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Vibrissa Movement, Sensation and Sensorimotor Control

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Introduction

p0005 Rats use their vibrissae, an array of long, pliable hairs that can be actively swept through space, to interrogate objects in their local physical environment (**Figures 1**(**a**) and **1**(**b**)). As rats search and locomote, they must be able to gauge the position of the ground beneath them and walls and obstacles around them. This suggests that the sense of touch is used in multiple ways. First, touch provides a means to establish the nature of a surface texture. Is it smooth or rough? Second, touch is used to establish the shape of an object. Third, touch is used as a means to determine the location of an object with respect to the body image of the rat. Is the object to the front or the side? The notion of interpreting touch in the context of body coordinates implies that reference signals of vibrissa position are an essential aspect of sensation.

p0010 The neuronal encoding of environmental and positional clues, and the anatomical circuitry that turns these clues into motor plans, form the material of this article. It begins by delineating a number of tasks that rats may be trained to accomplish solely through the use of their vibrissae. These serve to focus our presentation on neuronal pathways that are directly relevant to an understanding of vibrissa sensorimotor control. The article then discusses the anatomy of the vibrissa pathway in detail, with an emphasis on the mechanical properties of the vibrissa *per se*, as well as the motor plant that drives the vibrissae. This leads into a presentation of electrical signaling along the vibrissa pathways, followed by consideration of the neuronal computations that are supported by these signals. The article closes with a discussion of open issues. As an aid to reading the literature, common abbreviations are given in **Table 1**.

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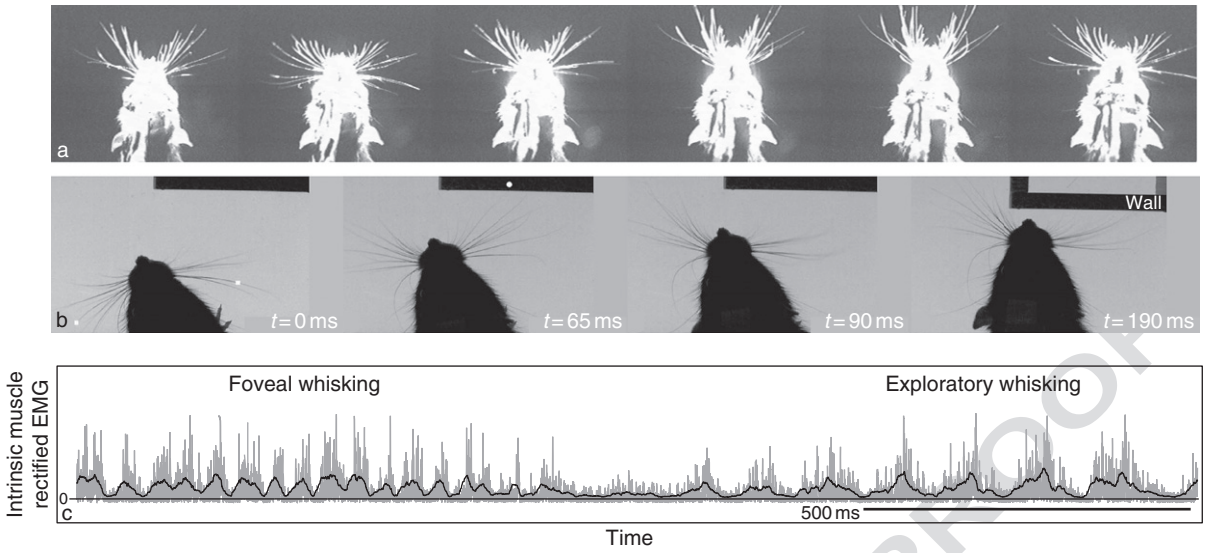
Behavior

p0015 Vibrissae somatosensation is an active sensory process. Rodents sweep their vibrissae through space largely in unison and with a rhythm that varies between 5 and 25 Hz. The dynamics of this process can be extracted from high-speed videography or from measurements of the electrical activity of the muscles that drive the vibrissae (**Figure 1**(**c**)). What tasks can animals accomplish with this active process? A basic function of the vibrissae is to evaluate the terrain in front of the animal. Thus, for example, blind rats with intact vibrissae will leap across wider gaps than rats without vibrissae. This observation is a building block of a commonly used paradigm to determine whether rats can discriminate among surfaces with different textures (**Figure 2**). Here, rats foveal whisk as they crane across each of two gaps (**Figure 1**(**c**)). This posture allows them to sense and evaluate a texture on the far side of the gap. Only one of the two textures is paired with a reward, that is, water or food, which the animal can receive by jumping across the gap. The accumulated data from these experiments suggest that trained animals may recognize a corrugated surface whose pitch is as fine as 15μm and differentiate among surfaces whose relative difference in pitch is as small as 5%. Last, these experiments reveal that the amplitude of whisking may change upon contact (**Figure 2**(**a**)(**2**)) and thus provides a means to manipulate sensorimotor feedback.

p0020 The vibrissae convey spatial information that is sufficient to allow rats to distinguish between barriers whose lateral distance from the snout varies by less than 5%. In one task, rats are trained to distinguish between a wide versus narrow aperture (**Figures 2**(**b**)(**1**) and **2**(**b**)(**2**)). A rat waits in a main chamber until a sliding door opens, after which it enters a small chamber that contains a nose poke, that is, a place for the snout that keeps the rat's head relatively fixed during the task. Once the snout is positioned, two panels close from the sides to form a symmetric, variable-width aperture. Animals are required to judge whether the aperture is the wider or narrower of two possible widths and report their choice by moving to additional nose pokes in the main chamber, that is, a right nose poke for the narrow aperture and a left nose poke for the wide aperture (**Figure 2**(**b**)(**1**)). The correct choice is rewarded. An interesting result is that, as the vibrissae are incrementally trimmed from the normal complement of 20 or more down to one and then zero, the performance on this task is a linearly decreasing function of the number of vibrissae that remain (**Figure 2**(**b**)(**2**)).

p0025 Variants of the above fine-discrimination task require the animal to report symmetric versus asymmetric apertures. In a related task, animals are trained to report the shift in the horizontal position between pins placed on each side of the face (**Figure 2**(**c**)(**1**)). This latter task probes the bilateral acuity of the vibrissa system. It is interesting that rats perform this task better with only a single column, referred to as arc, of vibrissae rather than all their vibrissae (**Figure 2**(**c**)(**2**)). The typical displacement that could be distinguished with an arc was 1.5 mm, which corresponds to an angular displacement of 6° in these experiments.



f0005 **Figure 1** Example data for different modes of whisking. (a) Exploratory whisking, also referred to as symmetric whisking. Shown are successive strobed video images of a rat, using darkfield illumination, as it moves its vibrissae during an exploratory whisk cycle. The animal was trained, while blindfolded, to whisk in search of a food tube (not shown). Successive frames are at intervals of 33 ms. Unpublished data. (b) Asymmetric whisking as a result of contact between the vibrissae and a wall. Protraction commences approximately synchronously on both sides of the snout; the filled white squares show the tracked vibrissae in the rear arcs. At $t = 65$ ms, a deflection occurs on a forward vibrissa; the filled white circle indicates the point of contact with the vertical surface. Protraction then ends on the side ipsilateral to the contact, and the contralateral vibrissae reach maximum protraction in the whisk cycle subsequent to the initial contact. Adapted from Mitchinson B, Martin CJ, Grant RA, and Prescott TJ (2007) Feedback control in active sensing: Rat exploratory whisking is modulated by environmental contact. *Proceedings. Biological Sciences/The Royal Society* 274(1613): 1035–1041. A similar pattern of asymmetric whisking as animals change their head position has been reported by Hartmann (Towal RB and Hartmann MJ (2006) Right-left asymmetries in the whisking behavior of rats anticipate head movements. *Journal of Neuroscience* 26: 8838–8846). (c) Example of sequential foveal and exploratory whisking observed via the rectified electromyogram of the intrinsic muscles. The solid line is the low-pass filtered signal. Adapted from Berg RW and Kleinfeld D (2003) Rhythmic whisking by rat: Retraction as well as protraction of the vibrissae is under active muscular control. *Journal of Neurophysiology* 89: 104–117.

p0030 Beyond issues of discrimination, rats make use of vibrissa somatosensation to encode the location of objects relative to their face as they explore their environment with large-amplitude whisks (**Figure 1(a)**). In part, the ability of rats to use their vibrissae to sense a platform across a gap implies that they are sensitive both to touch and to the forward thrust of their vibrissae. Nonetheless, the question remains as to whether rodents encode the position of their vibrissae as they whisk (**Figure 3(a)**). This issue was addressed in terms of an operant conditioning paradigm in which rats were trained to discriminate between different angles of a pin relative to the area of the cheek that hosts the vibrissae, called the mystacial pad (**Figure 3(b)**). These animals were trained to press a lever at a high rate if the rewarded stimulus (S+), corresponding to a pin at a specified location, was presented. No reward occurred for a stimulus at a second location (S−). Rats with a single vibrissa were able to perform this task (**Figure 3(c)**). Further, they performed it without bias to vibrissa location and with few, relatively brief contacts. This implies that rats must make use of a reference signal of vibrissa position as they determine where touch occurs relative to their mystacial pad.

Whisking

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p0035 Within laboratory settings, animals will typically whisk in bouts of five to 50 individual whisks with a continuum of behaviors. Nonetheless, three different motifs appear to be common. The first is exploratory whisking, which occurs when animals whisk in air without contact or with only light contact (**Figure 1(a)**). In this case the stroke on a given whisk approaches 70°, and a total field of up to 160° may be covered as the animal slowly shifts the set point of its whisk. Such whisking is extremely regular and typically occurs with a frequency between 7 and 12 Hz and a mean of 9 Hz. In particular, the bandwidth of exploratory whisking is at theoretical limits for a perfect oscillator, which implies that the motor drive may be described as a sinusoidal oscillation with a constant frequency.

p0040 The second whisking motif, asymmetric whisking, occurs when animals make contact with a large object, such as a wall, while they whisk (**Figure 1(b)**). It also occurs if they turn their head to the side while whisking. Asymmetric whisking lasts for only one to three whisk cycles. The final motif is referred to as foveal whisking and occurs when animals thrust all their

t0005 **Table 1** Common abbreviations

Abbreviation	*Meaning*
ALBSF	Anterior lateral barrel subfield, a region of parietal cortex
CPG	Central pattern generator
EMG	Electromyogram
FN	Facial nucleus
ICMS	Intracortical microstimulations
IoN	Infraorbital branch of the trigeminal nerve
L1, ..., L6	Neocortical layer 1, ..., layer 6
LFP	Local field potential
M1	Primary motor region of neocortex
MUA	Multiunit activity
PMBSF	Posterior medial barrel subfield, a region of parietal cortex
PO	Posterior medial nucleus, a region of dorsal thalamus (also POm)
PrV	Trigeminal nucleus principalis
RSU	Regular spiking unit
S1	Primary somatosensory region of neocortex (also SI)
S2	Secondary somatosensory region of neocortex (also SII)
SpVC	Spinal nucleus caudalis
SpVI	Spinal nucleus interpolaris
SpVO	Spinal nucleus oralis
TCU	Thalamocortical unit
TG	Trigeminal ganglion
TN	Trigeminal nucleus
VMCtx	Vibrissa primary motor cortex
VPM	Ventral posterior medial nucleus, a region of dorsal thalamus
VL	Ventral lateral nucleus, a region of dorsal thalamus
ZI	Zona incerta, a region of ventral thalamus

vibrissae forward to palpate an object ahead of them, as occurs when they try to detect a landing on the far side of a gap (**Figure 2(a)**). In this case the stroke is much reduced, typically to 20°, and the extrinsic muscles, the muscles that pull on the mystacial pad and include *m. nasolabialis*, *m. maxolabialis*, *m. nasalis*, and *m. transversus nasi*, are relatively inactive as they can apply little torque when the mystacial pad is fully extended. The frequency of foveal whisking is high, ranging between 15 and 25 Hz, and rats can readily switch between foveal and exploratory whisking (**Figure 1(c)**).

s0020 Systems Description of the Sensorimotor Plant

p0045 The anatomy of the vibrissa system provides the foundation for understanding the neuronal basis of whisking and vibrissa-driven behaviors. Like other sensorimotor systems, the vibrissa system is organized as a set of nested loops, with the vibrissae and the motor plant that drives the vibrissae as the common focus of all loops (**Figure 4**). The ascending branches of the loop receive and process sensory input, and the descending branches can control the motor plant that drives the vibrissae. It is important to remember that, as a closed feedback system, both sensory and motor signals can appear at all levels and stages of the nervous system. Only in extreme cases, such as induced paralysis of an identified pathway, can one isolate a touch signal from a motion signal that leads to touch.

The Follicle s0025

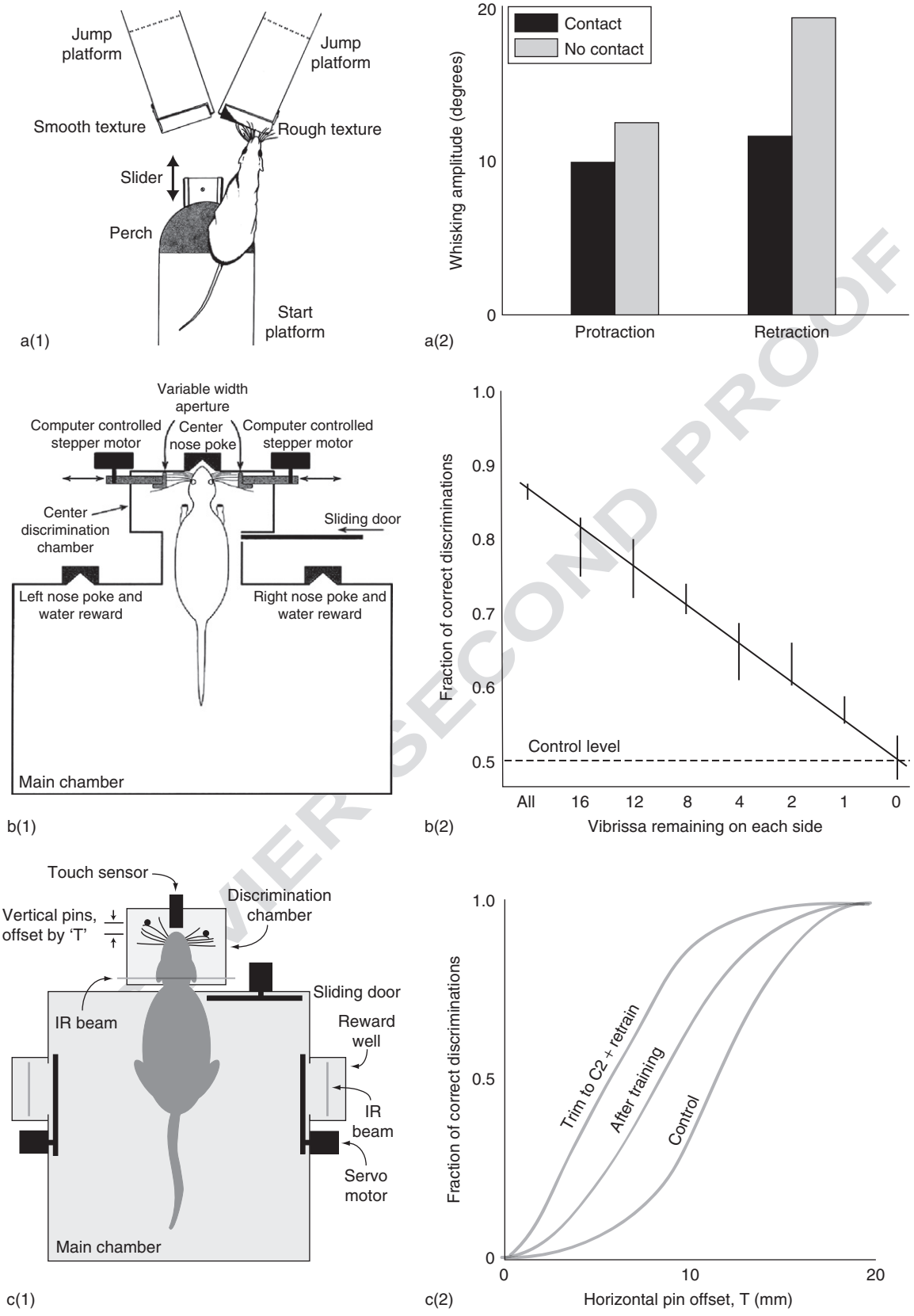
The front end of the vibrissa system is the vibrissa–follicle complex (**Figure 5**). The lower 4 mm of the vibrissa is buried in the follicle, which is innervated by two sets of trigeminal sensory nerve terminals that originate from the trigeminal nucleus. One set innervates the deep end of the follicle (DVN in **Figure 5**) and the other innervates the superficial end (SVN in **Figure 5**). Together, these nerve fibers form the infraorbital branch of the trigeminal nerve (IoN). p0050

