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REVIEW

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Object localization with whiskers

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Abstract Rats use their large facial hairs (whiskers) to detect, localize and identify objects in their proximal three-dimensional (3D) space. Here, we focus on recent evidence of how object location is encoded in the neural sensory pathways of the rat whisker system. Behavioral and neuronal observations have recently converged to the point where object location in 3D appears to be encoded by an efficient orthogonal scheme supported by primary sensory-afferents: each primary-afferent can signal object location by a spatial (labeled-line) code for the vertical axis (along whisker arcs), a temporal code for the horizontal axis (along whisker rows), and an intensity code for the radial axis (from the face out). Neuronal evidence shows that (i) the identities of activated sensory neurons convey information about the vertical coordinate of an object, (ii) the timing of their firing, in relation to other reference signals, conveys information about the horizontal object coordinate, and (iii) the intensity of firing conveys information about the radial object coordinate. Such a triple-coding scheme allows for efficient multiplexing of 3D object location information in the activity of single neurons. Also, this scheme provides redundancy since the same information may be represented in the activity of many neurons. These features of orthogonal coding increase accuracy and reliability. We propose that the multiplexed information is conveyed in parallel to different readout circuits, each decoding a specific spatial variable. Such decoding reduces ambiguity, and simplifies the required decoding algorithms, since different readout circuits can be optimized for a particular variable.

Keywords Vibrissae · Whiskers · Active sensing · Touch · Encoding · 3D

1 Introduction

The rat whisker system has been the subject of extensive behavioral and neuronal investigation, initiated by the pioneering studies of Vincent (1912). However, it is only in the last decade that measurement and theory have converged to the point of generating detailed and realistic network-models of sensory processing in this system that take into account mechano-neuronal transduction, primary sensory afferent activation, network dynamics as well as behavioral considerations and behavioral constraints. Here, we focus on recent advances in understanding the computation of the spatial location of objects in the neuronal structures of the whisker system. Critically, as the rat whisker system is an active sensing system, these advances have depended on both behavioral and neuronal measurements.

During exploration, rats use a combination of body, head and whisker movements to effectively comb the environment for interesting features. The immediate space which surrounds the snout of the rat can be geometrically described by any arbitrary set of three orthogonal axes. Here, we have chosen the axes that correspond to the geometry of the whisker pad to describe this space in head-centered coordinates (Fig. 1a): a vertical axis runs along the whisker arcs, a horizontal axis along whisker rows and a radial axis extends outward from the skin. In this scheme, we can describe movements of the whiskers in a whisker-centered frame in terms of angles of azimuth (Fig. 1b) and elevation.

How can the spatial location of objects be encoded in this space by contacting whiskers? A rat has five rows of whiskers, arranged in a grid-like manner on the whisker pad. By

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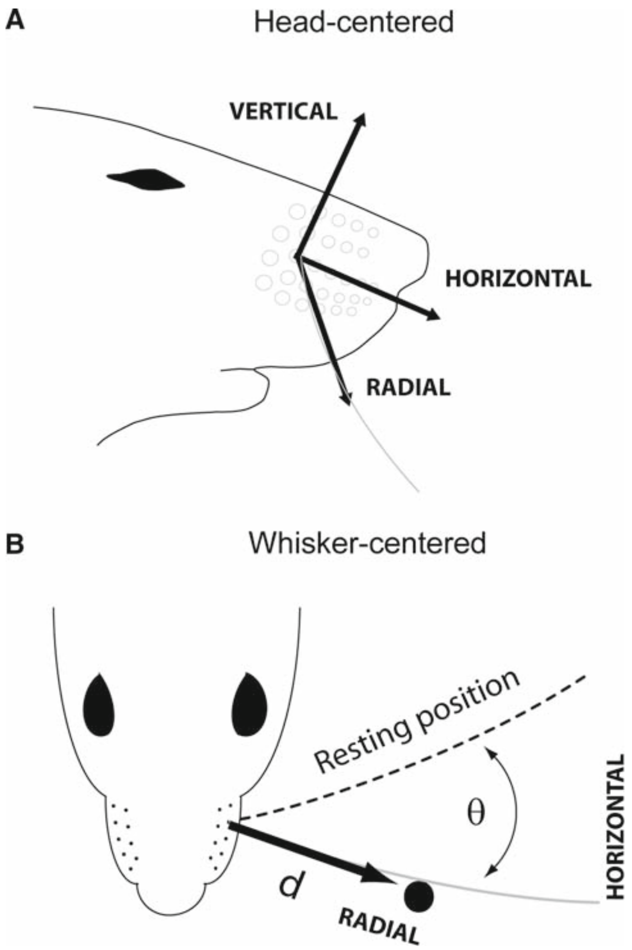

Fig. 1 Coordinate systems of the vibrissal system. **a** The space around one side of the snout of a rat can be described by a set of three axes defined with respect to the geometry of the whisker pad; (i) a vertical axis running along the whisker arcs, (ii) a horizontal axis along whisker rows and (iii) a radial axis extending outward from the skin. **b** Whisker movements primarily involve changes in the azimuthal angle (θ) of the whisker, defined with respect to the orientation of the whisker pad

