coding by timing: the order in which whiskers C2 and C3 contacted the object corresponds to a temporal code.

induced by muscle-driven contact, Bagdasarian and colleagues\* eliminated the operation of motor-sensory loops by anesthetizing rats and electrically stimulating the distal segment of a transected motor nerve (Figure 3a) to mimic natural whisker movements [18,19]. This paradigm deviates from classical paradigms using passive whisker deflections (Box 2). During passive movement, mechanoreceptors are activated by external forces applied to the whisker. During active movement, however, mechanoreceptors are activated both by forces owing to muscle protraction and reaction forces generated when whiskers contact objects. This difference leads to significantly different response characteristics of primary vibrissal afferents in the trigeminal ganglion (TG). During passive stimulation, TG cells are selective for deflection direction and velocity and can be characterized as slowly or rapidly adapting [18,20]. During active touch, TG neurons can be grouped into four major categories based on their response characteristics during whisking and touch [19]: contact, pressure, detach and whisking. Contact cells respond briefly and with short latency after a whisker contacts an object (Figure 3b). Pressure cells respond for as long as contact is maintained (Figure 3c). Detach cells respond only when the whisker detaches from the object (Figure 3d). Collectively, contact, pressure and detach cells are referred to as touch cells. The fourth class, whisking cells, respond to movement (Figure 3e) and are not affected by the presence of objects in the distal part of the whisking field; the sensitivity of these neurons to proximal contacts (<50% of whisker length) has not yet been tested. An additional class of cells (whisking/touch) respond during

whisking and increase their firing upon and during touch [19].

### Encoding object location with primary afferents

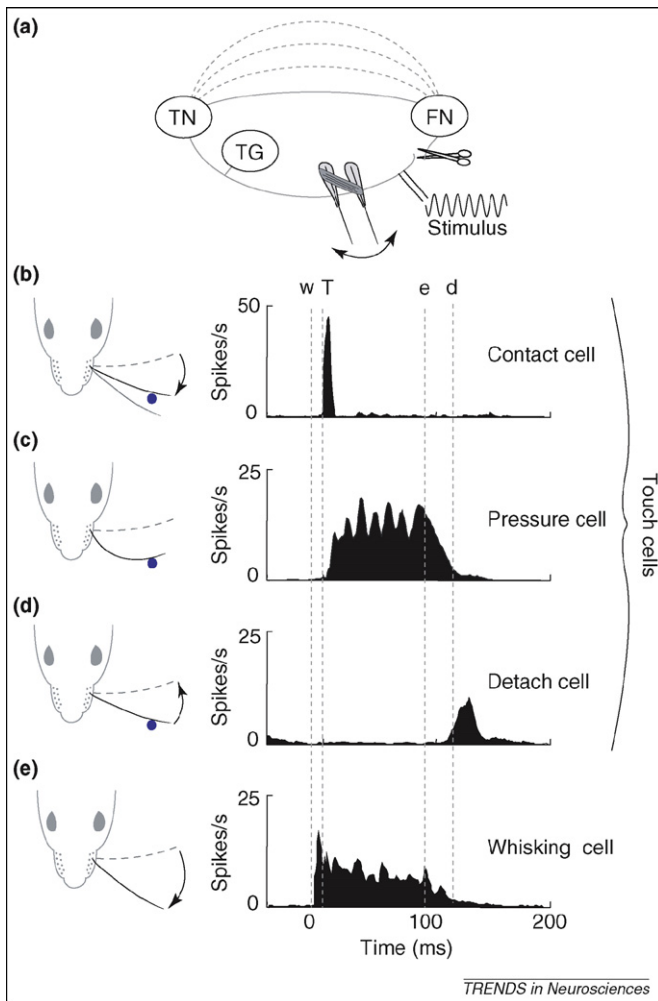
Using artificial whisking, Szwed and colleagues studied how TG neurons encode object position during active touch [19,21]. Encoding of the horizontal coordinate was studied by varying the azimuth angle of an object ( $\theta_{obj}$ ) within the movement trajectory of a whisker (Figure 4a). Touch-responsive cells (primarily contact cells) reliably encode the azimuth angle of the object by the latency from protraction onset to the first emitted spike in a whisking cycle [19], but not by spike count or spiking rate (Figure 4b,c). In order for a temporal code (such as spike latency) to be meaningful, read-out circuits must compare it with a reference signal such as an internal motor copy. A precise reference signal is the re-afferent information signaled by whisking cells (Figure 3e), whose activity is locked to specific phases of the movement cycle [19]. Thus, the azimuth angle of objects can be encoded by the relative timing of TG whisking and touch signals and, later, read out by circuits receiving both signals. The location and exact mechanism of the decoding circuit(s) is unknown; available data indicate that such circuits function downstream to the thalamus [22] and involve the somatosensory cortex†.