The sensory nerves contain eight morphologically distinct sensory terminals, for which two classes of responses appear to dominate. One is the rapidly adapting receptors, whose responses return to baseline within 200 ms of stimulation, and the other is the slowly adapting receptors, which enable the vibrissa to follow vibrations as fast as 1200 Hz over extended periods. The latter responses are believed to make use of small cells called Merkel cells, localized to the follicle as intermediates between the hair and the sensory nerve terminal. The follicles, although composed exclusively of soft tissue, contain cavities that are under the control of the autonomic nervous system and engorge with blood when the animal is active. This results in a fixture that is likely to form a stiff mechanical coupling between the vibrissa and the sensory nerve terminals. p0055

The sensory fibers in the follicle are sensitive to motion of the embedded vibrissa and thus encode contact between an object and the vibrissa. More information is gleaned if the impact on contact and the distance of the contact point to the skin, that is, the radial distance along the vibrissa, can be encoded. One likely possibility is that the reaction forces along the follicle shift as the point of impact moves relative to the center of mass of the vibrissa. Thus the pattern of these forces can be used to gauge the magnitude, distance, and direction of impact. p0060

The Mystacial Pad s0030

The cheek on each side of the rat's face contains a thickening in the skin that is called the mystacial pad. The pad contains an array of follicles organized as five rows and four or more arcs. In addition, there are p0065



f0010 **Figure 2** Behaviors that involve fine vibrissa-based comparisons. (a)(1) Schematic of a gap-crossing task in which rats crane across one of two equally spaced gaps to assess the relative roughness of textured tubes. Animals are trained to examine both textures and then jump from the perch on the start platform to the appropriate jump platform. The gap between the start and jump platforms can be adjusted

four additional large caudal vibrissae, denoted the straddlers, which interdigitate among the rows (insert, **Figure 5**). The hairs in the most dorsal row, that is, row A, point upward above the head and, curiously, are barbered as animals determine dominance. The hairs in the ventral row, that is, row E, tap the ground as the animal locomotes and presumably help maintain the altitude of the head. The middle rows, labeled B through D, appear important to exploration and the location of objects.

s0035 **Brain Stem Loop**

p0070 Sensory input from reaction forces generated in the follicles leads to a signal that transverses the IoN and projects to one or all four nuclei that form the trigeminal complex (**Figure 4**). These include the principal sensory nucleus (PrV) and the three spinal nuclei, denoted oralis (SpVO), interpolaris (SpVI), and caudalis (SpVC). The afferents form several somatotopic representations, referred to as barrelettes, of the ipsilateral vibrissae. Efferents from the PrV, SpVC, and SpVI nuclei project to motor neurons in the lateral subnucleus of the ipsilateral facial nucleus, which sends motor output to the muscles of the mystacial pad. This completes the lowest-order brain stem sensorimotor loop (∗ in **Figure 4**).

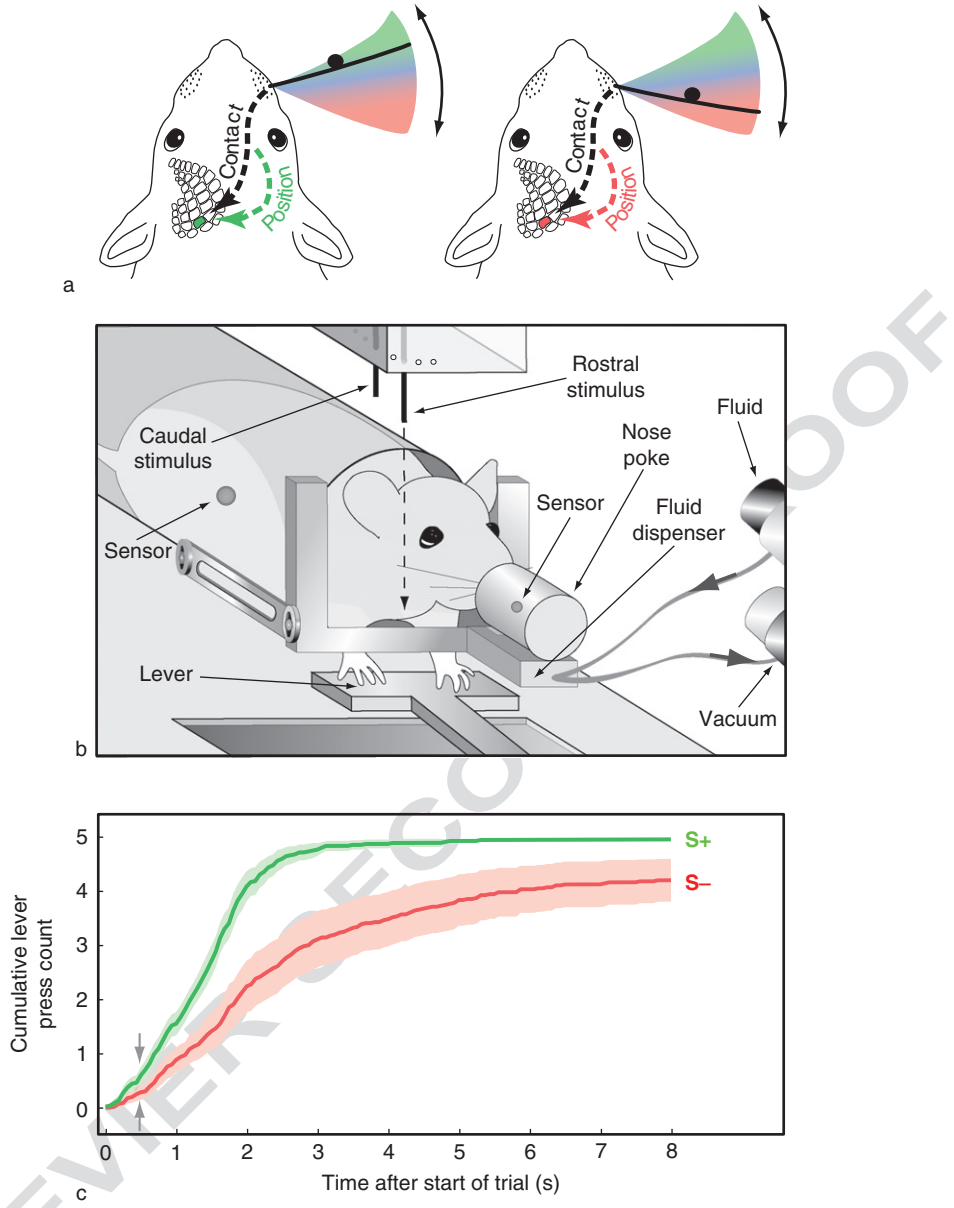
p9000 The trigeminal nuclei further interact among each other. Neurons in the PrV nucleus receive excitatory input from both the SpVC and SpVI nuclei and inhibitory input from the SpVi nucleus. The latter forms a local inhibitory loop that, possibly in concert with descending inputs from high-order areas, provides a means to filter sensory information at the level of the brain stem.

s0040 **Muscles of the Mystacial Pad**

p0075 What is the underlying musculature that drives the vibrissae? Protraction begins with contraction of the external protractor muscles in the skin, m. nasalis (**Figure 6(a)**). This shifts the center of mass of the follicle, as well as the point of egress of the vibrissae, toward the snout. A second group of muscles, which appear as slings that wrap around each follicle, contract next and rapidly propel the vibrissae forward. These muscles are unique to animals that whisk and are denoted the intrinsic muscles (**Figure 6(b)**). Last, as protraction reaches its maximum extent, activation of the sling muscles wanes and a pair of external retractor muscles, m. nasolabialis and m. maxolabialis, activate and restore the vibrissae to their initial position (**Figure 6(a)**). The measured sequence of muscle activation, together with the measured motion of the vibrissae along an anterior–posterior (A–P) axis, illustrates this process (**Figure 6(c)**). Last, it is possible to construct a mechanical model of the mystacial pad that is based on the known anatomy, elastic constants of the tissue, and force curves for the muscles (**Figure 6(d)**). The model serves as a means to reconstruct the position of the vibrissae from the measured electrical activation of the vibrissae.

p0080 Of critical importance, exploratory whisking occurs in the absence of sensory feedback. Moreover, the phase relation between the various muscle groups that mediate whisking is unchanged. This suggests the existence of coupled central pattern generators in the brain stem that drive the three phases of rhythmic whisking (**Figure 6(c)**).

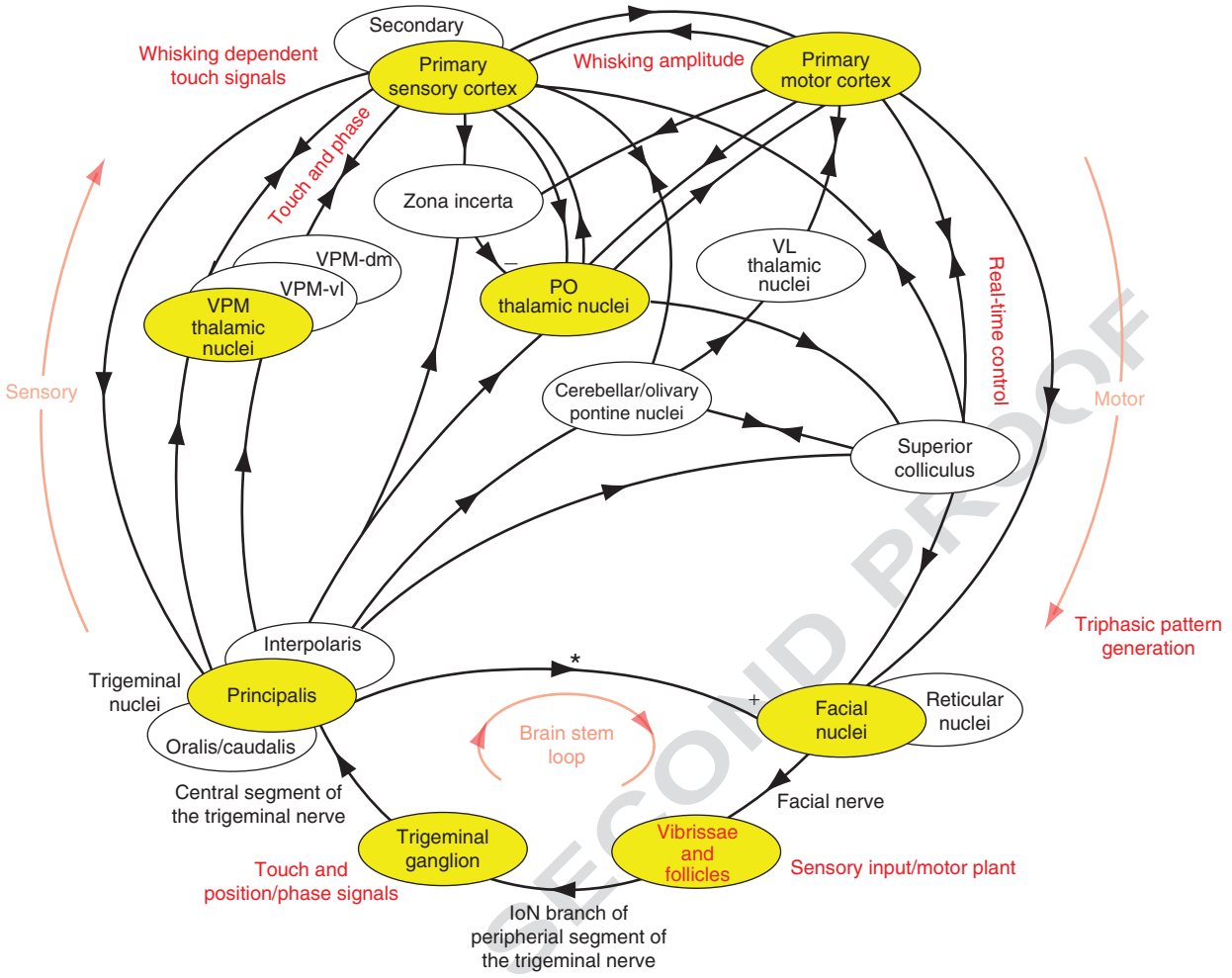
with a slider to change the difficulty of the task. (a)(2) The effects of surface contact on the amplitude of vibrissa movements in one rat. The angular displacement of different vibrissae are seen to decrease when they contact a texture as opposed to sweep the air without contact. Panels (a)(1) and (a)(2) adapted from Carvell GE and Simons DJ (1990) Biometric analyses of vibrissal tactile discrimination in the rat. *Journal of Neuroscience* 10: 2638–2648; see also Carvell GE and Simons DJ (1995) Task- and subject-related differences in sensorimotor behavior during active touch. *Somatosensory & Motor Research* 12: 1–9. A similar task was pioneered by Guic-Robles (Guic-Robles E, Valdivieso C, and Guajardo G (1989) *Behavioural Brain Research* 31: 285–289) and recently extended to mice (Celikel T and Sakmann B (2007) *Proceedings of the National Academy of Sciences USA* 104: 1395–1400). (b)(1) Apparatus for a task to test distance discrimination. The width of the aperture is adjusted between two values, 'narrow' or 'wide.' Differences of 1.5 mm, that is, 62 mm versus 63.5 mm, were generally irresolvable, but differences of 3 mm were resolvable. At the start of each session, the rat is placed in the outer reward chamber with the sliding door closed. When the door is opened, the rat enters the center discrimination chamber, centers in the nose poke, and samples the aperture with its vibrissae. The rat then backs into the outer reward chamber and pokes its nose into either the left or right nose poke to receive a water reward: a left nose poke if the aperture is narrow and a right nose poke if the aperture is wide. (b)(2) Mean percentage of correct discriminations for an ensemble of rats in which vibrissae were sequentially and systematically removed. Note the decrease in performance with the total number of vibrissae removed. Panels (b)(1) and (b)(2) adapted from Krupa DJ, Matell MS, Brisben AJ, Oliveira LM, and Nicolelis MAL (2001) Behavioral properties of the trigeminal somatosensory system in rats performing whisker-dependent tactile discriminations. *Journal of Neuroscience* 21: 5752–5763; see also Shuler MG, Krupa DJ, and Nicolelis MA (2002) Integration of bilateral whisker stimuli in rats: Role of the whisker barrel cortices. *Cerebral Cortex* 12: 86–97. (c)(1) Apparatus for a task to test fine discrimination in horizontal offsets of two bilaterally spaced bars. The horizontal locations of the poles were changed between trials in steps of 0.1 mm. At the start of each session, the rat enters the center discrimination chamber, centers in the nose poke, and samples the poles with its vibrissae. The rat then backs into the outer reward chamber and pokes its nose into either the left or the right reward cell to receive a water reward; a specific offset is randomly paired with a specific side for each rat. (c)(2) Distribution of performance thresholds after discrimination training with the complete C row of vibrissae, after trimming down to one vibrissa, C2, and retraining, and for control animals with no vibrissae. (c)(1) and (c)(2) adapted from Knutsen PM, Pietr M, and Ahissar E (2006) Haptic object localization in the vibrissal system: Behavior and performance. *Journal of Neuroscience* 26: 8451–8464.