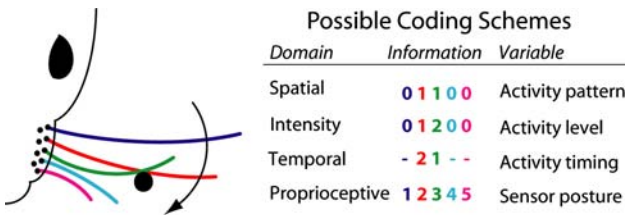

Fig. 2 Whisker behavior involves repetitive (periodic or non-periodic) forward (protraction) and backward (retraction) movements of the whiskers (*colored lines*). Whisker movements are largely synchronous on one side, but often occur with a phase-shift across the two sides of the snout. During whisker protraction, the location of an object (*black circle*) placed in the whisking path must be encoded by information derived from the contacting whiskers. Several sources, or domains, of information are available for the encoding of object location: *Spatial* the identities of contacting whiskers provide binary (0, 1) spatial information about which whiskers contacted the object; *Intensity* contact force intensity (caricaturized as 0, 1, 2, …) can be mapped onto response intensity of whisker-related neurons; *Temporal* the time of contact can be compared between different whiskers, or to a reference signal (relative times caricaturized as 1, 2); *Proprioceptive* current position of the contacting whisker(s), at the time of contact, can be conveyed by proprioceptive signals. These four encoding domains may be utilized in combination, and some in isolation, to encode the spatial coordinate of an object

and large, all whiskers move synchronously. Assuming that a single row of whiskers is protracted forward, we recognize that a rat may encode object location by more than just one parameter (Fig. 2). Here, we will limit our discussion to four possible domains of encoding space: spatial, intensity, temporal and proprioceptive encoding. We will start with a brief overview of candidate-encoding schemes for spatial object location, followed by a discussion of how recent behavioral and neurophysiological results constrain the possible encoding schemes for each spatial dimension.

When a whisker contacts an object, the forces applied to the whisker shaft are transduced into activity in the sensory nerves attached to the whisker follicle. This transduction process generates the sensory input to the nervous system. From the resulting spikes (i.e., action potentials) generated by object contact, the simplest parameter related to object location is the presence or absence of a spike. The identity of contacting whiskers will result in a unique pattern of activated sensory nerve fibers. Since the identity of contacting whiskers depends on the relative location of an object (Fig. 2), the identity of activated sensory nerve fibers carry information about location of the object. Typically, sensory afferents do not respond with a single spike, but at a certain rate of spiking. In general, the spike rate is positively correlated with the intensity of forces applied to the whisker shaft up to a point where the response saturates (Gibson and Welker 1983b). The intensity of evoked responses can either be measured instantaneously, as in a rate-code, or integrated over time, as in a spike-count code. In both cases, space is mapped onto different levels of intensity, such that each activity level across a population of sensory afferents indicates a specific location in space. The spatial resolution of an identity-based (labeled-line) code is limited by the spatial granularity of the sensor array, while the resolution of an intensity code is limited by the just noticeable difference (JND) in activity. These limits may be extended by additional levels of processing involving interpolation across sensory inputs. For instance, more exact localization of objects may be achieved by interpolation between activity levels of sensory afferents coding for neighboring whiskers (Barlow 1979).

Because the whiskers move, object location may also be temporally encoded, based on the timing of motor and sensory evoked activity (Fig. 2). The simplest form of such temporal coding is the timing of spikes relative to a reference event. This reference event may be the onset time of whisker movement, the evoked activity in other afferents, or an internal reference generated by the motor system.

The spatial and temporal encoding schemes discussed above assume an indirect measurement of object location: a signal is detected, which is then assumed to correspond with the location of an object with specific spatial coordinates. Object location may also be measured directly, by knowing the exact location of the whisker at any point in time. This concept is similar to path integration: a person navigating in the dark may know its spatial location by counting the number of steps, left-turns and right-turns. Similarly, a rat may know where it moved its whiskers to, either by proprioception (or an equivalent mechanoreceptor-based re-afferent signal) or by an efference copy. Thus, the location of the whisker encodes the location of the object when contact occurs. Such a proprioceptive coding scheme cannot encode radial location, since there is no proprioceptive signal for this dimension. Furthermore, this scheme must use contact signals in combination with positional signals.

2 Behavioral constraints

2.1 Horizontal (azimuth) coding

Behavioral evidence shows that rats are excellent at discriminating the horizontal location of objects. Rats trained to discriminate the relative horizontal location of two vertical poles (one on each side of the snout; Fig. 3a) can detect the closer pole when the difference in horizontal location between them differs by less than 1 mm (Knutsen et al. 2006). In comparison, the horizontal offset between two neighboring whiskers on the same whisker row is ∼5 mm at the typical radial location of contacted objects (Fig. 3a, right). Thus, rats outperform the horizontal acuity limit imposed by the granularity of the whisker array. Such performance is not unique to whisking rats, since also the visual system of humans is capable of such *hyperacuity* performance (Westheimer 1981). Similarly to visual hyperacuity (McKee et al. 1990), whisker-based hyperacuity requires the relative comparison of two spatial locations: when rats perform memory-based, absolute horizontal localization acuity drops by one order of magnitude (Mehta et al. 2007).

The hyperacuity resolution of rats excludes encoding mechanisms that are based on whisker identity alone, such as a labeled line code for horizontal location. Still, rats can achieve hyperacuity by interpolating spatial information collected from several neighboring whiskers. However, if all but one whisker are removed on each side of the snout (Fig. 3a), rats still reach hyperacuity and even improve their performance compared to rats localizing with all whiskers intact (Knutsen et al. 2006). Thus, behavioral observations alone constrain the possible coding schemes used for fine horizontal localization by ruling out spatially-based codes.