Unlike horizontal location, the radial coordinate of objects seems to be encoded by several neuronal variables, the primary being the spike rate of touch cells. When an object is positioned at increasing radial distances (Figure 4d), most touch cells respond with a decreasing

\* Bagdasarian, K. *et al.* (2002) Encoding of radial object position by rat whiskers: recordings from the trigeminal ganglion. *FENS Abstr.* 1, A052.3.

† Curtis, J.C. and Kleinfeld, D. (2006) Confluence of position and active touch in rat primary somatosensory cortex. *Soc. Neurosci. Abstr.* 32, 144–3.





**Figure 3.** (a) Method for artificially inducing whisker movements in the anesthetized rat. Sensory-motor feedback was cancelled by cutting the facial motor (VII) nerve, and whisker movements were controlled by electrically stimulating the distal segment of the nerve [19]. Solid lines indicate known connection and dotted lines indirect connections between trigeminal nuclei (TN) and facial nucleus (FN). During artificial whisking, an object was placed at different locations within the movement path. The most important events in each cycle with the object present (indicated by letters above dashed lines) were onset of movement (w), contact with the object (T), end of stimulation and whisker protraction (denoted with the letter e) and detach of the whisker shaft from the object (denoted with the letter d). TG neurons were grouped into four classes based on response characteristics to these events. (b) Contact cells responded only briefly to contact, but not to any other event. (c) Pressure cells responded to contact for as long as contact was maintained. (d) Detach cells responded only to object detaches. (e) Whisking cells responded to whisker movement and were not affected by object contact or detach. The whisking response was present regardless of the presence or absence of the object. Responses of a subpopulation of cells responding to whisker movement were augmented by object contact (whisking/touch cells, not shown). Adapted from Refs [19,21]. Abbreviations: FN, facial nucleus; TG, trigeminal ganglion; TN, trigeminal nuclei.

number of spikes per movement cycle [21] (Figure 4e,f). Other cells encode radial location by distinct thresholds and respond exclusively when the object is positioned at very proximal radial locations. Given the considerable variability between individual cells in their ability to encode radial location and the existence of cells that do not exhibit monotonic dependence on radial position [21], read-out mechanisms for radial location should be based on input from populations of touch cells rather than on individual cells.

The movement direction of the whiskers is along the plane of rows [15,23]. This, and the fact that TG neurons

always have single-whisker receptive fields [24], dictates that when a TG neuron is activated an object must have been present at the elevation of the row the whisker belongs to. Thus, the vertical coordinate of contact is encoded by neuron identity (Figure 1e).