f0015 **Figure 3** Behavior that involves the confluence of touch and position signals during exploratory whisking. (a) Cartoon that depicts a task to detect the position of an object relative to the rat's head with only one vibrissa. This task differentiates between labeled line-schemes that involve multiple vibrissae but no knowledge of vibrissa position and haptic-schemes that depend on both touch and position neural streams (dashed arrows) but do not require multiple vibrissa. (b) Details of the training and testing arena. Discrimination trials begin when an animal trips the nose poke sensor, which causes either the rostral or the caudal stimulus pin to descend into the vibrissa field. Lever presses in response to the rewarded, that is, S+, stimulus, either the rostral or caudal pin for each animal, result in a drop of water in the fluid dispenser. Lever presses in response to the unrewarded, that is, S−, stimulus have no effect. (c) Cumulative behavioral responses for one session, averaged separately over S+ and S− trials. The line and shaded regions give the mean ±2 standard error of measurement cumulative lever press counts. The gray arrows at 0.5 s mark the time after which the error regions remain nonoverlapping. Adapted from Mehta SB, Whitmer D, Figueroa R, Williams BA, and Kleinfeld D (2007) Active spatial perception in the vibrissa scanning sensorimotor system. *PLoS Biology* 5: e15.

s0045 ## Midbrain Loop

p0085 A intermediate-level loop incorporates the superior colliculus and includes connections that cross the midline (**Figure 4**). The superior colliculus is a laminar, midbrain structure in which each layer is nominally devoted to integrating sensory and motor information relevant to a particular sensory modality. In rat, the intermediate and deep layers of the colliculus appear to be devoted to general somatic sensorimotor processing, with the more



f0020 **Figure 4** Cartoon of the anatomy of nested, vibrissa sensorimotor loops. The proposed connections are gleaned from the work of very many laboratories and provide a coarse roadmap of the flow of neuronal signals. Only pathways of direct relevance to active sensing with vibrissae are shown, with the most studied areas, from the perspective of electrophysiology, shown in yellow. Subdivisions of each area that are not shown in the figure may be described below. Basal ganglion pathways (Mercier BE, Legg CR, and Glickstein M (1990) *Proceedings of the National Academy of Sciences USA* 87: 4388–4392; Deniau JM, Kita H, and Kitai ST (1992) *Neuroscience Letters* 144: 202–206), are not included as they have only recently received attention in the vibrissa community (Hoffer ZS, Arantes HB, Roth RL, and Alloway KD (2005) *Journal of Comparative Neurology* 488: 2–100). Nor has the loop between neocortex and the hippocampus been considered (Buzsaki G (1996) *Cerebral Cortex* 6: 81–92; Chrobak JJ, Lorincz A, and Buzsaki G (2000) *Hippocampus* 10: 457–465), a bias that reflects current ignorance in the role of these structures in sensorimotor control. The asterisk labels the shortest sensorimotor feedback pathway, which is a single-synapse from the principal trigeminal nucleus to the lateral aspect of the facial nucleus. **Hindbrain loops: (vibrissae → trigeminal ganglion)** The vibrissae are innervated by both slowly and rapidly adapting sensory afferents (**Figure 1**) that originate from the infraorbital nerve (Dorfl J (1985) *Journal of Anatomy* 142: 173–184; Rice FL A, Mance A, and Munger BL (1986) *Journal of Comparative Neurology* 252: 154–174; Leiser SC and Moxon KA (2006) *Journal of Neurophysiology* 95: 3125–3145). **(trigeminal ganglion → trigeminal nucleus)** Sensory inputs from the trigeminal ganglion project to the principal sensory nucleus (PrV) and the spinal trigeminal nuclei oralis (SpVO), interpolaris (SpVI), and caudalis (SpVC; Torvik A (1956) *Journal of Comparative Neurology* 106: 51–132; Clarke WB and Bowsher D (1962) *Experimental Neurology* 6: 372–383). The PrV and SpVI nuclei and the magnocellular portion of SpVC have somatotopic maps of the vibrissae ('barrelettes'; Ma PM and Woolsey RA (1984) *Brain Research* 306: 374–379); SpVO receives sensory input from the vibrissae yet does not contain a map (Belford GR and Killackey HP (1979) *Journal of Comparative Neurology* 188: 63–74; Belford GR and Killackey HP (1979) *Journal of Comparative Neurology* 183: 305–322). Last, there is particularly high internuclear connectivity among the SpVC and SpVO nuclei (Jacquin MF, Chiaia NL, Haring JH, and Rhoades RW (1990) *Somatosensory & Motor Research* 7: 399–420). The PrV nucleus receives collateral excitatory input from the SpVC and SpVI nuclei and inhibition from the SpVI nucleus (Furuta T, Timofeeva E, Nakamura K, et al. (2008) Inhibitory gating of vibrissal inputs in the brainstem. *Journal of Neuroscience* 28: 1789–1797). **(trigeminal nuclei → facial nuclei)** The facial nucleus contains five subnuclei, of which the lateral subnucleus is involved in vibrissa control (Papez JW (1927) *Journal of Comparative Neurology* 42: 159–191; Martin MR and Lodge D (1977) *Brain Research* 38: 206–210). Vibrissa areas SpVC, PrV, and SpVI connect to the lateral subnucleus, primarily through ipsilateral projections. The trigeminal loop is closed by direct projection from PrV, SpVC, and SpV1 to the facial nucleus (Erzurumlu RS and Killackey HP (1979) *Journal of Comparative Neurology* 188: 75–86; Hattox AM, Priest CA, and Keller A (2002) *Journal of Comparative Neurology* 442: 266–276) and indirect pathways within the hindbrain via the pontomedullary reticular formation (Dauvergne C, Pinganaud G, Buisseret P, Buisseret-Delmas C, and Zerari-Mailly F (2001) *Neuroscience Letters* 311: 109–112;

rostral and lateral areas responding to vibrissa-related inputs from the contralateral trigeminal nuclei. Descending afferents from the superior colliculus project to the lateral subnucleus of the contralateral facial nucleus to complete the loop. An additional input that converges to the same laminae arises from ipsilateral vibrissa primary motor (M1) cortex.

Zerari-Mailly F, Pinganaud G, Dauvergne C, Buisseret P, and Buisseret-Delmas CJ (2001) *Journal of Comparative Neurology* 429: 80–93). The direct projection, and possibly the indirect projection, is predominantly excitatory and results in positive feedback (Nguyen Q-T and Kleinfeld D (2005) *Neuron* 45: 447–457). **(facial nucleus → vibrissae)** The lateral aspect facial nucleus sends projections to the intrinsic muscles surrounding each vibrissa (Arvidsson J (1982) *Journal of Comparative Neurology* 211: 84–92; Dorfl J (1982) *Journal of Anatomy* 135: 147–154; Dorfl J (1985) *Journal of Anatomy* 142: 173–184; Arvidsson J and Rice F L (1991) *Journal of Comparative Neurology* 309: 1–16), and medial aspects are believed to project to the extrinsic muscles (**Figures 2(a)–2(c)**; Klein B and Rhoades R (1985) *Journal of Comparative Neurology* 232: 55–69; Isokawa-Akesson M and Komisaruk BR (1987) *Experimental Brain Research* 65: 385–398). The lateral subnucleus of the facial nucleus contains a somatotopic map of the vibrissae (Martin MR and Lodge D (1977) *Brain Research* 38: 206–210). **Midbrain loops: (trigeminal nuclei → superior colliculus)** The trigeminal nuclei project to vibrissa somatotopic areas of the superior colliculus (Drager UC and Hubel DH (1976) *Journal of Neurophysiology* 39: 91–101; Killackey H and Erzurumlu R (1981) *Journal of Comparative Neurology* 201: 221–242; Huerta M, Frankfurter A, and Harting J (1983) *Journal of Comparative Neurology* 220: 147–167; Steindler DA (1985) *Journal of Comparative Neurology* 237: 155–175; Bruce LL, McHaffie JG, and Stein BE (1987) *Journal of Comparative Neurology* 262: 315–330; Jacquin M, Barcia M, and Rhoades RW (1989) *Journal of Comparative Neurology* 282: 45–62; Benett-Clarke CA, Chiaia NL, Jacquin MF, and Rhoades RW (1992) *Journal of Comparative Neurology* 320: 323–338). Hemelt ME and Keller A (in press) Superior colliculus control of vibrissa movements. *Journal of Neurophysiology*. The connection from nucleus SpVI appears to be the strongest (Killackey H and Erzurumlu R (1981) *Journal of Comparative Neurology* 201: 221–242; Huerta M, Frankfurter A, and Harting J (1983) *Journal of Comparative Neurology* 220: 147–167; Jacquin M, Barcia M, and Rhoades RW (1989) *Journal of Comparative Neurology* 282: 45–62); it terminates in the intermediate and deep layers of the lateral and rostral aspects of the colliculus. The projections from the trigeminal ganglia to colliculus are likely to be collaterals of projections to thalamus (Benett-Clarke CA, Chiaia NL, Jacquin MF, and Rhoades RW (1992) *Journal of Comparative Neurology* 320: 323–338; Mantle-St. John LA and Tracey DJ (1987) *Journal of Comparative Neurology* 255: 259–271). **(superior colliculus → facial nucleus)** The intermediate and deep layers of the colliculus project to the lateral subnucleus of the facial nerve nucleus (Isokawa-Akesson M and Komisaruk BR (1987) *Experimental Brain Research* 65: 385–398; Miyashita E, Keller A, and Asanuma H (1994) *Experimental Brain Research* 99: 223–232; Miyashita E, and Shigemi M (1995) *Neuroscience Letters* 195: 69–71). **(trigeminal nuclei → cerebellum)** The trigeminal nuclei provide vibrissa sensory input to the cerebellum via a direct pathway, that is, the SpVI nucleus projects directly to the cerebellum (Woolston DC, LaLonde JR, and Gilson JM (1982) *Journal of Neurophysiology* 48: 160–173), and two indirect pathways, that is, the SpVI and SpVC nuclei project via the inferior olive climbing fibers and the PrV, SpVI, and SpVC nuclei project via pontine mossy fibers (Huerta M, Frankfurter A, and Harting J (1983) *Journal of Comparative Neurology* 220: 147–167; Steindler DA (1985) *Journal of Comparative Neurology* 237: 155–175; Jacquin M, Barcia M, and Rhoades RW (1989) *Journal of Comparative Neurology* 282: 45–62; Mantle-St. John LA and Tracey DJ (1987) *Journal of Comparative Neurology* 255: 259–271; Smith RL (1973) *Journal of Comparative Neurology* 148: 423–446; Watson CRR and Switzer III RC (1978) *Neuroscience Letters* 10: 77–82; Swenson RS, Kosinski RJ, and Castro AJ (1984) *Journal of Comparative Neurology* 222: 301–311). Projections from the trigeminal nuclei to the inferior olive overlap those from the olive to the cerebellum; the target areas in the cerebellum include *crura* I and II and the paramedian lobule and uvula (Huerta M, Frankfurter A, and Harting J (1983) *Journal of Comparative Neurology* 220: 147–167; Watson CRR and Switzer III RC (1978) *Neuroscience Letters* 10: 77–82); all these areas have facial receptive fields. **(superior colliculus ↔ cerebellum)** The colliculus sends projections to the cerebellar cortex, including target areas *crura* I and II, through both the inferior olive and the pons (Kassel J (1980) *Brain Research* 202: 291–305). The deep cerebellar nuclei send a projection back to the colliculus (Lee HS, Kosinski RJ, and Mihailoff GA (1989) *Neuroscience* 28: 725–734; Westby GW, Collinson C, and Dean P (1993) *European Journal of Neuroscience* 5: 1378–1388; Westby GW, Collinson C, Redgrave P, and Dean P (1994) *European Journal of Neuroscience* 6: 1335–1342) to form a 'colliculus → cerebellum → colliculus' loop. **Forebrain loops: (trigeminal nuclei → dorsal thalamus)** The PrV nucleus sends ascending projections to ventral posteromedial (VPM) thalamic nuclei, and the SpVI nucleus sends projections to posterior (PO) nuclei and to the ventral-lateral area of VPM (VPM-vl) thalamus as well as the dorsal-medial area of VPM (VPM-dm) thalamus (Lund RD and Webster KE (1967) *Journal of Comparative Neurology* 130: 313–328; Smith RL (1973) *Journal of Comparative Neurology* 148: 423–446; Erzurumlu RS and Killackey HP (1980) *Neuroscience*. 5: 1891–1901; Hoogland PV, Welker E, and Van der Loos H (1987) *Experimental Brain Research* 68: 73–87; Mantle-St. John LA and Tracey DJ (1987) *Journal of Comparative Neurology* 255: 259–271; Jacquin M, Barcia M, and Rhoades RW (1989) *Journal of Comparative Neurology* 282: 45–62; Killackey HP, Jacquin M, and Rhoades RW (1990) In: *Development of Sensory Systems in Mammals*, pp. 403–429. New York: Wiley; Chiaia NL, Rhoades RW, Bennett-Clark CA, Fish SE, and Killackey HP (1991) *Journal of Comparative Neurology* 314: 201–216; Benett-Clarke CA, Chiaia NL, Jacquin MF, and Rhoades RW (1992) *Journal of Comparative Neurology* 320: 323–338; Diamond ME, Armstrong-James M, Budway MJ, and Ebner FF (1992) *Journal of Comparative Neurology* 319: 66–84; Williams MN, Zahm DS, and Jacquin MF (1994) *European Journal of Neuroscience* 6: 429–453; Veinante P and Deschenes M (1999) *Journal of Neuroscience* 19: 5085–5095; Pierret T, Lavallee P, and Deschenes M (2000) *Journal of Neuroscience* 20: 7455–7462. Yu C, Derdikman D, Haidarliu S, and Ahissar E (2006) Parallel thalamic pathways for whisking and touch signals in the rat. *PLoS Biology* 4:e124; Simons DJ, Carvell GE, Kyriazi HT, and Bruno RM (2007) Thalamocortical conduction times and stimulus-evoked responses in the rat whisker-to-barrel system. *Journal of Neurophysiology* 98: 2842–2847; Masri R, Bezdudnaya T, Trageser JC, and Keller A. (in press) Encoding of stimulus frequency and sensor motion in the posterior medial thalamic nucleus. *Journal of Neurophysiology*.)The representation of the vibrissae forms a somatotopic map ('barreloids') in VPM thalamus (Van Der Loos H (1976) *Neuroscience Letters* 2: 1–6; Sugitani M, Yano J, Sugai T, and Ooyama H (1990) *Experimental Brain Research* 81: 346–351) and a diffuse map in PO thalamus (Nothias F, Peschanski M,

s0050 ## Cerebellar Loops

p0090 The pontine–cerebellar system appears to function at a hindbrain level in a loop that involves direct connections from the contralateral SpVI nucleus and indirect connections between contralateral trigeminal nuclei and the ipsilateral superior colliculus (**Figure 4**). For the latter case, the trigeminal nuclei project to both the pons and the inferior olive, which in turn directly project to crura 1 and 2 in the cerebellum. Similar inputs, which project to the same crura in cerebellum,