2.2 Radial coding

Rats are nocturnal animals, and often dwell in extensive networks of underground tunnels (Whishaw and Kolb 2005). In such an environment, the texture and position of tunnel walls provide rich tactile experiences as rats navigate around their living quarters. The proximity of a tunnel wall is an important stimulus, as it regulates running direction and velocity (Horev et al. 2007). As a consequence, rats are easily trained and quite efficient at discriminating the radial distance of objects (Fig. 3b), reaching a radial acuity of about 3 mm (Krupa et al. 2001; Shuler et al. 2002). Behavioral experiments demonstrate that radial discrimination does not require the whiskers to be moved relative to the head, since the motor nerve supplying these muscles can be cut without negatively affecting performance. Instead, the whiskers contact the objects through whole-body movements (Krupa et al. 2001). Unlike horizontal localization, there is a positive correlation between the number of available whiskers and radial localization performance (Fig. 3b). However, radial localization does not depend in any way on the identity of the whiskers that contact the object. Thus, as with horizontal object localization, behavioral observations constrain the possible encoding schemes for radial localization. First, temporal coding is probably not involved since the whiskers are not required to move during localization. Second, simple spatial, labeled-line codes are also not involved since the identity of the whiskers that contact the objects does not influence performance.

2.3 Vertical (elevation) coding

Two observations limit the available codes for vertical object location. First, receptive fields of first-order trigeminal afferents are always single-whisker (Zucker and Welker 1969; Gibson and Welker 1983a; Lichtenstein et al. 1990; Szwed et al. 2003). Second, whisker movements are largely constrained to the horizontal axis (Fig. 3c): movements along the vertical axis are small, and typically smaller than the spacing between two neighboring rows (Bermejo et al. 2002). These vertical movements are caused by the activity of extrinsic muscles that act to move the whole whisker-pad together. Thus, even if the absolute elevation of the whiskers may vary, the change in relative elevation of different whiskers is always much smaller. Together, these observations suggest that the vertical dimension is most likely spatially encoded, possibly using a labeled-line code. Thus, the identities of activated whiskers indicate the vertical coordinate of an object in pad-related coordinates. For example, if only whiskers of

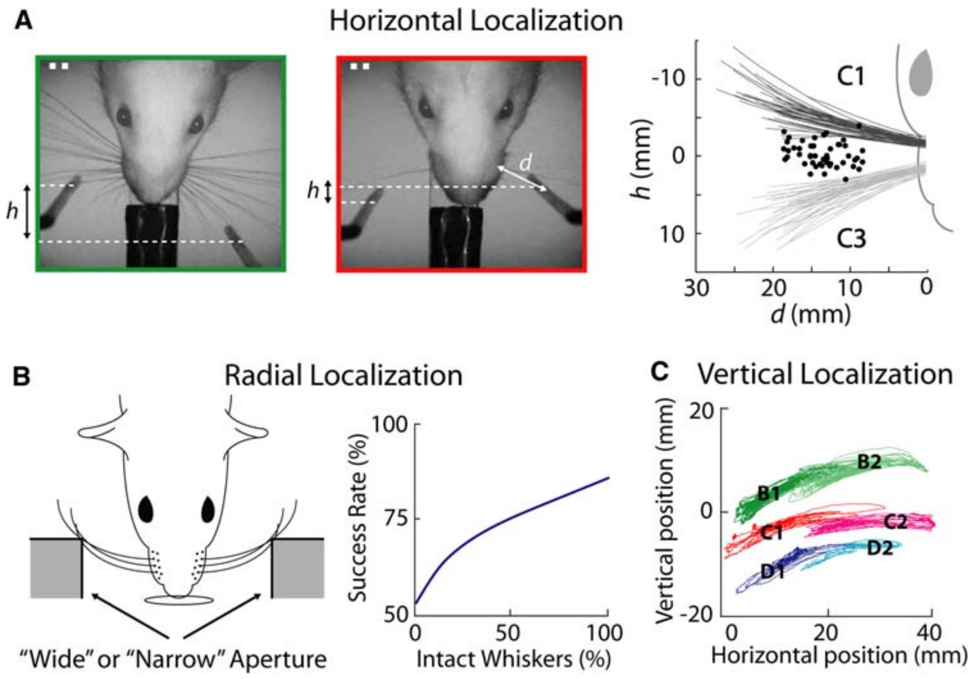

Fig. 3 Behavioral evidence of spatial encoding. **a** Horizontal object localization (adapted from Knutsen et al. 2006). Rats can be trained to discriminate the relative horizontal (anterior–posterior) offset (h) between two vertical poles. *Left* Rats require all or a significant subset of the whiskers to be intact in order to learn this localization task. *Middle* With training, rats can also learn to localize the objects accurately with a single whisker intact on each side of the snout. *Right* The performance in an experimental session can be measured by the localization threshold, which indicates the smallest difference in horizontal offset that a rat was able to discern. These performance thresholds were often smaller than the average horizontal distances between neighboring whiskers on the same row (*C-row* the C2 whisker was located at $h = 0$, and the *gray lines* indicate the average distances of C1 and C3 whiskers from the C2 whisker in individual test trials). On average, neighboring whiskers were horizontally separated by 4.8 mm at the radial contact location. On the basis of Monte Carlo simulations, the upper bound of the discrimination threshold of a population of tested rats was found to be 7.1 mm when all whiskers were intact, 2.8 mm when a single whisker was intact, and 1.5 mm when an arc of whiskers was intact. Individual rats, however, reached lower thresholds: *black dots* indicate the lowest thresholds obtained by individual rats, some as low as just 0.24 mm. **b** Radial object localization (Krupa et al. 2001). *Left* Rats can be trained to classify presented apertures as being either narrow or wide in the radial dimension. *Right* Performance (success rate) in this radial discrimination task is positively correlated with the number of intact whiskers; performance drops as whiskers are gradually trimmed, reaching chance-performance if only a single whisker is left intact on each side of the snout. **c** *Vertical localization* During whisking, movement primarily occurs along the horizontal dimension. Here, the horizontal and vertical movements of individually tracked whiskers from *B*, *C* and *D* rows were measured 20 mm from the whisker base. The results were obtained with stereo-videography and 3D reconstructions (unpublished results, P.M. Knutsen, A. Biess and E. Ahissar; see Bermejo et al. 2002 for similar results)

row B contact an object, the vertical coordinate of the object must be at the level of row B and not at the level of any other row.