### Behavior and performance during object localization

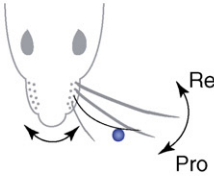
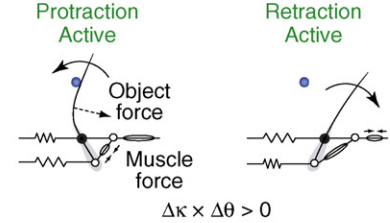
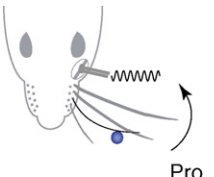
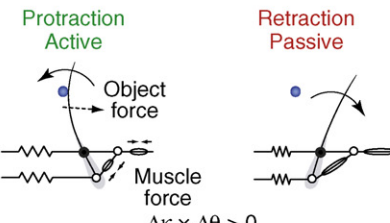
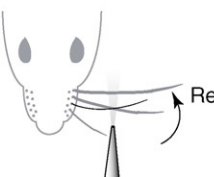
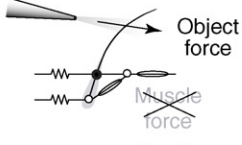
The ability of rats to localize objects, the motor strategies employed and the conditions for localizing along horizontal and radial dimensions has been studied by isolating spatial dimensions and removing sub-sets of whiskers [3,5,25–27]. Such behavioral studies support neuronal-driven hypotheses of how object location is encoded. Knutsen *et al.* [3] trained rats to discriminate the relative horizontal location of two objects (Figure 5a). The ability of the rats to perform such discriminations was correlated with the initial whisker-array configuration used during learning of the task and the amount of whisking, as measured by the spectral power of whisking (Figure 5b). Rats could localize with a single whisker intact on either side of the snout, but only if the rats had initially been trained with multiple whiskers intact. Both with multiple or single whiskers intact, rats reached hyperacuity resolution. That is, rats could localize with a resolution ( $1\text{--}5^\circ$ ) significantly better than the limit imposed by the spacing of adjacent same-row whiskers ( $\sim 20^\circ$ ) [3]. Such performance levels preclude encoding of horizontal location by whisker identity. Instead, the correlation between localization acuity and whisking power indicates that temporal events associated with whisker movement are, as expected from primary afferent responses, important for encoding the horizontal dimension. Indeed, the same study showed that rats that were unable to move their whiskers during discrimination, except through the use of head movements, after bilateral lesions of the facial motor nerves were unable to discriminate horizontal offsets between objects (Figure 5b). In a similar study, hyperacuity performance was not achieved when rats had to determine the horizontal coordinate of a single object without a reference to a second, simultaneously presented object [5]. In such an absolute localization task, which is in essence memory guided, localization acuity ( $\sim 15^\circ$ ) drops to the order of the typical inter-whisker spacing. In an analogy, visual hyperacuity ( $\sim 0.001^\circ$ ) is only achieved when stimuli are localized relative to each other and not when stimuli need to be localized in space without a reference, in which case acuity drops to  $\sim 0.01^\circ$  (i.e. to the order of photoreceptor spacing [28]).

The ability of rats to localize features along the radial dimension has been studied during absolute and relative discriminations. In an absolute, memory-guided task, Krupa and colleagues [26] trained rats to discriminate apertures with varying radial widths as either ‘narrow’ or ‘wide’. In a variation of this task, Schuler *et al.* [27] trained rats to make relative, bilateral discriminations and judge the two walls of the apertures as ‘equidistant’ or ‘non-equidistant’ (Figure 5c). During performance of both tasks, whisking was absent and whiskers brought in contact with the walls primarily through head and body movements. Performance during absolute radial localization was reliable even after complete facial motor-nerve lesions

Box 2. Active versus passive touch

During naturally, self-generated whisking by freely-moving animals, both whisker protraction and retraction are active and controlled by groups of intrinsic and extrinsic muscles [11,40]. Forces, thus, act directly on the whisker follicles both upon contact and detach with an object (Figure 1a). Upon contact with an object (blue sphere), contacting whiskers bend as a function of whisker material properties, head-position, muscle forces and object location. Thus, not every contact yields identical whisker curvatures. How rats exploit this to encode object position is unknown because response features of primary afferents in behaving animals have not yet been characterized. Clues to how afferents encode object position can be obtained from artificially whisking anesthetized rats. Artificial whisking is generated by electrically activating the facial motor nerve [19] (Figure 1b). This method activates all muscles simultaneously and, thus, does not preserve the normal phase relationship between muscles associated with protraction or retraction [11]. The net outcome of artificial whisking is protraction, although the detailed motions differ somewhat from self-generated whisking. As occurs

during self-generated whisking, whiskers bend upon contact with an object, and both muscular and object induced forces are applied to the follicle-whisker complex. During these conditions, primary afferents exhibit selectivity for either touch or whisking, or both [19]. A common technique for probing afferent activity, which ignores the active nature of vibrissal touch, is deflections of passive, stationary whiskers using mechanical stimulators or air pressure. During such stimulation, no muscles are activated and the whisker is merely deflected from its resting position (Figure 1c). Thus, passive stimulation only mimics the forces applied to the whisker shaft during contact. As a result, the induced mechanical changes are different. For example, passive deflections induce curvature and angle changes in opposite directions, whereas active touch induces curvature and angle changes in the same direction. Owing to these mechanical differences, neural selectivity revealed during active and passive touch is qualitatively different and usually cannot be deduced from each other even when the same neuron is recorded in both conditions [19,21,41,42].