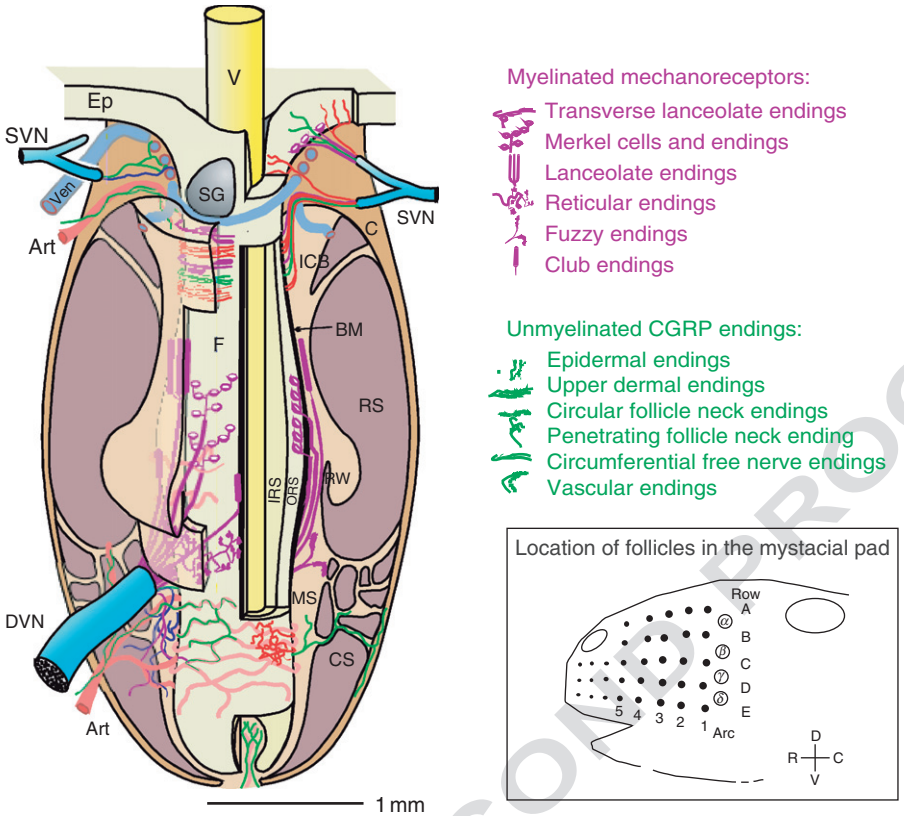
and Besson J-M (1988) *Brain Research* 447: 169–174; Fabri M and Burton H (1991) *Brain Research* 538: 351–357) and VPM-vl (Pierret T, Lavallee P, and Deschenes M (2000) *Journal of Neuroscience* 20: 7455–7462). **(trigeminal nuclei → zona incerta)** Nuclei in zona incerta (ZI) consist exclusively of inhibitory projection neurons; those involved in vibrissa somatosensation receive input from SpVI (Kolmac CI, Power BD, and Mitrofanis J (1998) *Journal of Comparative Neurology* 396: 544–555). ZI forms a negative (**-**) feedback connection to PO thalamus (Trageser JC and Keller A (2004) *Journal of Neuroscience* 24: 8911–8915; Lavallee P, Urbain N, Dufresne C, Bokor H, Acsady L, and Deschenes M (2005) *Journal of Neuroscience* 25: 7489–7498) that is inactivated only by descending input from vibrissa cortex Urbain N and Deschenes M (2007) Motor cortex gates vibrissal responses in a thalamocortical projection pathway. *Neuron* 56: 714–725 **(dorsal thalamus ↔ neocortex)** Thalamic regions VPM, PO, and ZI project to primary (S1), secondary (S2), and posterior ventral areas of sensory cortex, and cortex sends feedback projections to VP, PO, and the trigeminal nuclei (Wise SP and Jones EG (1977) *Journal of Comparative Neurology* 175: 129–158; Donoghue JP, Kerman KL, and Ebner FF (1979) *Journal of Comparative Neurology* 183: 647–664; Donoghue JP and Kitai ST (1981) *Journal of Comparative Neurology* 201: 1–13; Carvell GE and Simons DJ (1987) *Journal of Comparative Neurology* 265: 409–427; Hoogland PV, Welker E, and Van der Loos H (1987) *Experimental Brain Research* 68: 73–87; Koralek K, Jensen KF, and Killackey HP (1988) *Brain Research* 463: 346–351; Welker E, Hoogland PV, and van der Loos H (1988) *Experimental Brain Research* 73: 411–435; Jacquin MF, Wiegand MR, and Renehan WE (1990) *Journal of Neurophysiology* 64: 3–27; Chiaia NL, Rhoades RW, Bennett-Clark CA, Fish SE, and Killackey HP (1991) *Journal of Comparative Neurology* 314: 201–216; Chiaia NL, Rhoades RW, Fish SE, and Killackey HP (1991) *Journal of Comparative Neurology* 314: 217–236; Diamond ME, Armstrong-James M, Budway MJ, and Ebner FF (1992) *Journal of Comparative Neurology* 319: 66–84; Deschênes M, Bourassa J, and Parent A (1996) *Neuroscience* 72: 679–687; Lévesque M, Charara A, Gagnon S, Parent A, and Deschênes M (1996) *Brain Research* 709: 311–315; Shepherd GM and Svoboda K (2005) *Journal of Neuroscience* 25: 5670–5679; Landisman CE and Connors BW (2007) VPM and PoM Nuclei of the rat somatosensory thalamus: Intrinsic neuronal properties and corticothalamic feedback. *Cerebral Cortex.* 17: 2853–2865, Urbain N and Deschenes M (2007) A new thalamic pathway of vibrissal information modulated by the motor cortex. *Journal of Neuroscience* 27: 12407–12412; Bokor H, Acsady L, and Deschenes M (2008) Vibrissal responses of thalamic cells that project to the septal columns of the barrel cortex and to the second somatosensory area. *Journal of Neuroscience* 28: 5169–5177); The projection from ZI thalamus to S1 cortex is unique in providing an inhibitory input (Chapin JK, Schneider JS, Nicolelis M, and Lin C-S (1990) *Science* 248: 1553–1556; Nicolelis MAL, Chapin JK, and Lin RCS (1992) *Brain Research* 577: 134–141). **(direct intercortical connections)** Vibrissa S1 cortex forms reciprocal projections with other vibrissa sensory areas in neocortex (Carvell GE and Simons DJ (1987) *Journal of Comparative Neurology* 265: 409–427; Chapin JK, Sadeq M, and Guise JLU (1987) *Journal of Comparative Neurology* 263: 326–346; Welker E, Hoogland PV, and van der Loos H (1988) *Experimental Brain Research* 73: 411–435; Fabri M and Burton H (1991) *Journal of Comparative Neurology* 311: 405–424; Hoffer ZS, Hoover JE, and Alloway KD (2003) *Journal of Comparative Neurology* 466: 525–544; Chakrabarti S and Alloway KD (2006) *Journal of Comparative Neurology* 498: 624–636) and with vibrissa motor (M1) cortex (White EL and deAmicis RA (1977) *Journal of Comparative Neurology* 175: 455–482; Fabri M and Burton H (1991) *Journal of Comparative Neurology* 311: 405–424; Aroniadou VA and Keller A (1993) *Journal of Neurophysiology* 70: 1493–1553; Keller A (1993) *Cerebral Cortex* 3: 430–441; Miyashita E, Keller A, and Asanuma H (1994) *Experimental Brain Research* 99: 223–232; Izraeli R and Porter LL (1995) *Experimental Brain Research* 104: 41–54; Veinante P and Deschenes M (2003) *Journal of Comparative Neurology* 464: 98–103; Hoffer ZS, Arantes HB, Roth RL, and Alloway KD (2005) *Journal of Comparative Neurology* 488: 82–100; Chakrabarti S and Alloway KD (2006) *Journal of Comparative Neurology* 498: 624–636). The representation of the vibrissae forms a somatotopic map in S1 cortex (Woolsey TA, Welker C, and Schwartz RH (1974) *Journal of Comparative Neurology* 164: 79–94; Durham D and Woolsey TA (1977) *Brain Research* 137: 169–174)-'barrels'- and S2 (Carvell GE and Simons DJ (1986) *Somatosensory Research* 3: 213–237; Kleinfeld D and Delaney KR (1996) *Journal of Comparative Neurology* 375: 89–108). Note that M1 is taken as the parasagittal agranular medial area. **(indirect intercortical connections)** Feedback from neocortex to thalamus via projections from cortical layer 6 provides a pathway for different cortical columns and regions to intact in thalamus (Deschenes M, Veinante P, and Zhang Z-W (1998) *Brain Research Reviews* 28: 286–308). This effect is enhanced by an effective intrathalamic connection mediated by thalamoreticular and recticulothalmic projections (Crabtree JW, Collingridge GL, and Isaac JT (1998) *Nature Neuroscience* 1: 289–394; Crabtree JW and Isaac JT (2002) *Journal of Neuroscience* 22: 8754–8761; Golomb D, Ahissar E, and Kleinfeld D (2005) *Journal of Neurophysiology* 95: 1735–1750). **(neocortex → superior colliculus)** Both sensory and motor cortices send descending projections to the superior colliculus (Wise SP and Jones EG (1977) *Journal of Comparative Neurology* 175: 129–158; Killackey H and Erzurumlu R (1981) *Journal of Comparative Neurology* 201: 221–242; Welker E, Hoogland PV, and van der Loos H (1988) *Experimental Brain Research* 73: 411–435; Mercier BE, Legg CR, and Glickstein M (1990) *Proceedings of the National Academy of Sciences USA*87: 4388–4392). Cellular interactions between the descending cortical M1 projection to colliculus and from the colliculus to the facial nucleus support the relay of motor commands to the facial nucleus (Miyashita E and Shigemi M (1995) *Neuroscience Letters*195: 69–71). **(motor cortex → reticular nuclei)** A direct connection from vibrissa M1 cortex to nuclei in the reticular formation (Miyashita E, Keller A, and Asanuma H (1994) *Experimental Brain Research* 99: 223–232; Hattox AM, Priest CA, and Keller A (2002) *Journal of Comparative Neurology* 442: 266–276) is suggestive of a central pattern generator (CPG) by analogy with the CPG for mastication (Nozaki S, Iriki A, and Nakamura Y (1986) *Journal of Neurophysiology* 55: 806–825) and provides descending control of the vibrissae. The ambiguus and parvocellular reticular nuclei in the medulla, as well as the pontine reticular nucleus, are capable of evoking vibrissa movement and further receive input from M1 cortex (Hattox AM, Priest CA, and Keller A (2002) *Journal of Comparative Neurology* 442: 266–276). Critically, direct input from M1 terminates in the lateral facial nucleus and may directly drive the vibrissae (Grinevich V, Brecht M, and Osten P (2005) *Journal of Neuroscience* 25: 8250–8258).

t0010 **Table 2** Afferent nuclei to the lateral aspect of the facial nucleus

Afferent nucleus	*VMCtx afferent*	*Evoked movement*	*Transmitter*
Myelencephalon (medulla)			
Dorsal motor nucleus of the vagus	x		
Reticular nucleus of the medulla	x		
Intermediate reticular nucleus	x		GABA, Gly
Lateral reticular nucleus	x		
Ambiguus nucleus	x	x	
Gigantocellular reticular nucleus	x		GABA, Gly, 5-HT
Parvocellular reticular nucleus	x	x	
Spinal vestibular nuclei	x		GABA, Gly
External cuneate nucleus			
Nucleus solitary tract			
Raphe magnus, pallidus, obscurus			5-HT
Paragigantocellular reticular nucleus			
Spinal trigeminal nucleus			GABA, Gly
Hypoglossal nucleus			
Metencephalon (pons)			
Pontine reticular nucleus	x	x	GABA, Gly
Ventral parabrachial nucleus	x		
Kölliker-Fuse nucleus	x		
Paralemniscal nucleus	x		GABA, Gly
Lateral parabrachial nucleus	x		
Subpedencular tegmental nucleus	x		
Intertrigeminal nucleus	x		
Subcoeruleus nucleus	x		
Ventral nucleus of the lateral lemniscus			
Motor trigeminal nucleus			
Pediculopontine tegmental			
Medial parabrachial nucleus			
Mesencephalon (midbrain)			
Deep mesencephalic nucleus	x		
Oculomotor nucleus	x		
Central gray	x		
Superior colliculus	x	x	
Red nucleus	x	x	
Edinger-Westphal nucleus	x		
Pararubral nucleus	x		
Nucleus raphe dorsalis			
Interstitial nucleus of medial longitudinal fasciculus			
Retrorubral nucleus			
Nucleus Darkschewitsch			
Substantia nigra			
Primary motor cortex (VMCtx)	–	x	Glutamate

The listings are based on anatomical studies. Neurons in the lateral facial nucleus integrate inputs from about 40 presynaptic sources (Fay RA and Norgren R (1997) *Brain Research Reviews* 25: 276–290). These include reticular motor nuclei that are potentially involved with the generation of the oscillatory drive for rhythmic whisking, such as the parvocellular nucleus (Mogoseanu D, Smith AD, and Bolam JP (1994) *Experimental Brain Research* 101: 427–438; Hattox AM, Priest CA, and Keller A (2002) *Journal of Comparative Neurology* 442: 266–276), reticular nuclei that are involved with other oromotor behaviors (Travers JB (1995) In: Paxinos G (ed.) *The Rat Nervous System*, 2nd edn., pp. 239–255. San Diego: Academic Press), such as suckling and licking, trigeminal sensory nuclei, whose input to the facial nucleus completes a feedback loop that encompasses the vibrissae; cerebellar deep nuclei, whose input also completes a feedback loop (Huerta M, Frankfurter A, and Harting J (1983) *Journal of Comparative Neurology* 220: 147–167), input from the superior colliculus (Miyashita E, Keller A, and Asanuma H (1994) *Experimental Brain Research* 99: 223–232; Miyashita E and Shigemi M (1995) *Neuroscience Letters* 195: 69–71), and direct input from the primary motor cortex (Grinevich V, Brecht M, and Osten P (2005) *Journal of Neuroscience* 25: 8250–8258). The column labeled 'VMCtx afferent' denotes that the nucleus receives a projection from primary motor cortex. VMCtx, vibrissa primary motor cortex. The column labeled 'Evoked movement' indicates that activation of this region in anesthetized animals leads to vibrissa movement.

arise from the intermediate and deep layers of the superior colliculus. The relative means by which these inputs contribute to a pronounced sensory response in crus 2, and a more restricted response in crus 1, is unknown. Finally, the cerebellar Purkinje cells form synapses on the cerebellar nuclei, which provide output projections to superior colliculus to complete this intermediary-level loop.



f0025 **Figure 5** The follicle contains both superficial (SVN) and deep (DVN) nerve terminals that report both self-movement and contact of the vibrissa. The follicle sits in the mystacial pad as part of an array of five rows and roughly ten arcs of follicle/vibrissa units (**insert in lower right corner**). Rows are labeled by letters and arcs by numbers. The four posterior vibrissa, referred to as straddlers, are labeled by Greek letters. In the awake and aroused animal, the sinuses (CS and RS) are engorged with blood, which stiffens the structure. Both self-movement and touch are presumed to be coded by both the superficial and deep nerves, which project to the trigeminal ganglion and have similar passive response properties (Waite PME and Jacquin MF (1992) *Journal of Comparative Neurology* 322: 233–245). The DVN ultimately projects to the PrV, SpVO, SpVI, and SpVC trigeminal nuclei (Hayashi H (1985) *Journal of Comparative Neurology* 237: 195–215; Jacquin MF, Stennett RA, Renehan WE, and Rhoades RW (1988) *Journal of Comparative Neurology* 267: 107–130), and the SVN has been reported to project only to SpVC (Martin Deschenes, unpublished observations). This illustration was adapted from Arvidsson J and Rice FL (1991) Central projections of primary sensory neurons innervating different parts of the vibrissae follicles and intervibrissal skin on the mystacial pad of the rat. *Journal of Comparative Neurology* 309: 1–16; see also Rice FL, Fundin BT, Pfaller K, and Arvidsson J (1994) *Experimental Brain Research* 99: 233–246. A mechanical model of the follicle is given by Mitchinson B, Gurney KN, Redgrave P, et al. (2004) *Proceedings of the Royal Society of London, Series B: Containing Papers of a Biological Character* 271: 2509–2516. V, vibrissa; SG, sebacceous gland; RW, ringwulst; RS, ring sinus; ORS, outer root sheath; MS, mesenchymal sheath; IRS, inner root sheath; ICB, inner conical body; F, follicle; Ep, epidermis; CS, cavernous sinus; C, follicle-sinus-complex capsule; BM, basement membrane; CGRP, calcitonin gene-related peptide; and Art, arteriole.