3 Neuronal constraints

3.1 Primary afferent signals

Evidently, one would like to look at the neuronal signals entering the trigeminal system while rats perform behavioral tasks requiring them to localize objects in space. Such experiments are challenging and difficult to perform in a manner that allows a systematic study of the neuronal variables that encode object location. Primarily, this is because the behavioral variability involved in such experiments impedes traditional approaches, such as trial averaging, to detect relevant signals against the ongoing background activity in awake, behaving animals (Erchova et al. 2002). Although efficient paradigms for limiting behavioral variability have been developed (Bermejo et al. 1996), the closed-loop nature of vibrissal touch suggests that applying such methods to perceptual discrimination paradigms may adversely affect performance. Sensory acquisition in the vibrissal system is active, in the sense that the nature of the acquired data depends on whisker movements. Thus, the range of movements should be selected by rats during task performance in ways that optimize the collection of relevant information. For example, while rats are capable of producing rhythmic, repetitive movements during exploration in free-air (Fig. 4a), this behavior is replaced by a continuously altered pattern of movement when whisking against objects in an object

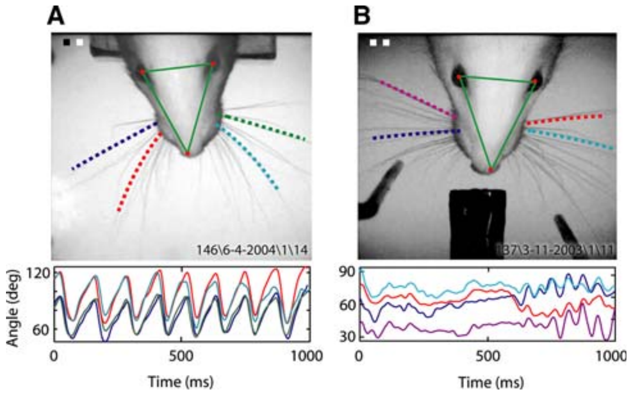

Fig. 4 Influence of object contact and context on whisking behavior. **a** Typical whisking pattern observed during exploratory free-air whisking. Whisking is highly rhythmic and the movements of whiskers on both sides synchronized. **b** During object localization, rats repeatedly contact the objects with their whiskers. Whisker movements during such behavior are less rhythmic and protraction/retraction cycles shorter. Also, synchrony between whiskers on the different sides of the snout is reduced

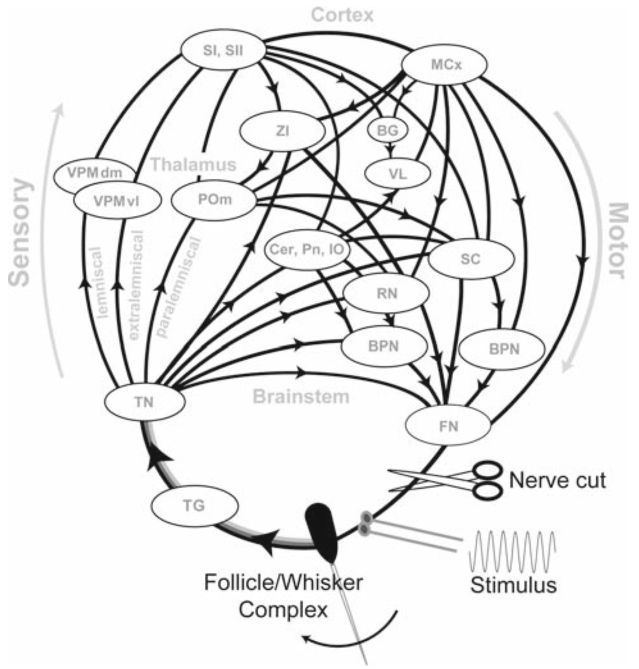

Fig. 5 Closed-loop connections of the vibrissal system. Sensory activity is transmitted by multiple pathways through the sensory regions of the brain, and feed-back to motor circuits of the neocortex, cerebellum, midbrain and brainstem. In awake animals, these closed-loops function to modulate and optimize behavior for the collection of relevant sensory inputs. In anesthetized animals, the sensory signals can be studied by opening the loops by cutting the motor nerve (preventing sensory feedback from modulating whisker movement) and control whisker movement directly by applying patterns of electrical stimulation to the intact, distal part of the motor nerve (Zucker and Welker 1969; Szwed et al. 2003). *Oval circles* indicate the brain regions involved in vibrissal sensory-motor processing [TG trigeminal ganglion; TN trigeminal brainstem nuclei; RN red nucleus; VPM ventroposteromedial complex of the thalamus; SI primary somatosensory cortex; SII secondary somatosensory cortex; ZI zona incerta; VL ventrolateral thalamic nucleus; MCx motor cortex; BG basal ganglia; Cer cerebellum; Pn pontine nuclei; IO inferior olive; SC superior colliculus; POm posteromedial thalamic nucleus; BPN brainstem premotor nuclei (arbitrarily divided into two oval circles); FN facial nucleus]. *Black lines* connecting brain regions indicate anatomical connections. *Arrows* indicate the direction of information flow between brain regions. Connections not labeled with *arrows* are reciprocal. For a more complete review on closed-loop connections within the vibrissal system, see Kleinfeld et al. (1999)

localization task (Fig. 4b). Such dynamic control of whisker movement is probably the most readily available mechanism for rats to increase localization acuity and reliability (Carvell and Simons 1990; Knutsen et al. 2006). However, while being beneficial for the rat, this dynamic control harms attempts to systematically characterize sensory encoding.