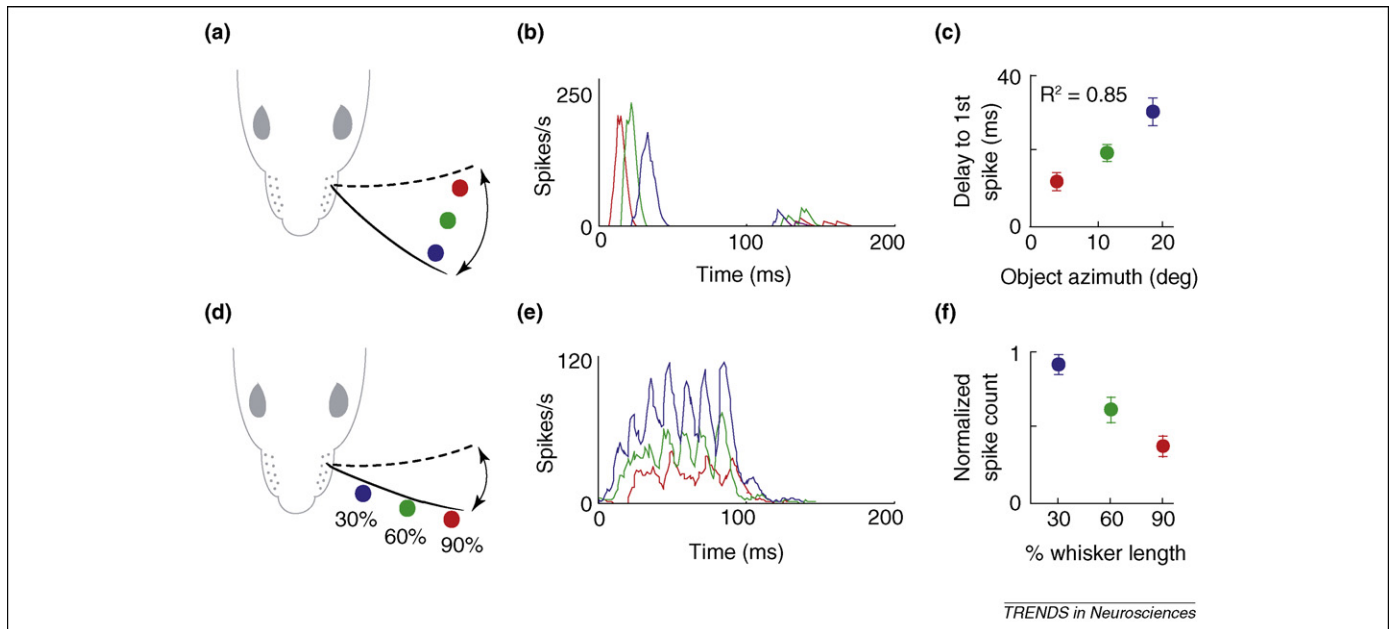
	Control	Mechanics	Selectivity
(a) Self-generated whisking	Adaptive closed loop 	<div>Protraction Active</div> <div>Retraction Active</div>  $\Delta\kappa \times \Delta\theta > 0$	?
(b) Artificial whisking	Open loop 	<div>Protraction Active</div> <div>Retraction Passive</div>  $\Delta\kappa \times \Delta\theta > 0$	Whisking Touch Whisking/touch
(c) Passive whisker deflection	Open loop 	<div>Retraction Passive</div>  $\Delta\kappa \times \Delta\theta < 0$	Slow or rapidly adapting Stimulus direction Stimulus intensity