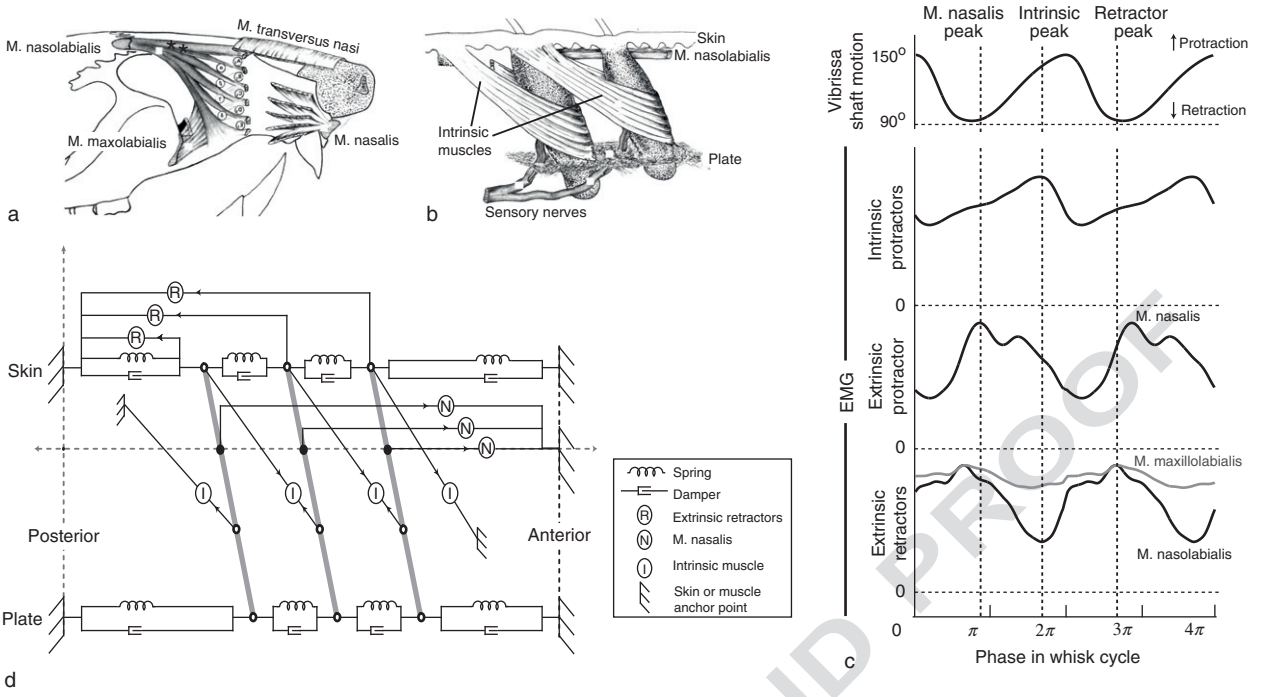
s0055 ## Thalamic-Forebrain Loop

p0095 Multiple structures in ventral and dorsal thalamus receive input from the trigeminal nuclei. Only one of these, zona incerta (ZI) in the ventral thalamus, projects directly back to the superior colliculus (**Figure 4**), where it forms inhibitory connections with the superior colliculus. Thus, ZI thalamus appears to function as a forebrain-level intermediary in a loop that involves the trigeminal nuclei and the colliculus. Further, inhibitory projections from ZI thalamus serve to gate afferents from PO thalamus to vibrissa SI cortex. This gate is removed by descending inputs from vibrissa M1 cortex.

s0060 ## Neocortical Loop

p0100 Cortex receives input from the trigeminal nuclei along four streams that pass through the thalamus (**Figure 4**):

1. The well-known lemniscal pathway that ascends from the PrV nucleus via the central region of the ventral posterior medial (VPM) thalamus and projects to vibrissa primary somatosensory (S1) cortex. Neurons in VPM thalamus rapidly respond to stimulation of a single vibrissa in anesthetized animals, whose receptive fields are referred to as barreloids. Similarly, neurons in the granular layer



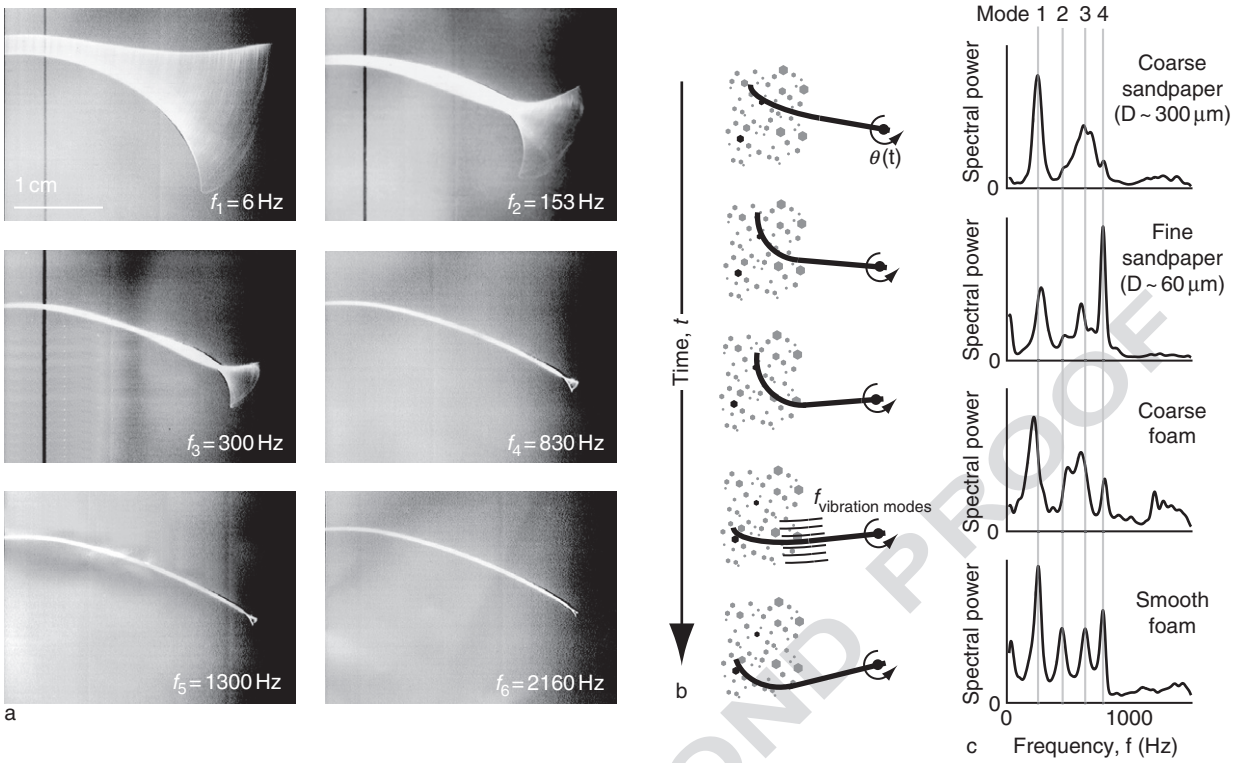
f0030 **Figure 6** Geometry, musculature, and motion of the follicles and vibrissae. (a) Drawing of extrinsic musculature in mouse; a similar pattern occurs in rat. Four extrinsic muscles invade the mystacial pad while maintaining external attachment points. The retractor M. nasolabialis attaches dorsal–caudal to the pad and runs superficially below the skin. A second retractor, m. maxillolabialis, attaches ventral–caudal to the pad and fuses with the fibers of m. nasolabialis as they invade the pad. M. nasalis attaches rostral to the pad at the nasal septum and runs deep to the follicles as it extends caudally. M. transversus nasi lies transverse to the snout and runs superficially through the pad. (b) Drawing of intrinsic musculature in mouse. The intrinsic muscles join adjacent follicles (insert in **Figure 5**) of a single row. Each muscle attaches medially and laterally to the superior part of the caudal follicle while forming a sling around the lower third of the rostral follicle. The skin and other connective tissue, such as the fibrous plate, provide a passive restoring force. Superficial extrinsic muscles run just below the skin. (c) A mechanical model of a row of three vibrissae, shown in the rest state, to illustrate how the extrinsic and intrinsic muscles pull on the vibrissae. The attachment points are illustrated for the springs, dampers, and muscles, which together from an active vasoelastic element. The approximate relationship between these points is conserved, but the figure is not drawn to scale. Arrows indicate the direction of muscle forces, which point away from the attachment points. (d) Average vibrissa motion and muscle activity from a head-restrained rat. Each whisk was linearly mapped from time onto the range of 0 to 2π radians and the average taken across phase. Average traces (1750 whisks) are repeated to display two cycles; only motion along the A–P axis is shown. The rectified electromyogram values were normalized by the maximum voltage of each trace. The dashed vertical lines indicate the three phases of average muscle activity. The drawings in panels (a) and (b) were adapted from Dorfl J (1982) The musculature of the mystacial vibrissae of the white mouse. *Journal of Anatomy* 135: 147–154; see also Dorfl J (1985) The innervation of the mystacial region of the white mouse: A topographical study. *Journal of Anatomy* 142: 173–184, and the model and data in panels (c) and (d) from Hill DN, Bermejo R, Zeigler HP, and Kleinfeld D (2008) Biomechanics of the vibrissa motor plant in rat: Rhythmic whisking consists of triphasic neuromuscular activity. *Journal of Neuroscience* 28: 3438–3455.

of S1 cortex respond to stimulation of a single vibrissa, whose receptive fields are formed by afferents from VPM thalamus and are referred to as barrels.

2. The well-known paralemniscal pathway that ascends from the rostral part of the SpVI nucleus, passes through posterior medial (PO) thalamus, and projects down to the superior colliculus as well as up to agranular layers 1 and 5 in S1 cortex, vibrissa secondary somatosensory (S2), and vibrissa motor (M1) cortices. Neurons in PO thalamus receive inhibitory projections from ZI thalamus; this inhibitory block is relieved by projections from M1 cortex to PO thalamus.

3. A recently described extralemniscal pathway that ascends from the caudal part of the SpVI nucleus, passes through the ventrolateral border of VPM (VPM-vl) thalamus, and projects to S1 and S2 cortices. Neurons in VPM-vl thalamus rapidly respond to stimulation of multiple vibrissae in anesthetized animals.

4. A recently described extralemniscal pathway that ascends from the part of the PrV nucleus that contains large neurons with multivibrissa responses, passes through the dorsomedial border of VPM (VPM-dm) thalamus that lies next to PO thalamus, and projects to S1 cortex. Neurons in VPM-dm thalamus rapidly respond to stimulation of multiple vibrissae in anesthetized animals.



f0035 **Figure 7** Dynamics of a single vibrissa. (a) Photographs of the motion of the straddler vibrissa γ (see insert, **Figure 5**) at successive resonant frequencies. The vibrissa was glued to a small voice coil that was driven by a wave generator. Note that the displacements are shifted to the finer and more distal parts of the vibrissa at progressively higher-order modes. Data was taken in the laboratory following reports by Hartmann (Hartmann MJ, Johnson NJ, Towal RB, and Assad C (2003) Mechanical characteristics of rat vibrissae: Resonant frequencies and damping in isolated whiskers and in the awake behaving animal. *Journal of Neuroscience* 23: 6510–6519) and Moore (Neimark MA, Andermann ML, Hopfield JJ, and Moore CI (2003) Vibrissa resonance as a transduction mechanism for tactile encoding. *Journal of Neuroscience* 23: 6499–6509; Ritt JT, Andermann ML, and Moore CI (2008) Emdodied information processing: vibrissa mechanics and texture features shape micromotions in actively sensing rats. *Neuron* 57: 599–613). (b) Cartoon that shows how the drag on a vibrissa can couple to the intrinsic mechanical vibrations (modes) of the vibrissa via 'stick–slip' friction. This effect may be relevant for the encoding of texture. Adapted from Mehta SB and Kleinfeld D (2004) Frisking the whiskers: Patterned sensory input in the rat vibrissa system. *Neuron* 41: 181–184. (c) Spectral power of the vibrations measured at the base of a vibrissa artificially whisked across different textures, in support of a model in which different surfaces preferentially excite different modes of a vibrissa (Moore CI and Andermann ML (2005) In: Ebner FF (ed.) *Neural Plasticity in Adult Somatic Sensory-Motor Systems.* Boca Raton, FL: CRC Press). Adapted from Fend M, Bovet S, Yokoi H, and Pfeifer R (2003) An active artificial whisker array for texture discrimination. In: *Proceedings of the IEEE/RSJ International Conference on Intelligent Robots and Systems* (IROS), Las Vegas, NV, October.