Whisker movements are controlled by the activity of vibrissal motoneurons (vMNs) in the facial nucleus of the brainstem. The vMNs receive inputs from several other sensory brainstem nuclei, placing the vMNs just two synapses away from the primary afferents. Also, the vMNs receive direct inputs from the vibrissal motor cortex (Grinevich et al. 2005)—a pathway connecting vMNs to the sensory input by four or more synapses. Including a number of other control pathways, vMNs are thus dynamically controlled by multiple sets of nested closed-loops (Fig. 5). Counting delays between primary afferent and efferent (motor) activation, response latencies in this system range from a few to hundreds of milliseconds (Nguyen and Kleinfeld 2005). In comparison, the duration of a single protraction–retraction cycle ranges from 50 to 200 ms. Thus, studying sensory processing in behaving animals is a challenge since sensory-evoked efferent responses may interfere with sensory response on relatively fast time scales. To eliminate such effects, Szwed et al. (2003) opened this system of closed-loops by anesthetizing rats and cutting the facial motor nerve. They then attached electrodes to the distal part of the motor nerve and applied patterns of electrical stimulation that produced movements mimicking natural free-air whisking (Zucker and Welker 1969). The mechanics of whisker movement in this whisking mode differs in several respects from natural whisking. In awake animals, both whisker protraction and retraction can be active, using different muscles (Berg and Kleinfeld 2003), while during artificial whisking retraction is always passive. Electrically-driven whisking often includes a small stimulus-locked component superimposed on the main protraction trajectory. Also, artificially generated whisking cycles are nearly identical, while natural whisking patterns animals may vary considerable from cycle to cycle (see Fig. 4b). Furthermore, sympathetic and parasympathetic activation fills the follicle with blood during natural whisking, possibly affecting movement parameters and mechanoreceptor activation (Fundin et al. 1997): it is not known to what extent such effects are also present during artificial whisking.

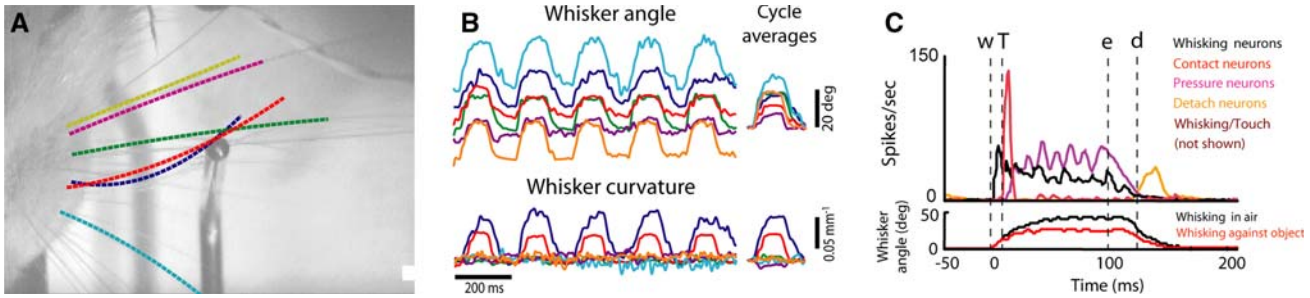

Fig. 6 Kinematics and primary afferent activity during artificial whisking. **a** Anesthetized rats were made to artificially whisk by electrically stimulation the distal part of the transected motor nerve (see Fig. 5; method developed by K. Bagdasarian). A *vertical bar* was positioned at various locations within the path of the moving whiskers. Whisker movements were recorded with high-speed video (1000 frames/s) and then tracked offline using image processing techniques (Knutsen et al. 2005). Image shows a single video frame at the peak of whisker protraction together with six tracked whiskers (*colored*, *dotted lines*). **b** Whisker angle and curvature at whisker base was computed from the tracked whisker movements. Due to the intrinsic curvature of the whisker pad, different whiskers have different resting angles. The whiskers move synchronously, but reach different angular amplitudes depending on the identity of the whisker and whether it contacted the object. The whisker curvature changes significantly when the whisker contacts an object (*blue* and *red traces*). **c** During artificial whisking, the responses of TG primary afferents can be classified according to three main categories, whisking (W), touch (T) and whisking/touch. Touch cells can further be divided into three classes: (i) contact neurons that respond briefly upon contact, (ii) pressure neurons that respond for as long as contact is maintained with the object, and (iii) detach neurons that respond when the whisker detaches from the object