TRENDS in Neurosciences

**Figure 1.** Three different paradigms of whisker stimulation and the resulting mechanics and neuronal activity. (a) During self-generated whisking, both muscle and contact forces influence whisker mechanics. The neuronal activity of individual primary afferents during such stimulation is unknown (denoted ?). (b) Artificial whisking evoked by direct motor-nerve stimulation enables experimental control of active whisking but does not fully reproduce all aspects of normal behavior. Retraction is initiated by cessation of electrical stimulation and is therefore passive, whereas during self-generated whisking dedicated muscles contribute to fast whisker retraction. Neuronal activity during artificial whisking is highly selective to specific events within the whisk cycle, such as contact and motion. (c) Passive deflection is the most utilized method of whisker stimulation. During passive deflection, muscle contraction is absent and neuronal selectivity is delineated as a function of adaptation time constants, directional tuning and stimulation intensity thresholds. In the left column, Pro and Re denote protraction and retraction, respectively. In the middle column  $\Delta\kappa$  denotes the induced change in whisker curvature and  $\Delta\theta$  the induced change in whisker angle.

(Figure 5d). Performance, however, was significantly affected by the number of intact whiskers available to the rat, although it did not depend on the identity of contacting whiskers [26] (Figure 5d). The fact that whisker movements were not required, and typically not present during radial localization, indicates that temporal cues are not important for radial localization. Furthermore, simple spatial codes, such as a labeled-line code, can be ruled out

because the identities of intact whiskers were not a determining factor for performance. Although measurements of localization acuity were not an explicit objective in the relative radial discrimination study, stable performance (86% correct) was reported only at a radial offset of 11 mm [27]. In the absolute radial discrimination task, rats were capable of discriminating aperture widths as small as 3 mm [26]. Thus, a similar advantage as that conferred