All four thalamic areas receive feedback projections from the infragranular layers of S1 and S2 cortices. Further, VPM-dm thalamus receives feedback projections from M1 cortex.

p0105 There is evidence for the segregation of neuronal signals among the different pathways. The lemniscal pathway appears to convey a combination of touch and position signals while the extralemniscal pathway appears to convey primarily touch-based signals. The evidence for signaling along the paralemniscal pathway is inconsistent. Activation of neurons in PO thalamus in anesthetized animals occurs via feedback from S1 cortex. On the other hand, during whisking neurons in PO thalamus may be driven directly by sensory input and report vibrissa position. Independent of this segregation of information, the thalamic nuclei interact via reciprocal connections to the reticular thalamic nucleus, which may lead to a mixing of touch and position signals, among others. Further, sensory and motor cortex interact through corticocortical projections, and there is considerable feedback among thalamic-mediated connections between cortical areas (**Figure 4**). This implies that sensory and motor functions are likely to be distributed throughout these areas.

p0110 The cortical loop is closed by corticospinal-like projections from M1 cortex to the vibrissa areas of the facial nucleus, as well as by projections from both S1 and M1 cortices to the superior colliculus, which in turn sends descending projections to motor neurons in the facial nucleus. By analogy with the

anatomy of corticospinal projections in primates, there may be undiscovered projections from vibrissa S1 cortex to the facial nucleus.

s0065 **Back to the Brain Stem**

p0115 Two more points bear on the nested topology of the vibrissa system. The first is that a single synaptic connection from neurons in the trigeminal complex to those in the facial nucleus (* in **Figure 4**) is paralleled, from hindbrain to midbrain to forebrain, by connections of increasing complexity. The second and related issue is that the motor neurons in the lateral facial nucleus appear as arbitrators of activity from loops at all levels, receiving input from neurons in nearly 40 identified nuclei (**Table 2**). This makes the motor neurons arbitrators of motor commands to the vibrissae.

s0070 Mechanics of the Vibrissae

p0120 The vibrissae are shaped as round, tapered beams. Videographs of the vibrissae as rats whisk clearly show that the vibrissae flex as a consequence of the muscular forces that propel them forward at their base as well as the forces that act on contact (**Figure 1(b)**). A result of this flexibility is that, as for all extended mechanical systems, individual vibrissae exhibit a set of resonances (**Figure 7(a)**). The lowest-order resonance exhibits bending all along the vibrissae, while higher-order resonances exhibit bending that is localized toward the tip.

p0125 What are the potential ethological roles that vibrations of the vibrissae can play? One is that a vibrissa can twang when it contacts an object, so that touch will yield a rapid succession of taps rather than a single tap. The frequency of these taps will depend on the location of contact along the shaft of the vibrissa but will be in the order of the roughly 100 Hz resonant frequencies. This rate is sufficient to induce short-term synaptic plasticity; so mechanical resonance may contribute to the transmission probability of a contact event.

p0130 The vibrations of the vibrissae may also play a role in sensing texture. The vibrissae may alternately stick and slip as they are dragged across a rough surface (**Figure 7(b)**). As the vibrissa slips, the resultant vibrations of the shaft will be a superposition of the intrinsic vibrations of the vibrissa. It is natural to posit that differences between surfaces are expressed by the extent to which different modes are favored. In particular, when the tip of a vibrissa is moved across surfaces of differing roughness, the set of frequencies of the vibration is essentially the same for all surfaces, but the relative amplitude associated with each vibration will depend on the detailed properties of the surface (**Figure 7(c)**).

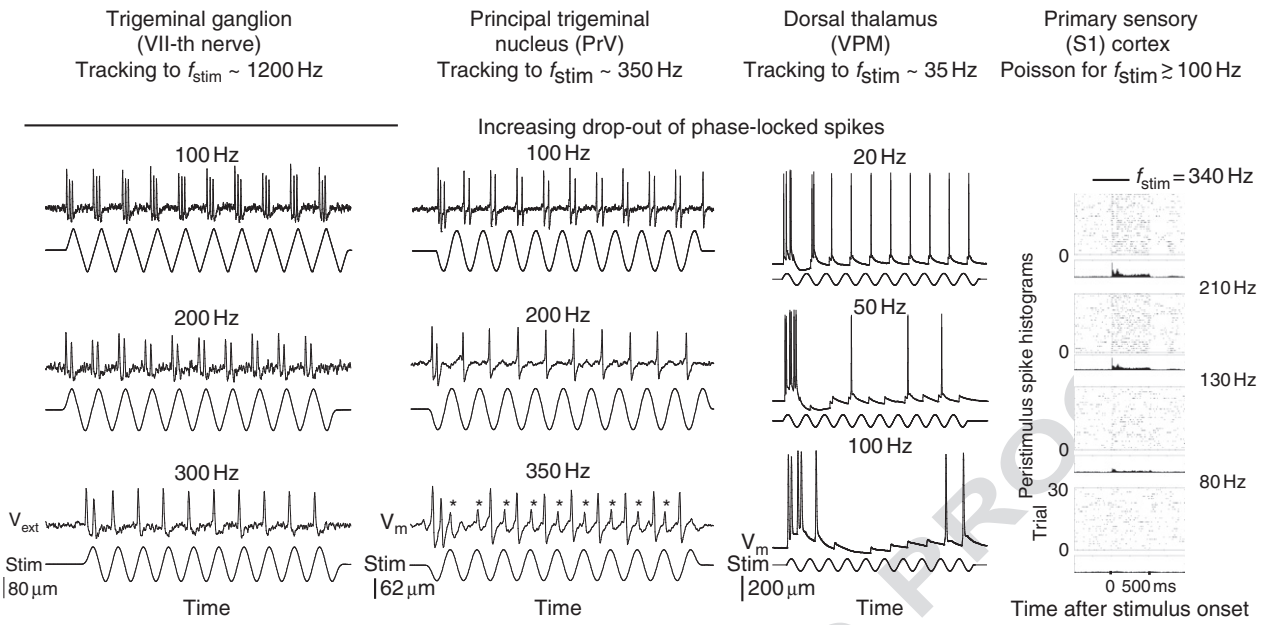
Transmission of High-Frequency Signals s0075

The timing of neuronal signals from the initial contact of a vibrissa with an object to their representation in vibrissa S1 cortex is central to perception. This timing is heavily dependent on the state of the animal, that is, sessile versus aroused, as mediated through synaptic changes and cellular adaptation. While modulation of the timing might complicate the processing of sensory signals, simplicities appear in two limits as signals ascend the lemniscal pathway (**Figure 4**). For punctate signals, as might occur with a sharp initial contact, there is a high probability that the signal will successfully propagate up through cortex. In contrast, for steady-state periodic signals, the probability of transmission can be low (**Figure 8**). At the level of primary sensory neurons, periodic signals are faithfully transduced up to frequencies of ~1200 Hz. However, this signal begins to degrade at the level of the PrV nucleus in brain stem, such that for vibration frequencies above ~350 Hz, roughly half the spikes are dropped (* in bottom row, second column, of **Figure 8**). By the level of VPM thalamus, roughly half the spikes are dropped for frequencies above ~35 Hz, and by the level of S1 cortex, roughly half the spikes are dropped for frequencies above ~5 Hz. Thus the ability of individual neurons to faithfully follow rapid movements of the vibrissa degrades with higher-order structures in the sensorimotor system. p0135

How are high-frequency events, such as vibrations, encoded in cortex? First, even the response in the primary sensory cells may be insufficient to track the finest surface detail. In particular, the maximum response frequency of 1200 Hz corresponds to the rhythmic motion of the tip of a vibrissa across a corrugated surface with a pitch of only ~200 μm, which is rather coarse. Second, while neurons in S1 cortex cannot track the phase of periodic inputs above ~35 Hz, at least in anesthetized animals the high-frequency sensory inputs are coded as an approximate Poisson process (right column in **Figure 8**). It is interesting that the rate of this spike process is proportional to the logarithm of the vibration frequency of the vibrissa, that is, p0140

$$\text{Firing Rate} \propto 2 \ln \{\text{Vibration Frequency}\} + \text{Constant}.$$

This is in the form of Weber's Law, but for frequencies rather than intensity. The coarseness of logarithmic coding suggests that comparisons of rhythmic inputs with slightly different frequencies will be problematic. p0145

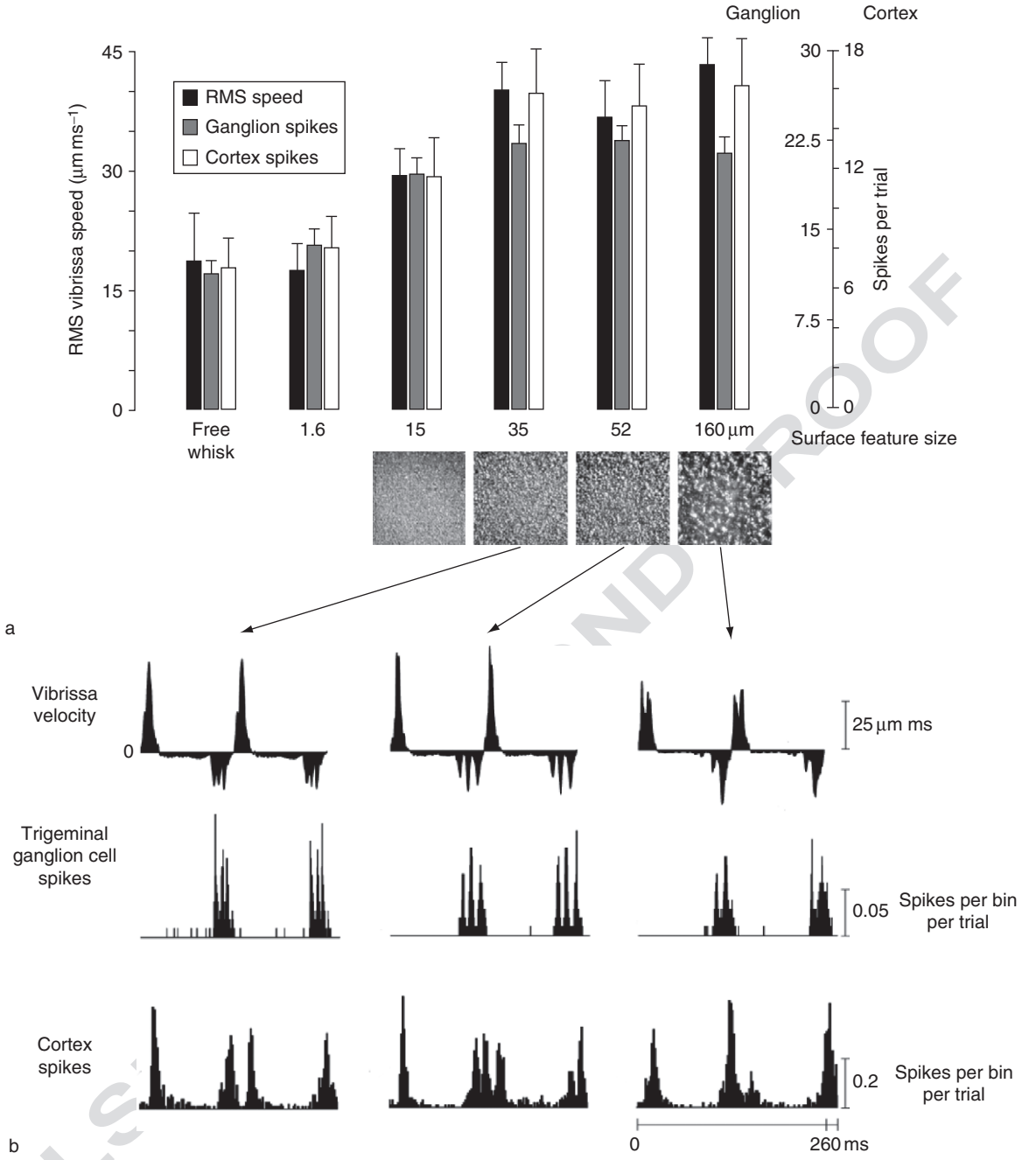


f0040 **Figure 8** Loss in phase-locked spiking with ascending activation of vibrissa brain centers as the frequency of periodic stimulation is increased. In all cases a sinusoidal stimulus was applied to a single vibrissa in an anesthetized animal. The extracellular, single-unit responses are shown in the first and fourth columns, and intracellular responses are shown in the second and third columns. Individual units in the trigeminal ganglia respond reliably up to 1200 Hz stimulation of the vibrissa (Gottschaldt KM and Vahle-Hinz C (1981) *Science* 214: 143–186), and essentially all units respond reliably to 300 Hz. By the anatomical level of the ventral posterior medial nucleus of dorsal thalamus (VPM), the responses are phase locked to the stimulus but rather infrequent; that is, most spikes are dropped. By the level of the PrV, the responses are still phase locked to the stimulus but drop-outs (*) are significant by 350 Hz. At the level of cortex, the drop-out rate is apparently so high that phase-locked spiking is not apparent at high frequencies, yet for stimulation frequencies near 100 Hz and above, the neurons appear to fire in a largely asynchronous manner, that is, as an inhomogeneous Poisson process. Note that, at all levels, the onset of stimulation always leads to transient activation. Data in the first three columns from Deschenes M, Timofeeva E, and Lavallee P (2003) The relay of high-frequency sensory signals in the whisker-to-barreloid pathway. *Journal of Neuroscience* 23: 6778–6787, and data in the final column from Arabzadeh E, Petersen RS, and Diamond ME (2003) Encoding of whisker vibration by rat barrel cortex neurons: Implications for texture discrimination. *Journal of Neuroscience* 27: 9146–9154. The responses are different in aroused animals or anesthetized animals with activation of their cholinergic system; the responses in VPM thalamus (Castro-Alamancos MA (2002) Different temporal processing of sensory inputs in the rat thalamus during quiescent and information processing states in vivo. *Journal of Physiology* 539: 567–578.) extend to higher frequencies before attenuation, while the frequency dependence of the response in vibrissa S1 cortex is largely unchanged (Castro-Alamancos MA (2004) Absence of rapid sensory adaptation in neocortex during information processing states. *Neuron* 41: 455–464) and may further exhibit bursts of spikes (de Kock C and Sakmann B (in press) High frequency action potential bursts (100 Hz) in L2/3 and L5B thick tufted neurons in anaesthetized and awake rat primary somatosensory cortex. *Journal of Physiology*; Ewert TA, Vahle-Hinz C, and Engel AK (2008) High-frequency whisker vibration is encoded by phase-locked responses of neurons in the rat's barrel cortex. *Journal of Neuroscience* 14: 5359–5368).