Despite these differences, electrically driven whisking is an approximation to natural whisking while differing from passive stimulation in two crucial ways. With passive stimulations, sensory activation is studied by applying an external force to a non-moving whisker. During behavior, however, when whiskers are actively moved against an object, a force is applied to the whisker–follicle complex by the muscles and a reaction force applied to the external shaft of the whisker by the object. As a result, active whisker touch is often accompanied by appreciably curving of the whisker shaft (Knutsen et al. 2005). The curvature that develops during active touch (Fig. 6a, b) represents the moment at the base of the whisker (Solomon and Hartmann 2006). Such curvatures never develop with passive stimulations, as these stimulations are applied only to the external shaft of the whisker. Furthermore, passive stimulations induce unnatural whisker–follicle interactions, which mechanoreceptors are extremely sensitive to; minute ($<0.1°$) passive deflections may elicit significant sensory responses (Gibson and Welker 1983b). As a result, passive stimulations activate almost all afferent neurons indiscriminately (Szwed et al. 2003). Most individual primary afferents, as measured by the extracellular activity of single-cells in the trigeminal ganglion (TG), can be characterized during passive touch by their selectivity to the direction velocity and acceleration of the applied force, and by their adaptation dynamics (slowly-adapting, SA, or rapidly adapting, RA) (Zucker and Welker 1969; Gibson and Welker 1983b; Lichtenstein et al. 1990; Jones et al. 2004b; Arabzadeh et al. 2005; Stuttgen et al. 2006). In contrast, during active touch, TG neurons are primarily characterized by their selectivity to the components of active touch, a selectivity that cannot be observed during passive touch (Fig. 6c). Critically, these active characteristics cannot be inferred from passive response characteristics (Szwed et al. 2003). During active touch, one class of TG neurons responds exclusively to whisking movements. These cells, termed Whisking cells (W) do not alter their activity levels when the whisker contacts an object along the distal part of the whisker shaft (i.e. at radial positions above 50% of the whisker length). Another class of TG neurons is not sensitive to whisker movement, but instead responds to various phases of contact. Collectively, these cells are referred to as Touch neurons (T), and can be divided into three categories: (i) contact cells that respond briefly upon contact, (ii) detach cells that respond briefly upon detach from an object, and (iii) pressure cells that respond continuously while contact is maintained. A third class of cells responds to both whisking and touch—they respond to whisking and increase their activity levels upon and throughout contact (whisking/touch neurons, WT).

3.2 Horizontal (azimuth) coding

The responses of TG neurons during active touch transmit information about the horizontal coordinate of an object using a temporal code. The timing of the response onset of touch cells (both contact and pressure cells) coincides with object contact (Fig. 7A). During movement, the time elapsed between protraction onset and the contact moment is correlated with the azimuthal angle, θ, upon contact (Fig. 1b). Thus, the timing of contact and pressure cell response onset indicates the horizontal location of an object (Szwed et al. 2003). No other parameter of TG cell activity is known that encodes horizontal object location (Szwed et al. 2003). As in any temporal-coding scheme, the timing of response events must be measured with respect to some reference event. In the

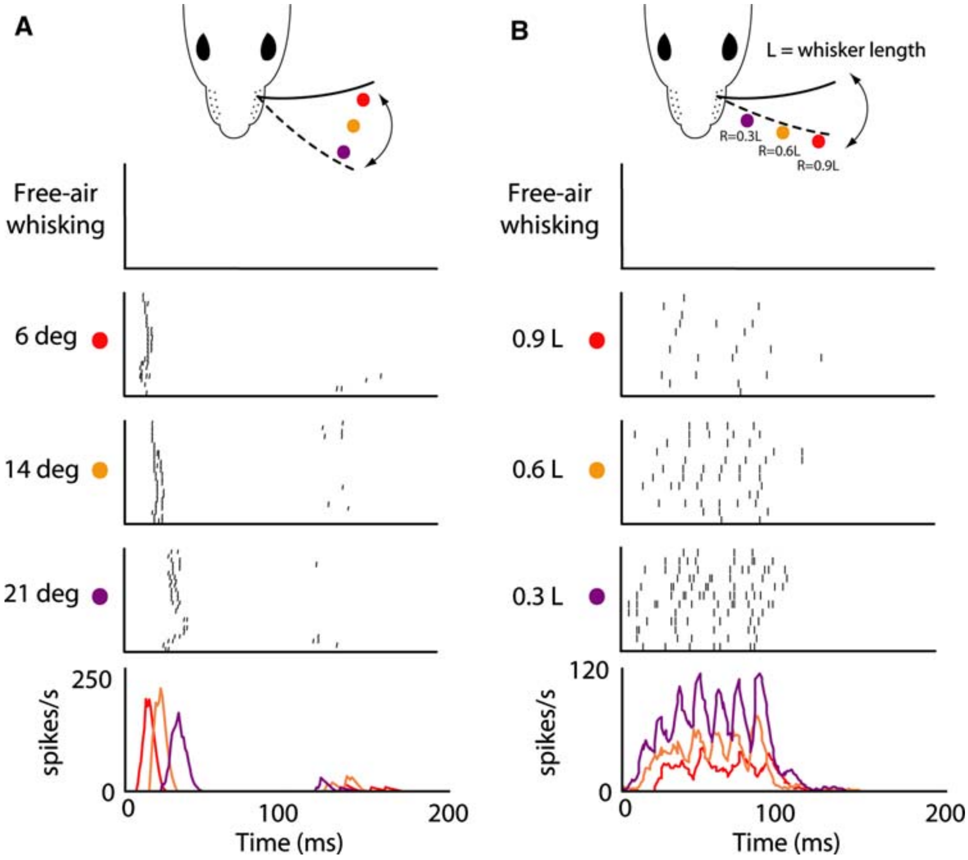

Fig. 7 Neuronal encoding of object location. **a** The horizontal coordinate of an object can be encoded by a temporal code based on the activity timing of touch cells. During free-air whisking (*top*), Touch cells do not respond and thus report that no object was present. Upon contact, the latency of the on-response of touch cells measured from the onset of whisker movement (time = 0 ms) correlates with the horizontal location of the object; response latencies increase as the object is moved further away along the horizontal axis (adapted from Szwed et al. 2003). **b** The radial coordinate of an object is encoded by the activity intensity of touch cells. As the object is positioned at more distal radial locations, the firing-rate and spike-count of touch cells generally drops monotonically (adapted from Szwed et al. 2006)