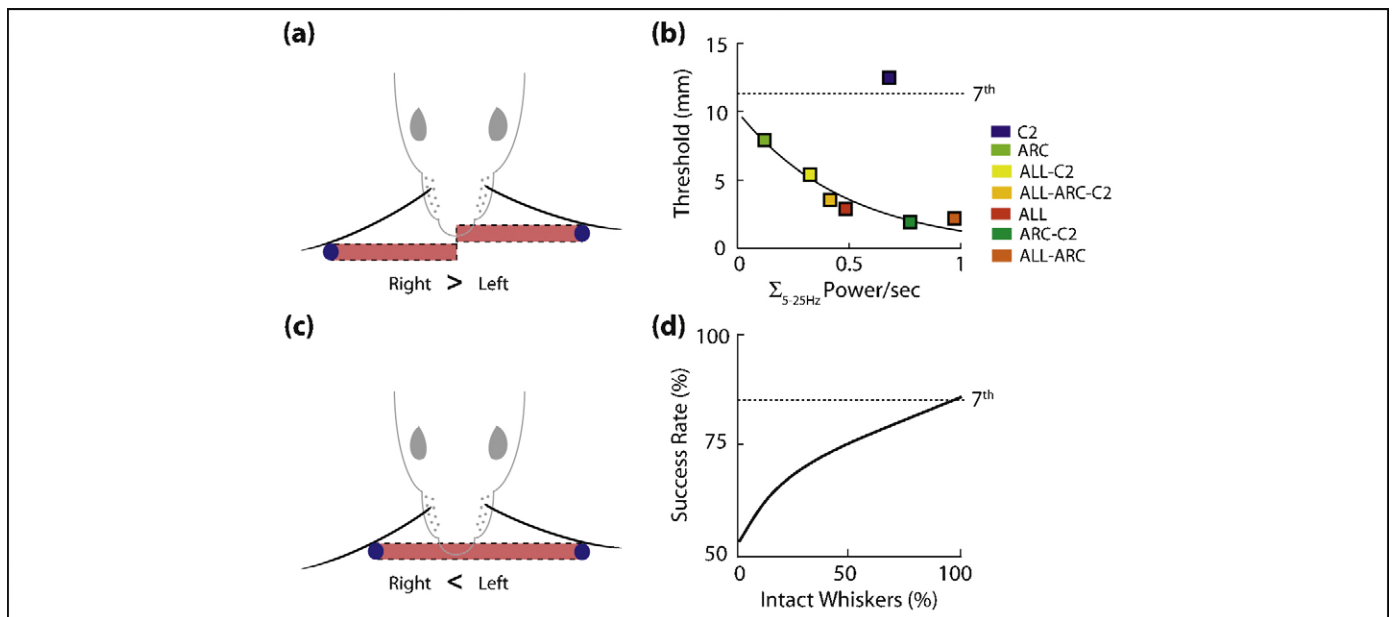


**Figure 4.** (a-c) Touch cells encode the horizontal location of objects. Artificial whisking was induced in anesthetized rats and an object placed at different azimuth angles. Touch cells reliably encoded object azimuth by increasing latency to the first spike with increasing object angle. Average response latencies shown in (c) are for a single touch cell. (d-f) Pressure cells encode the radial location of objects. Pressure neurons encoded the radial location by reducing the net spike count during protraction as the radial location became more proximal. The correlation between spike count and radial location shown in (f) include all recorded pressure cells ( $n = 38$ ). Adapted from Refs [19,21].

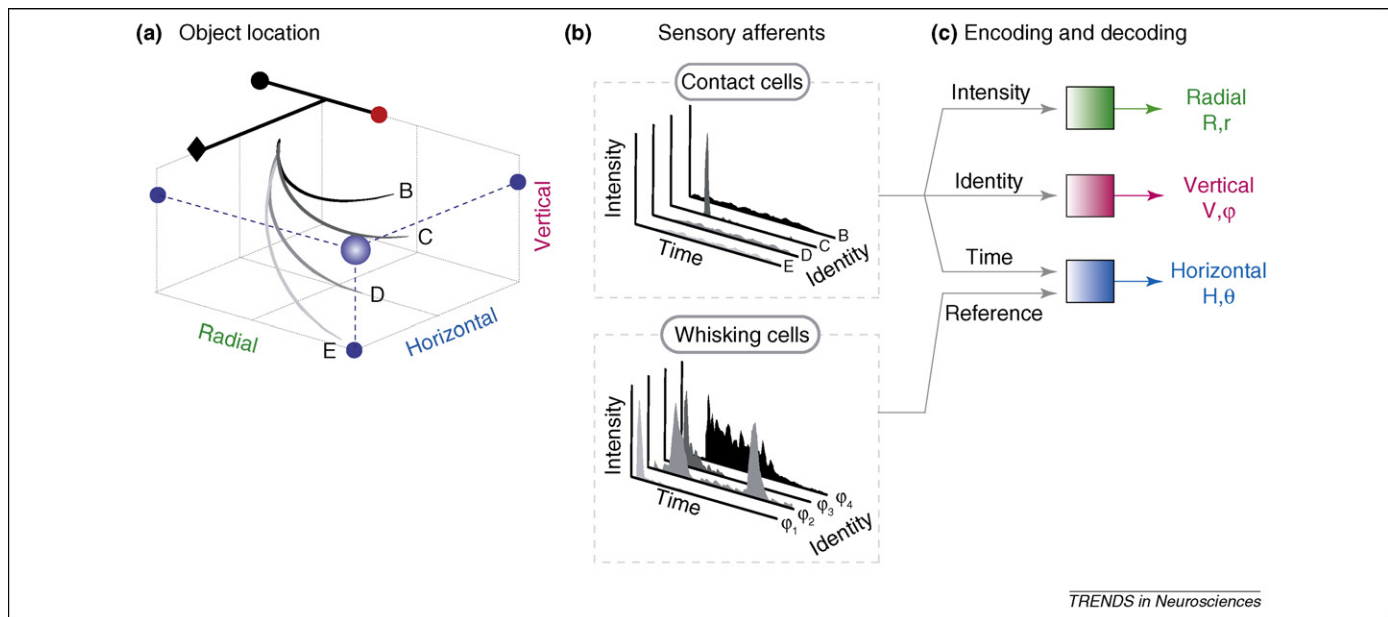
by making simultaneous comparisons between two objects during horizontal localization [3] has not been demonstrated for radial localization. This might be related to the coding scheme used in each case. When sensory acuity depends on movement-dependent temporal cues, acuity can be improved by controlling whisker movements. The actual motor patterns used to acquire the high-resolution data, however, might not be stored in memory and will,

thus, not be available for comparisons during absolute horizontal localization. By contrast, sensory data that do not depend on sensor motion, such as population firing rates that seem to encode radial location, contain all necessary information for future comparisons, albeit with lower resolution.