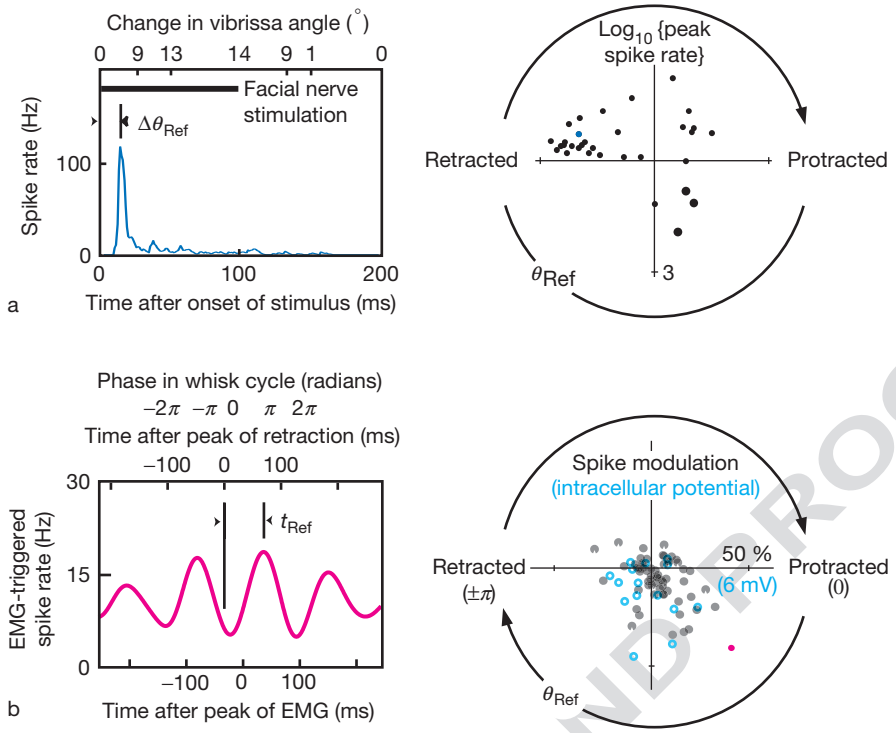
s0080 ## Sensory Representation of Texture

p0150 Studies on the coding of texture typically make use of irregular surfaces of differing roughness, such as sandpapers, as stimuli. In one paradigm, artificial whisking with anesthetized animals is used to ensure a repeatable pattern of motion of individual vibrissae, whose detailed positions can be recorded with high-speed videography (**Figure 9**). Artificial whisking makes use of electrical stimulation of the facial nerve, with trains of pulses to induce rhythmic sweeps. Yet artificial whisking provides a practical means to study the variation in vibrissa movement across surfaces for the same muscular drive. Further, once the motion is recorded, one can use the stored waveforms to control piezoelectric manipulators that move the vibrissa in a repeatable manner. The caveats of this approach are twofold: first, the resultant motion is abnormal in that the three phases of natural motor activity (**Figure 6(c)**) are reduced to one and, second, sensation may be altered in that extrinsic movement of the vibrissae approximates self-induced movement.

p0155 The motion of the vibrissae across different sandpapers in the artificial whisking paradigm has been characterized in two ways. First, variations in motion were quantified in terms of the root-mean-square (RMS) speed of the shaft of individual vibrissae. The RMS speed initially increased in a progression from smooth to rough surfaces, then reached an asymptote as the size of the surface features reached ~35 μm (**Figure 9(a)**). Concomitant with this asymptote in



f0045 **Figure 9** Evidence that vibrissa motions induced by textured surfaces are encoded by both average spike rate and temporal variations in the rate. (a) Texture coding by the average rate of neuronal firing. The spike rate is plotted for texture-induced vibrations, quantified by the root-mean-square (RMS) speed of the horizontal vibrissa motion, averaged across 100 trials of 500 ms each. The average spike count per trial was pooled from ten trigeminal ganglion neurons and 12 neurons in vibrissa S1 cortex (granular layer); note the different scales for spike counts. The insets show the surfaces. (b) Texture coding by patterns in the firing rate for three examples. The top line shows variations in velocity of a vibrissa as it moves across one of three different textures. The second line shows the peristimulus time histograms, with 0.2-ms bins, for a unit in the trigeminal ganglion. The final line shows the peristimulus time histograms for a unit in S1 cortex. Each profile is the average of 100 trials. Data adapted from Arabzadeh E, Zorzin E, and Diamond ME (2005) Neuronal encoding of texture in the whisker sensory pathway. *PLoS Biology* 3(e17): 155–165; the discrimination of different textures is discussed by von Helmendahl M, Itskov PM, Arabzadeh E, and Diamond ME (2007) Neuronal activity in rat barrel cortex underlying texture discrimination. *PLoS Biology* 5: e305.



f0050 **Figure 10** Encoding of vibrissa position in the hindbrain and forebrain. (a) Spiking output from primary sensory neurons of the trigeminal ganglion was recorded during vibrissa motion induced by 5 Hz electrical stimulation of the facial motor nerve. The left panel shows the trial-averaged response of the reference signal for one neuron; the angle $\Delta\theta_{Ref}$ is the extent of protraction, relative to the initial retracted position, at the peak of the neuronal response. The right panel summarizes the data for all cells. From Szwed M, Bagdasarian K, and Ahissar E (2003) Encoding of vibrissal active touch. *Neuron* 40: 621–630. The radial coordinate is the logarithm of the peak spike rate, and the angular coordinate is the phase within the whisk cycle. (b) Responses in vibrissa S1 cortex measured as animals whisked without contact. The data on the left show an example of the correlation between spiking and the peak of the electromyogram (EMG). The scale on top accounts for the lag between vibrissa position and the EMG (Berg RW and Kleinfeld D (2003) *Journal of Neurophysiology* 89: 104–117); the time t_{Ref} is the peak of cortical spiking relative to the fully retracted position. The panel on the right summarizes the data for all cells from these extracellular measurements, for which the radial coordinate is the modulation of the spike–EMG correlation, as well as cells from recent intracellular studies, for which the radial coordinate is the maximum intracellular depolarization. The bias in spiking as a function of phase in the whisk cycle comes slightly earlier than that for the membrane depolarization, as expected for a threshold process. Data from Fee MS, Mitra PP, and Kleinfeld D (1997) Central versus peripheral determinants of patterned spike activity in rat vibrissa cortex during whisking. *Journal of Neurophysiology* 78: 1144–1149; Mehta SB and Kleinfeld D (2004) Frisking the whiskers: Patterned sensory input in the rat vibrissa system. *Neuron* 41: 181–184; and Crochet S and Petersen CCH (2006) Correlating whisker behavior with membrane potential in barrel cortex of awake mice. *Nature Neuroscience* 9: 608–609.

speed, the spike rate of units in both the trigeminal ganglion and vibrissa S1 cortex also achieved an asymptotic value. This implies that average measures cannot distinguish among different coarse surfaces. In contrast, a second analysis considered the full time dependence of the velocity for motion across surfaces of different roughness. This measure exhibited clear changes as surface features doubled and tripled in size (**Figure 9(b)**). Further, neurons in the trigeminal ganglion faithfully tracked these changes, with directional preference, consistent with their ability to track high-frequency vibrations (**Figure 8**). At the level of S1 cortex, there were repeatable differences in the spike rate for all sandpapers, although many details of the timing were not tracked (**Figure 9(b)**).

p0160 The data suggest that the motion of a vibrissa across a textured surface is dominated by stick–slip events (**Figure 7(b)**), this conclusion has been partially verified with awake animals in natural textural settings. Further, while primary sensory cells can encode different textures, the algorithm for encoding a natural ensemble of textures in terms of cortical spike rates remains an open issue, as does the issue of the fidelity of that encoding.

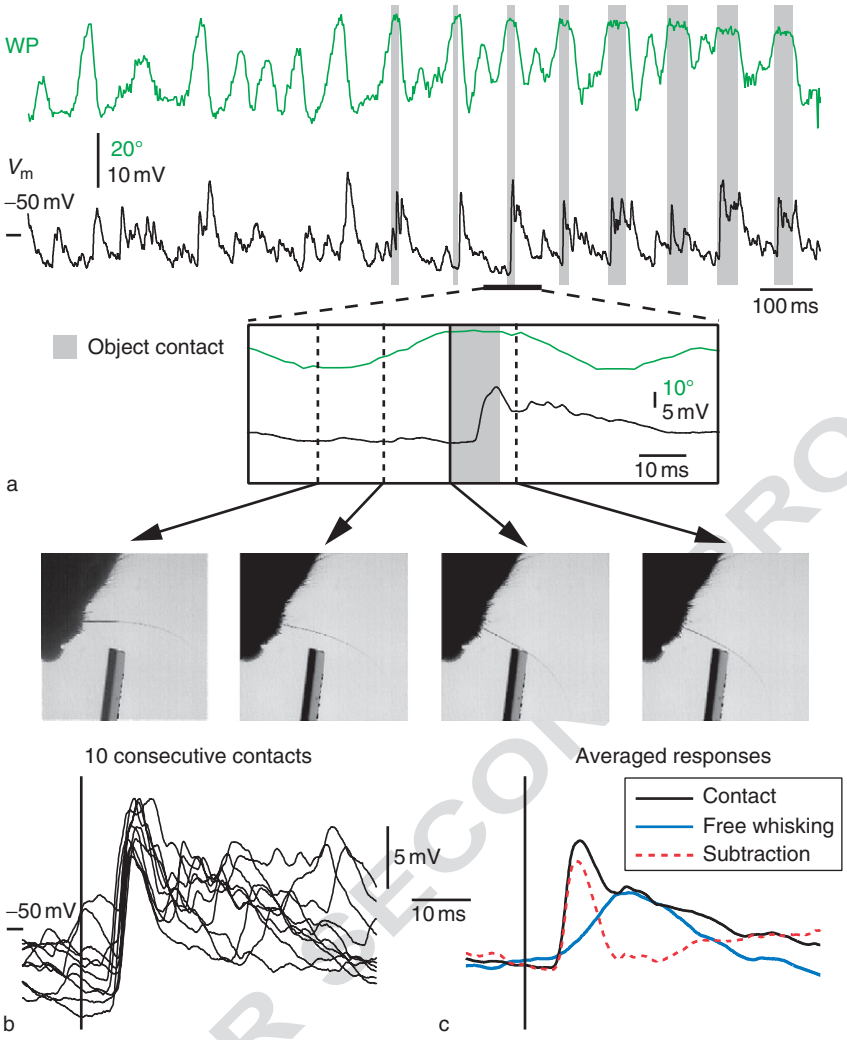
Sensory Representation of Object Location

s0085

Neuronal Signals of Vibrissa Position

s0090

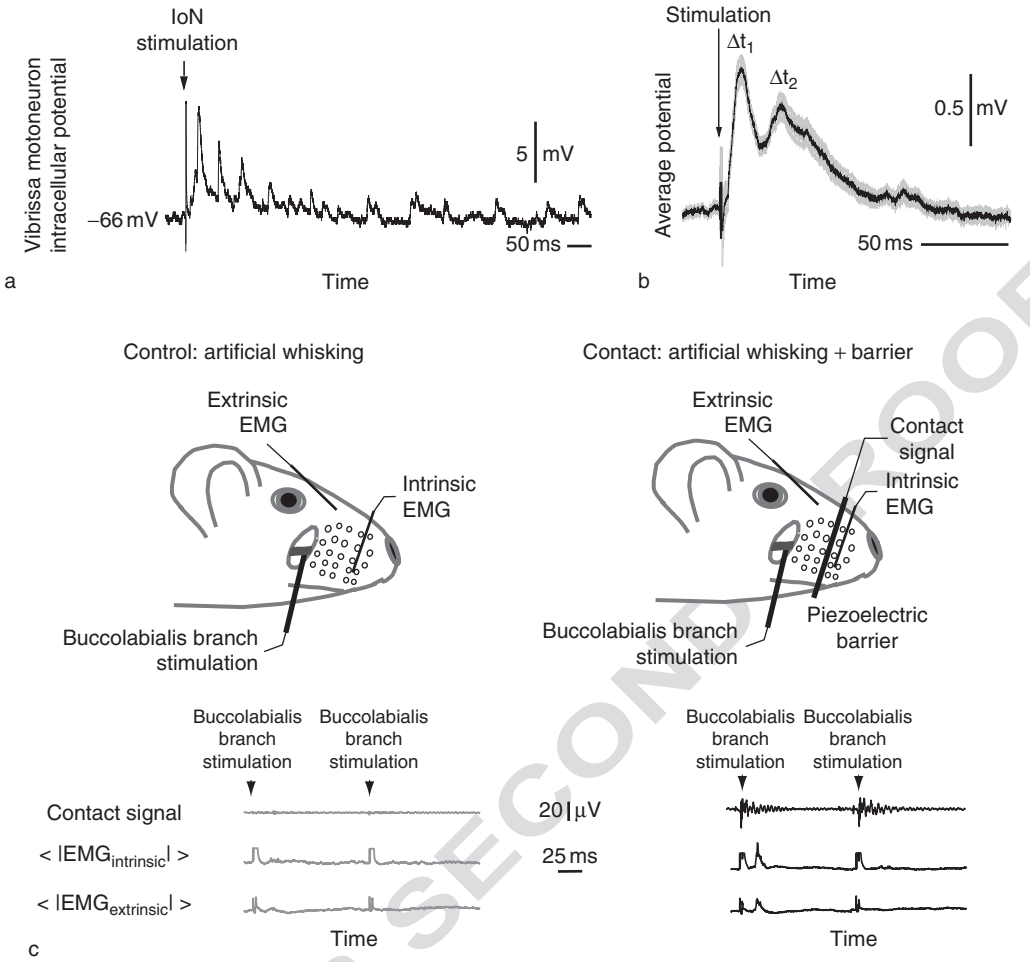
p0165 There is a lack of evidence for spindle fibers, the transduction mechanism for proprioception, in the facial musculature, as well as a lack of evidence for descending inputs to primary sensory neurons.



f0055 **Figure 11** Intracellular potential of neurons in primary vibrissa cortex of a head-fixed mouse during active touch. (a) The mouse whisked in air both without contact (left sides of top two traces) and with contact against an object (right sides) when it thrust its vibrissae forward. The intracellular potential is marked by V_m (black), the videographed vibrissa position is marked by WP (green), and contact is marked by a gray bar. Note that the rest level of the cell is relatively depolarized. The box corresponds to an expansion of one contact event, with videographs of the contact event shown below. (b) The superposition of ten consecutive contacts shows the reliability and temporal precision of the intracellular response. (c) Intracellular responses evoked by contact with an object were averaged (blue) and compared with the average response aligned with respect to the peak of the vibrissa position for whisking in air (WP in (a)). The response evoked by contact was faster and larger than that evoked by free whisking; dashed red line marks the subtraction of the two responses. Adapted from Crochet S and Petersen CCH (2006) Correlating whisker behavior with membrane potential in barrel cortex of awake mice. *Nature Neuroscience* 9: 608–609.

Nonetheless, the results of experiments with the artificial whisking paradigm report the presence of reference signals for vibrissa position in a subset of primary sensory neurons (left panel in **Figure 10(a)**). Different neurons preferentially spiked at different angles during the whisk cycle (right panel in **Figure 10(a)**), with a bias toward protraction from the retracted position. These data, together with nerve block experiments, imply that the position signal originates from peripheral reafference.

p0170 At the level of vibrissa S1 cortex, experiments with awake animals trained to whisk in air show that the spike rates of individual cortical neurons are locked to the rhythmic motion of the vibrissae, as inferred from the electromyogram (EMG) of the intrinsic muscles (left panel of **Figure 10(b)**). This constitutes a reference signal of vibrissa position. The distribution of preferred angles extends over the entire whisk cycle, with a bias toward retraction from the protracted position. Further, intracellular measurements with head-fixed awake animals find a similar distribution of preferred angles for the peak of the excitatory postsynaptic potential. The bias in spiking as a function of phase in the whisk cycle comes earlier than that