case of horizontal location coding, this reference event could be the onset of whisker protraction (of the cycle in which the contact occurred), an event that is signaled at high-precision by TG whisking cells. In fact, TG whisking cells signal not only the onset of protraction but also the relative phase of protraction (Szwed et al. 2003). A version of such reference signal exists also in the barrel cortex (Fee et al. 1997; Brecht et al. 2006; Crochet and Petersen 2006; Derdikman et al. 2006). This cortical reference signal is locked to the phase of the mystacial EMG (Fee et al. 1997), and thus also to motion (Carvell et al. 1991). The timing of the contact signal should also be conveyed reliably to enable an accurate comparison with the reference signal. Work in the passive anesthetized rat show that first-order neurons reliably transmit vibrissal contacts at sub-millisecond resolution (Jones et al. 2004a; Arabzadeh et al. 2005). Thus, the horizontal coordinate of an object can be reliably read out by comparison between precisely timed reference and contact signals in the trigeminal pathway (Szwed et al. 2003).

3.3 Radial coding

Radial object location is encoded by several TG activity parameters. During active touch, both the spiking-rate and spike-count of TG touch neurons during the protraction phase are modulated by the radial distance of an object (Szwed et al. 2006). Overall, TG neurons shows a higher spike-rate or spike-count as an object is moved closer to the whisker pad along the radial dimension (Fig. 7b). Since the resolution obtained by individual touch neurons is limited to about 30% of whisker length, more accurate encoding of radial location requires integration across populations of touch neurons (Szwed et al. 2006), consistent with the improved encoding accuracy of passive stimuli obtained by integrating response rates of different TG neurons (Shoykhet et al. 2000). A small proportion of touch cells also exhibit all-or-none responses to radial position—some units respond only when the object is positioned near the base of the whiskers. This observation is consistent with the observation that TG neurons show discrete threshold levels in response to passive whiskers deflections (Gibson and Welker 1983b). In summary, the radial location of objects is encoded by the population firing intensity of TG neurons, and in extreme cases such as proximal touch, also by identity (labeled-line) code.

3.4 Vertical (elevation) coding

TG receptive fields contain only a single whisker also during artificial whisking (Szwed et al. 2003). Thus, no experiments are required to verify that labeled-line is the only code

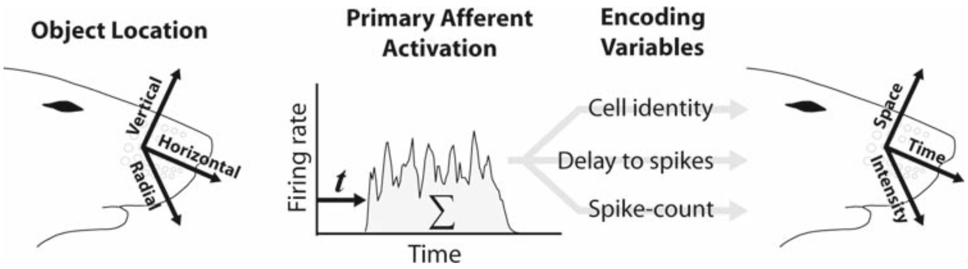

Fig. 8 An orthogonal neuronal coding scheme for 3D object location based on whisking behavior. The activity profiles of individual touch neurons transmit information about each spatial dimension. During whisking, a particular vertical coordinate is scanned only by a subset of whiskers belonging to the same row. When a specific touch cell responds, this means that an object was contacted at the vertical scanning plane of the whisker composing its receptive field. Thus, the vertical coordinate of an object is encoded by the identity of activated Touch cells. The same touch cell also encodes the horizontal and radial location of the object using temporal and intensity codes, respectively (see Fig. 7). Information about the spatial dimensions of an object is therefore encoded by an orthogonal triple-code carried by individual touch cells

possible with artificial whisking in anesthetized rats. In this condition, the fact that a Touch neuron fires in a whisking cycle means that an object was located at the elevation of the whisker to which that cell is attached.

4 Discussion

4.1 An orthogonal coding scheme for object localization

A combination of behavioral and neuronal observations now converges to the following encoding scheme of object location in the whisker system (Fig. 8). The location of an object in three dimensions can be defined according to head (and whisker) centered coordinate systems defined by three orthogonal axes: horizontal (azimuth), vertical (elevation) and radial (along the whisker shaft). These orthogonal axes are encoded in three orthogonal neuronal domains: the horizontal coordinate is encoded in time, the radial coordinate by intensity and the vertical coordinate by identity (Fig. 8).

Rats can accurately localize objects along the horizontal axis with just a single whisker intact (Knutsen et al. 2006; Mehta et al. 2007). Thus, contact and proprioceptive, but not spatial, information is available for the animal to process (Fig. 2). The temporal encoding of horizontal object location must rely on a comparison between contact–time signal and a whisker–position reference signal. Two such reference signals are known that may interact with a contact signal in order for a read-out circuit to decode the temporal code of horizontal location: (i) the timing of whisker protraction onset, and (ii) the whisker position at the time of contact. Such signals are conveyed by the primary afferent whisking cells (Szwed et al. 2003), and exist in both the somatosensory thalamus (Yu et al. 2006) and barrel cortex (Fee et al. 1997; Brecht et al. 2006; Crochet and Petersen 2006; Derdikman et al. 2006; Kleinfeld et al. 2006). The exact location and identity of the neurons that implement the read-out circuit for the temporal code of horizontal location is not yet known. Recent work suggests that neurons of the barrel cortex have a preferred whisker phase (i.e. fire more spikes during a particular phase of the protraction-retraction cycle), and the responses to touch are higher during the preferred-phase than during the remainder of the whisk cycle (Curtis and Kleinfeld 2006: Confluence of position and active touch in rat primary somatosensory cortex. 144.3/F4, Soc for Neurosci). These coincidence responses might reflect a read out of the temporal code of horizontal location. Recordings from the second somatosensory cortex (S2) suggest significant involvement of S2 neurons in decoding horizontal location as well (Yu et al. unpublished data).