Coding of different spatial dimensions use different neuronal variables and are optimized with compatible



**Figure 5.** (a) Rats were trained to discriminate the relative horizontal offsets of two vertical poles (blue) [3]. (b) During horizontal object localization, performance did not depend on the number or identity of intact whiskers. Instead, performance was related to the order in which whisker-array configurations were exposed to the task and the amount of whisking executed during test trials. Rats with a single whisker intact are C2, those with an arc of whiskers intact are denoted ARC and those with all whiskers intact are denoted ALL. Colored squares denote the order of whisker-array configurations rats were exposed to. Lesioning the facial motor nerve reduced performance to chance level (dashed line). (c) Rats were trained to discriminate the radial offset between two bilaterally placed objects. The task variations included judging the objects as equidistant or non-equidistant (as shown) [26] or to detect the location of the 'near' or 'far' object (not shown) [27]. (d) Performance during the relative radial object localization was correlated with the number of intact whiskers. Lesioning the facial motor nerve did not affect radial localization performance (dashed line).



**Figure 6.** Orthogonal coding of object location. **(a)** Different whiskers (gray lines) interact with an object differently owing to their lengths or position on the whisker pad. Here, whiskers in rows B–E belonging to the same arc are shown in a protraction position, contacting an object at the level of row C (blue sphere). **(b)** During whisking and touch, the activation of whisking and contact primary afferents can be characterized by the identity of activated cells, the intensity of activation (firing rate or spike-count) and the timing of activation. The onset timing, or phase, of whisking cell activation is typically consistent for a given cell and location but varies across the whisking cell population ( $\varphi_1$ – $\varphi_4$ ). **(c)** When a contact primary afferent is activated, the whisker in its receptive field contacted an object. Because within any given whisking cycle a particular vertical coordinate is scanned only by a subset of whiskers, the firing of a contact primary afferent within that cycle indicates the elevation (vertical coordinate) of the object. The timing of the contact signal, relative to the firing timing of whisking afferents, indicates the azimuth (horizontal coordinate) of the object (Figure 4a–c). The net spike count emitted by the contact afferent during that cycle encodes the radial coordinate of the object (Figure 4d–f).

whisking strategies. Yet, during natural exploration, the location of an object in all three spatial dimensions must be encoded simultaneously to enable targeted actions. In nature, rats must optimize behavior simultaneously across all dimensions. Observations obtained to date indicate that dynamic movement control is probably the most readily available tool for rats to increase acuity in real time and is undoubtedly used by rats while solving challenging tasks.

### Orthogonal encoding of object location

By combining the neuronal and behavioral observations reviewed earlier, we suggest the following encoding scheme for object localization during whisking (Figure 6). In both head- and whisker-centered coordinate schemes, the three orthogonal coordinates, horizontal, vertical and radial ( $\theta$ ,  $\varphi$  and  $r$ ;  $H$ ,  $V$  and  $R$  in Box 1), are encoded using three orthogonal neuronal codes: a spatial code for the vertical (elevation) coordinate, a temporal code for the horizontal (azimuth) coordinate and an intensity code for the radial distance. Intensity coding of radial position is likely to be based on interpolating firing intensity across multiple whiskers. Temporal encoding of horizontal position should use a comparison of contact time with a reference signal of a proprioceptive nature (meaning that the reference signal represents the motion of the whisker), such as (i) the timing of protraction onset or (ii) whisker position at the time of contact. Both these signals are conveyed by peripheral whisking neurons [19] and exist in the somatosensory thalamus [22] and somatosensory cortex [29–31]<sup>†</sup>.

In principle, individual TG touch neurons could convey information about the three coordinates simultaneously

within one whisking cycle. The fact that particular touch cells are activated conveys information about the vertical coordinate of an object, the onset time of firing conveys information about the horizontal coordinate and the intensity of firing conveys information about the radial coordinate of an object (Figure 6). One feature of orthogonal coding is that the output signals of touch cells can be conveyed in parallel to different, specialized decoding (readout) circuits, each of which decodes a particular neural variable. Although the specific read-out mechanisms are yet to be discovered, already-known neural circuits could be used for decoding the signals of touch cells. The vertical coordinate can be read out by threshold detectors, the horizontal coordinate by phase-locked loops or phase detectors [19] and the radial distance by neural integrators, peak detectors, attractor neural networks or synfire chains. Orthogonal coding reduces the ambiguity of afferent signals and, thus, simplifies these decoding algorithms. Through evolution, algorithms can become optimized for decoding a particular variable without dedicating resources to discriminating between input afferents because readout circuits should be specific to a variable but not necessarily to a neuronal population.