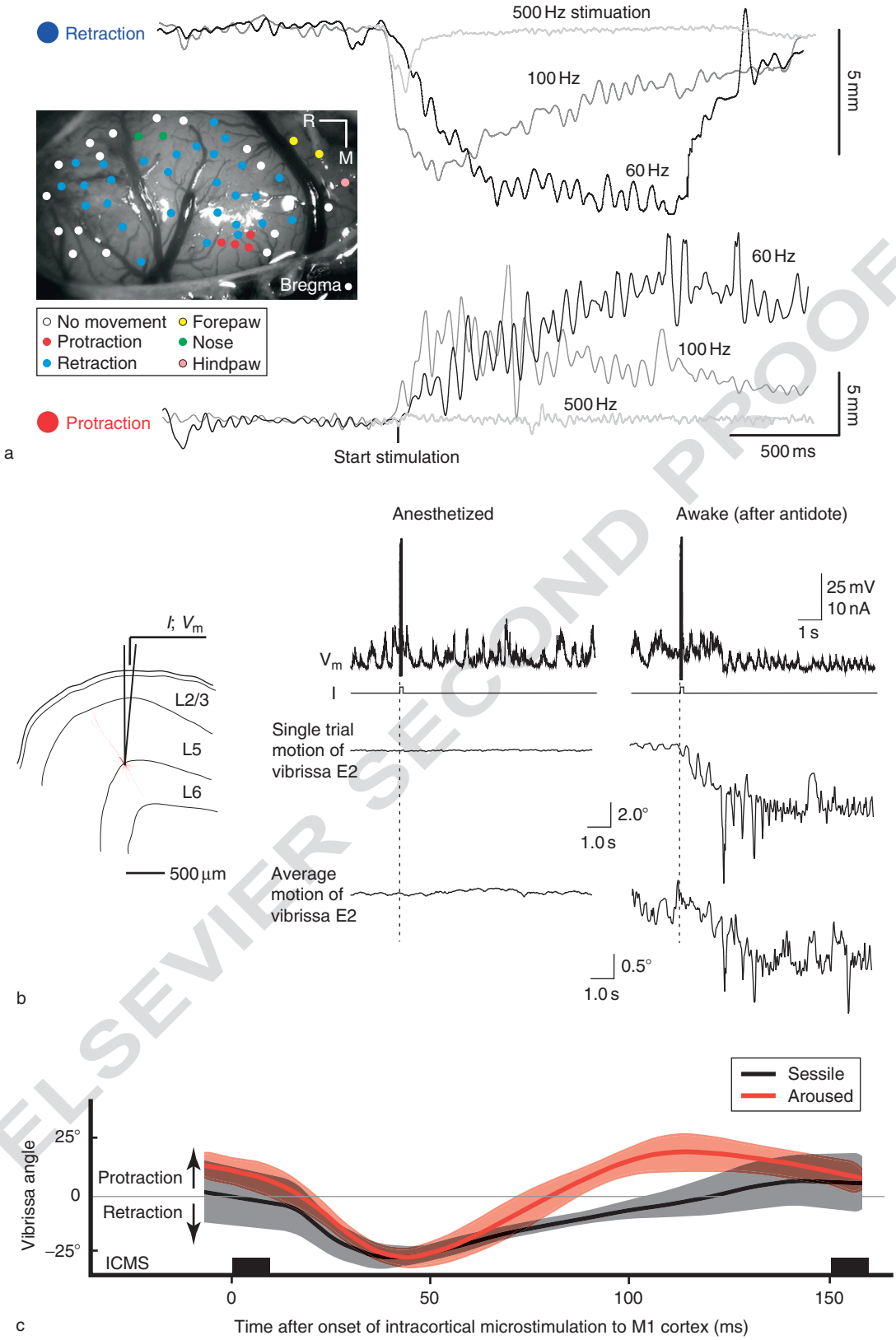
f0060 **Figure 12** Sensorimotor feedback in the hindbrain (brain stem) loop. This closed loop is formed by the vibrissae follicle → trigeminal ganglion → trigeminal nuclei → facial nuclei → follicle musculature pathway; trigeminal nucleus principalis and spinal nucleus interpolaris are likely to mediate the trigeminal pathway (**Figure 6**). (a) Data from a brain stem slice preparation of juvenile animals (postnatal days 10–15) that preserves the connectivity, except that excitation of sensory terminals is replaced by shock to the infraorbital nerve (IoN), which excites vibrissa neurons in the trigeminal ganglion, and muscle output is replaced by intracellular recording from facial motor neurons in the lateral aspect of the facial nucleus. Shown are excitatory postsynaptic potentials in a motor neuron following suprathreshold stimulation (average of 20 responses) of the IoN in a slice. (b) Trial and preparation averaged intracellular response to nerve stimulation. The responses from ten trials each of 25 motor neurons were averaged together; mean, black trace; standard error of measurement, gray band. (c) The electromyogram (EMG) responses elicited by vibrissa contact in a ketamine xylazine-anesthetized adult rat. The cartoon in the top row shows the experimental setup for the contact experiment during artificial whisking (**Figure 9(a)**), for which the facial motor nerve (buccolabialis branch, driving the retractors m. nasolabialis and m. maxillolabialis; **Figure 6(a)**) is stimulated at 8 Hz with 9-mA, 50-s pulses to make the vibrissae protract. Shown are the contact signals (top traces, with control trials on the left and contact trials on the right) and consecutive averaged rectified EMG responses recorded simultaneously in intrinsic (middle traces) and extrinsic (bottom traces) vibrissa muscles. Note that the contact-induced EMG signals adapt after a single contact. Each trace is the average of 30 sweeps. Data from Nguyen Q-T and Kleinfeld D (2005) Positive feedback in a brainstem tactile sensorimotor loop. *Neuron* 45: 447–457.

for the membrane depolarization, as expected for a threshold process. Collectively, these data imply that rats ascertain the position of their vibrissa at the time of contact.

p0175 Finally, the fidelity of the reference signal in cortex depends on reward. Whisking in air that is coupled to a food reward is a factor of 2 to 3 times more coherent with vibrissa position than whisking in air that is unrewarded. This shows that reward, which is likely to heighten the attentional state of the animal, can strongly bias the nature of its sensorimotor processing.

Whisking-Dependent Contact Signals s0095

p0180 A reliable and robust response to contact is observed at the level of the trigeminal ganglion in awake animals. The spike rate of primary sensory cells increases with increasing impact, or velocity, of contact until a



F0065 **Figure 13** Real-time control of vibrissa position by primary motor cortex. (a) Intracortical microstimulation (ICMS) of vibrissa M1 cortex leads to retraction at a majority of stimulation sites (blue dots and associated traces at top; magnification of 3 by 5 mm image) but protraction in a medial region of frontal cortex (red dots and associated traces at bottom of image). The amplitude of the response as a function of the frequency of the microstimulation was greater for low-versus high-frequency stimulation (cf. 60 vs. 500 Hz). Data from

saturation level is reached for angular speeds on the order of $500^{\circ}s^{-1}$. There is also evidence that the radial distance to the contact point is encoded independent of the velocity.

p0185 Experiments with anesthetized animals indicate that there are robust spike responses to the initial deflection of a vibrissa along the entire ascending lemniscal pathway. Yet a systematic study of spiking at all levels in the sensorimotor hierarchy in awake animals remains to be completed, including the essential issue of spiking induced by animal-initiated contact. Nonetheless, preliminary observations of the nature of the subthreshold input to neurons in the upper layers of vibrissa S1 cortex have revealed the coexistence of whisking-related changes in subthreshold potential and changes in potential that are locked to contact (**Figure 11**). Contact signals that are referenced to vibrissa position could, in principle, be computed from the observed signals.

s0100 ## Sensory Modulation of Vibrissa Motion

p0190 The observation of changes in whisking on contact of the vibrissa with a wall (**Figure 1(a)**), along with changes in whisking amplitudes for whisking in air versus against a target (**Figure 2(a)**), provides evidence for changes in whisking strategy based on the task. How can this occur?

s0105 ### Brain Stem Mechanisms

p0195 Recent work shows that the brain stem loop exerts a transient positive feedback (**Figure 12**). At the level of *in vitro* physiology, sensory feedback from the trigeminal input to the motor neurons was measured in a brain stem slice preparation that preserves the vibrissa sensorimotor feedback pathway; see brain stem loop in **Figure 4**. Stimulation of the IoN leads solely to excitatory postsynaptic potentials in the motor neurons of the facial nucleus (**Figure 12(a)**). The latency of the response has two components, a fast Δt_1 component that presumably reflects disynaptic (IoN → trigeminal nuclei → facial nucleus) input and a slower Δt_2 component that is involved in trisynaptic or higher-order feedback in brain stem (**Figure 12(b)**). The critical issues are that feedback is both positive and rapid, that is, $\Delta t_1 \sim 10$ ms compared with the ~100 ms timescale of whisking.

At the level of *in vivo* physiology, the brain stem can p0200 be functionally isolated through the use of anesthesia. The artificial whisking paradigm is then used to drive the vibrissa muscles at physiological whisking rates. As a means to study sensorimotor feedback, a rigid contact detector is introduced in the trajectory of the vibrissae during alternate measurements to ascertain whether EMG responses could be elicited by contact of the vibrissae with the detector (**Figure 12(c)**). Consistent with positive feedback, contact led to a transient increase in the amplitude of the rectified EMG for both intrinsic and extrinsic muscles. This effect rapidly adapted for stimulation frequencies above 5 Hz. These data show that positive, transient feedback can lead to an increase in motor force.

Behavioral data to support transient positive sensori- p0205 motor feedback come from measurements of changes in whisking force coincident with contact. When animals whisked symmetrically yet made contact with a sensor on only one side of the face, the amplitude of the mystacial EMG on the contact side was transiently increased by 25%. These data show that the vibrissa feedback loops act to transiently increase the interval and force of contact.

Cortical Mechanisms s0110

We conjecture that changes in whisking strategies, p0210 as opposed to transient changes in force, are regulated at the thalamocortical level. Three classes of experiments support this view. As a means to delineate the sensory representation of rhythmic input in M1 cortex, the first experimental effort made use of awake, head-fixed animals that were trained not to whisk. The observed response captured only the fundamental frequency of the input pattern for pulsatile stimuli delivered at frequencies that ranged from 5 to 20 Hz, that is, the range of exploratory whisking. This nonlinear transformation resembles the synthesis of a sinusoidal feedback signal for servocontrol of a motor.

A second class of experiments showed that vibrissa p0215 M1 cortex supports oscillations in extracellular current flow that are phase locked to whisking. These

Haiss F and Schwarz C (2005) Spatial segregation of different modes of movement control in the whisker representation of rat primary motor cortex. *Journal of Neuroscience* 25: 1579–1587. (b) Intracellular stimulation of a single neuron in M1 cortex with current I has little effect on the membrane potential V_m as well as on the motion of the vibrissae in the anesthetized state but leads to protraction of vibrissa E2 in the awake animal. Data from Brecht M, Schneider M, Sakmann B, and Margrie T (2004) Whisker movements evoked by stimulation of single pyramidal cells in rat motor cortex. *Nature* 427: 704–710. (c) Videographic data of vibrissa position in sessile versus aroused animals in response to ICMS of motor cortex. Note that ICMS in the sessile case led to retraction of the muscles, whereas stimulation in the aroused case led to a whisk cycle with retraction followed by a protraction phase. Data from Berg RW and Kleinfeld D (2003) Rhythmic whisking by rat: Retraction as well as protraction of the vibrissae is under active muscular control. *Journal of Neurophysiology* 89: 104–117. Early studies also considered the direction of motion induced by ICMS to M1 cortex (Sanderson KJ, Welker Wand Shambes GM (1984) *Brain Research* 292: 251–260; Gioanni Y and Lamarche M (1985) *Brain Research* 344: 49–61).

signals are preserved after lesions of the IoN to block sensory input. Further, ablation of M1 cortex leads to alteration of the whisking patterns. Thus, motor cortex generates rhythmic signals that can drive normal exploratory whisking.

p0220 A final class of experiments, highlighted in **Figure 13**, explored the motion of the vibrissa in response to activation of vibrissa M1 cortex in both anesthetized and behaving animals. From a functional perspective, there are two contiguous motor areas. For the largest region (blue dots in **Figure 13(a)**), activation of tissue with a brief train of extracellular current pulses, or even depolarization of a single cell, leads to retraction of the vibrissae. For a smaller region near the midline (red dots in **Figure 13(a)**), activation with a brief train of extracellular current pulses leads to protraction. It is interesting that stimulation of neurons in this region with a continuous train of high-frequency pulses, rather than a brief train, can induce rhythmic whisking.

p0225 The ability of M1 motor cortex to drive whisking is enhanced when rats are awake as opposed to anesthetized. Further, this enhancement is profoundly increased in the attentive, as opposed to sessile, awake state. First, stimulation of even a single projection neuron in vibrissa M1 cortex can lead to movement of one or more vibrissae. In the awake animals, this movement is dramatically increased (**Figure 13(b)**). Second, while stimulation of the major fraction of vibrissa M1 cortex leads to retraction when animals are anesthetized or awake but sessile, this motion is transformed into a full whisk, with protraction and retraction, when animals are in the awake and aroused state (**Figure 13(c)**). This effect is mimicked by cholinergic activation of cortex, a key component of attention. Collectively, these data show that M1 cortex, in principle, can subsume full control of vibrissa movement.

s0115 Epilog

p0230 The vibrissa system in rodents has a multitude of features that make it ideal for the study of sensorimotor control in a mammal. It preserves the basic architectonics of nested feedback loops (**Figure 4**), yet the lissencephalic cortex of rodents makes all structures of the brain very accessible. Critical for studies of active sensation, work to date has refined a number of behavioral paradigms that tax the active nature of this sensorimotor system and define strategies for processing the sense of vibrissa-based touch (**Figures 2** and **3**).

p0235 Electrophysiology studies with awake, behaving animals have begun to elucidate the algorithms involved in active sensing. For texture discrimination, this is likely to include the detailed timing of spikes in vibrissa S1 cortex (**Figure 9**). For touch in face-centered coordinates (**Figure 3**), this is likely to involve the merge of touch and reference signals of vibrissa position (**Figures 10** and **11**). Experimental progress is anticipated to be critical to a proper understanding of active sensing in two broad, open issues.

How Do Rats Map the Space about Their Vibrissa? s0120

The main issue is whether rats maintain an abstract representation of objects that is independent of which vibrissa makes contact with an object. Or is this representation based solely on a single vibrissa (which would suggest little interaction between columnar representations)? A number of immediate issues within the realm of representation are ripe for study: p0240

- There is evidence that rats encode texture by the time between stick–slip events. How is this used to form a perception? By analogy with flutter coding in somatosensory experiments in monkeys, do rats count the number of events in a period? Or are individual periods stored? Beyond this lies the issue of whether stick–slip events are encoded across different vibrissae.
- There is evidence that primary sensory neurons can encode the radial distance of contact. How is radial distance separated from impact on contact?
- The notion of object location depends on the presence of a neuronal response that encodes contact conditioned on vibrissa position in the whisk cycle. At what level of the sensorimotor pathways do such responses first occur?
- There is evidence that the phase of the vibrissae within a whisk cycle, rather than the absolute position, is encoded. How is this accomplished? One hypothesis is that it relies on adaptation at the level of the primary sensory neurons.
- Adaptation of the neuronal response at all levels of sensory processing, and particularly at the level of thalamocortical synapses, is strong. Thus steady state responses are much different from transient responses. How does this play into the representation of sensory signals?

How Do Rats Change Their Motor Output in Response to Vibrissa-Based Touch? s0125

The main issue is how touch leads to changes in body position, whisking dynamics, and locomotion. p0245

- Rhythmic whisking can occur in the absence of sensory feedback and in the absence of high-level control. Where are the pattern generators for rhythmic whisking? Further, what form of circuitry allows these generators to stabilize at a different, single frequency from bout to bout?

- The superior colliculus is capable of driving patterned, stereotyped motor behaviors. What is the role of the colliculus in transforming vibrissa sensory inputs into motor commands?
- Motor neurons can potentially receive feedback from sensory pathways at all levels of the brain. How are these inputs arbitrated?

See also: Barrel cortex circuits (00167); Sensorimotor Integration: Attention and the Premotor theory (01108); Sensorimotor Integration: Barrels, vibrissae and topographic representations (01109); Sensorimotor integration: models (01426).

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Non-Print Items

Abstract:

Rats sweep their vibrissae through space to locate objects in their immediate environment. In essence, their view of the proximal world is generated through pliable hairs that tap and palpate objects. The texture and shape of those objects must be discerned for the rat to assess their value. Further, the location of those objects must be specified with reference to the position of the rat's head for the rat to plan its future movements. This article reviews the nature of the sensors and motor plant that govern whisking, along with the neuronal circuitry and signaling that underlie vibrissae-based sensation and sensorimotor control.

Keywords: Barrels; Barreloids; Extrinsic muscles; Foveal whisking; Infraorbital nerve; Intrinsic muscles; Phase locking; Rat; Triangulation; Vibrissae

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