The intensity coding scheme for radial position is most likely based on a population code, given the overall low encoding quality of individual primary afferents (Szwed et al. 2006). In this scheme, each neuron contributes with a noisy input signal (firing-rate or spike-count) to a read-out circuit that either interpolates or averages the activity across all touch cells. In addition, since some TG neurons exhibit discrete activation thresholds (Gibson and Welker 1983b; Szwed et al. 2006) proximal radial location may also be encoded by an identity code.

In addition, the orthogonal triple-coding scheme allows efficient transmission of information from the whisker follicle and into the brain. Information about all three spatial dimensions is multiplexed into the activity profile of each individual touch cell—the fact that a touch cell is activated conveys information about the vertical coordinate of an object, the onset of firing its horizontal coordinate, and the intensity of firing the radial coordinate (Fig. 8). This scheme of same-neuron-different-codes provides provides several advantages over same-code-different-neurons schemes.

First, by conveying orthogonal information by orthogonal codes, the amount of cross-talk of information along afferent channels is significantly reduced. Secondly, the decoding circuits do not have to limit themselves to a specific sub-group of afferents—they can extract their relevant variable (firing, latency and intensity) from all touch afferents coming from the same whisker, and sometimes from different whiskers, indiscriminately, and integrate them. This provides about three-fold augmentation of the number of channels that can be integrated, over same-code-different-neurons schemes, in which different neurons should be allocated to each spatial dimension. Such an advantage is significant, since integration of channels is necessary due to inevitable gradual changes in whiskers' morphology, mechanics, and configurations. Behavioral studies indicate that multi-whisker integration is involved in some perceptual tasks. For instance, multi-whisker integration facilitates radial localization acuity (Krupa et al. 2001) as well as learning-ability in a horizontal localization task (Knutsen et al. 2006). Such behavioral studies have not yet addressed integration across afferents related to the same whisker.

At present, it is not known how and where the output signals of touch cells are decoded. One possibility is that the output signals of these neurons are conveyed in parallel to different readout circuits, each of which decodes one specific variable. The vertical coordinate can be read out by simple threshold neurons. The horizontal coordinate can be read out by temporal-to-rate converters or phase detectors (Ahissar 1998; Szwed et al. 2003). The radial distance can be read out by neural integrators (Barlow 1979), peak detectors, attractor neural networks (Hopfield 1982), or synfire chains (Abeles 1982). Experimental evidence shows that some response features (touch and whisking) of the primary afferents are indeed segregated into different anatomical pathways at the level of the sensory thalamus (Yu et al. 2006). This segregation of the information flow is consistent with experiments suggesting that horizontal object location may be decoded by specific thalamo-cortical or cortical circuits (Ahissar et al. 2001; Ahissar and Kleinfeld 2003).

The orthogonal coding described here allows three different codes to be conveyed by each neuron. This allows the nervous system to use a scheme of different-codes-same-neurons instead of the same-code-different-neurons scheme which is traditionally considered. In the different-code-same-neurons scheme, the receiving circuitry can evolve to optimally decode a selected variable, without making assumptions about the source of the information or the context it occurred in as would be required with a same-code-different-neurons scheme.

4.2 The role of whisking behavior: Perception versus sensory processing

Perception is not a sensory process—it is a motor-sensory process. Behavioral observations repeatedly demonstrate that object localization is achieved via actively generated body, head and whisker movements (Krupa et al. 2001; Knutsen et al. 2006; Mehta et al. 2007). During horizontal localization, for example, rats repeatedly contact objects through discrete cycles of protraction and retraction. Through each such whisk-cycle, the rat's brain may be considered to acquire a discrete chunk of information, from which its future actions are determined (Knutsen et al. 2006). Such an iterative active sensing process may also be important for the encoding of spatial coordinates. Thus, sensory coding schemes proposed earlier, which neglect this iterative process of repeated contacts and possibly re-alignments of the head and body, only partially describe the perceptual process leading to localization.

Until recently, studies aimed at elucidating the encoding mechanisms of object location have relied on a simplified, experimental model system void of behavior and sensory-feedback (Szwed et al. 2003, 2006; Derdikman et al. 2006). Evidently, in order to obtain a more complete picture of the localization process, future experimental models must incorporate behavior and/or sensory feedback. The importance of the latter is evidenced by the obvious change in motor behavior as rats shift from free-air whisking to palpation against objects (Fig. 4). Furthermore, the proposed encoding schemes may not be absolute: individual rats may use sensory variables differently by shifting the motor strategy in any particular task. For example, during horizontal object localization (Knutsen et al. 2006), one rat might use synchronous bilateral whisking to measure the time difference between left and right contacts as the primary sensory variable for encoding the relative horizontal location of objects, while another rat may employ fine motor control in each side independently to achieve accurate proprioceptive measure of contact upon contact. Evidently, contact times will be important in the sensory-motor process in both cases, but will serve as a perceptual cue only in the former. Thus, the sensory variables that serve perceptual processing need not be the same that convey the primary sensory signals. The former depend on behavioral strategies, whereas the latter depend on vibrissal motor-sensory interactions.

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