### Perceptual coding versus sensory coding: role of motor strategies

Perception is a motor-sensory process, in which motor strategies determine the type and quality of sensory data. Rodents modify their whisking patterns when challenged with different perceptual tasks. For example, for texture identification rats typically employ continuous scanning profiles [32,33], whereas during exploration they seem to employ a minimal impingement strategy by which they



contact obstacles with as many whiskers as possible with very light touch [4]. In whisking rodents, object localization is achieved via body, head and whisker movements [3,5,26]. Thus, the sensory coding scheme described here is only one component involved in the perceptual process of localization. Individual rats can use these sensory codes differently, depending on their motor strategy. For example, during horizontal position discrimination, some rats might employ synchronous bilateral whisking and use the time difference between left and right contacts as a primary cue for discrimination [3]. Other rats might instead contact synchronously on both sides and use the bilateral angular difference as the primary cue for discrimination. Evidently, whisker angle and contact time are crucial in both sensory-motor processes, but each serves as a perceptual cue only in one of the strategies and as a sensory-motor coordinator in the other.

Thus, sensory cues that serve perceptual comparisons are not necessarily the same cues that convey primary sensory data (where by primary sensory data we refer to the manner of receptor activation). Perceptual comparisons depend on motor strategies, which involve multiple levels of sensory-motor control loops encompassing body, head and whisker movements [10], whereas sensory data depend only on the peripheral level of vibrissal interaction with the external world. Thus, a perceptual coding scheme, unlike a sensory coding scheme, must include motor variables in its definition. These motor variables change from task to task and between exploration epochs and whisking cycles. Therefore, with active sensing, perceptual coding cannot be based on fixed internal representations. Rather, during active sensing, internal representations are always functions of both external features and motor activity.

### Conclusive remarks

Neuronal recordings in anesthetized rats and behavioral observations in rats performing localization tasks indicate that the vibrissal sensory organs implement an orthogonal coding scheme to encode object location: spatial coding for vertical coordinates, temporal for horizontal and intensity for radial coordinates. The decoding of object location by internal circuits must consider whisker reference signals. As several motor-sensory strategies can potentially be employed, examination of decoding algorithms should involve awake behaving animals [31–36]<sup>†</sup>. Furthermore, other potential encoding schemes must be examined in more detail. For instance, high-threshold afferents might additionally encode radial location by a labeled-line code [21], and it has been suggested that horizontal location might also be encoded, in part, by a labeled-line code owing to interactions between torsional whisker rotation and directional tuning of afferents [15]. A common requirement for several of the identified, putative codes is active sensing via whisking. The closed-loop architecture of the vibrissal system enables efficient adaptive control of vibrissal touch [4,37]. It remains to be seen to what extent adaptive behavior is, indeed, manifested during perceptual tasks, which motor variables are controlled in given contexts and how they are controlled. Improving our understanding of adaptive behavior will also facilitate our

understanding of how tactile perception emerges during active sensing.

### Acknowledgements

Work in the Ahissar laboratory is supported by the Israel Science Foundation ([www.isf.org.il](http://www.isf.org.il)), the Minerva Foundation ([www.minerva.mpg.de](http://www.minerva.mpg.de)) funded by the Federal German Ministry for Education and Research, the United States-Israel Binational Science Foundation ([www.bsf.org.il](http://www.bsf.org.il)), the Human Frontiers Science Program ([www.hfsp.org](http://www.hfsp.org)) and the EU FP7 BIOTACT project (ICT-215910; [www.biotact.org](http://www.biotact.org)). P.M.K. is a Human Frontier Science Program Long-Term Fellow. E.A. holds the Helen Diller Family Professorial Chair of Neurobiology.

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