A night in the life of a rat: vibrissal mechanics and tactile exploration

Mitra J. Z. Hartmann

Departments of Biomedical Engineering and Mechanical Engineering, Northwestern University, Evanston, Illinois

Address for correspondence: Mitra J. Hartmann, Departments of Biomedical Engineering and Mechanical Engineering, Northwestern University, 2145 Sheridan Road, Evanston, IL 602028. m-hartmann@northwestern.edu

The rat vibrissal (whisker) system is an increasingly important model for the study of the sense of touch. This paper describes recent results obtained from high-speed videography of rat exploratory behavior and from modeling studies of vibrissal biomechanics. We review several features of vibrissal touch, including the mechanics of contact versus noncontact whisking, the coordination between head and whisker movements, and the use of information obtained from the whiskers to detect, localize, and extract the spatial properties of objects. This work highlights the idea that mechanics are critical to an understanding of sensory systems and describes some new tools to monitor the spatiotemporal patterns of whisker–object contact during natural tactile exploratory behavior.

Keywords: trigeminal; whisker; vibrissa; somatosensory; biomechanics

Introduction

Rats inhabit a world of touches and smells. Each evening, they leave the safety of their burrows and—in complete darkness—navigate intricate systems of underground tunnels[1] to surface and scavenge for food. Once outside, their keen olfactory sense guides the search for food and water and helps them elude nocturnal predators.[2] The rat's exploratory behavior is dominated by intense, synchronized sniffing and "whisking," rhythmic sweeps of the vibrissae (whiskers) at frequencies between 5 and 25 Hz that provide a continuous flow of tactile information to the rat's brain.[3,4]

The vibrissae are arranged in a dense, grid-like pattern on both sides of the face.[5] Each vibrissa inserts into a sense organ (follicle) containing an array of mechanoreceptors,[6] exquisitely sensitive to vibrissal motion and bending. An understanding of vibrissal-based touch must therefore begin with a quantification of vibrissal mechanics.

To provide a perspective on the functional importance of the vibrissal sensorimotor system, we follow an imaginary rat as it uses its whiskers to explore and navigate its world during one night of its life. We imagine the rat as it leaves its nest, using its whiskers to follow the walls of a tunnel, and to scan the open space immediately around the tunnel exit. As it scans, its whiskers make unexpected contact with an object, and the rat then explores the object to extract the details of its shape. This fictional narrative highlights several features of the biomechanics of touch, including the mechanics of contact versus noncontact whisking, the coordination between head and whisker movements, and the use of whisker inputs to detect, localize, and extract the spatial properties of objects.

The behavioral results presented in the narrative are based on an analysis of behavior of the freely exploring rat using high-speed video to resolve movements of the vibrissae, head, and body. Figure 1 illustrates measurements made during a typical experiment.[7] The rat's head is tracked with three points on the snout and ears (Fig. 1A). The angle of the head is then determined in the standard "laboratory frame," that is, in a fixed Cartesian coordinate system (Fig. 1B, left) that does not move as the animal moves in the environment. The rostral-most and caudal-most whiskers are individually tracked (Fig. 1A,B), and their movements are analyzed both in the laboratory frame as well in "head-centered" coordinates (Fig. 1B, right). In head-centered
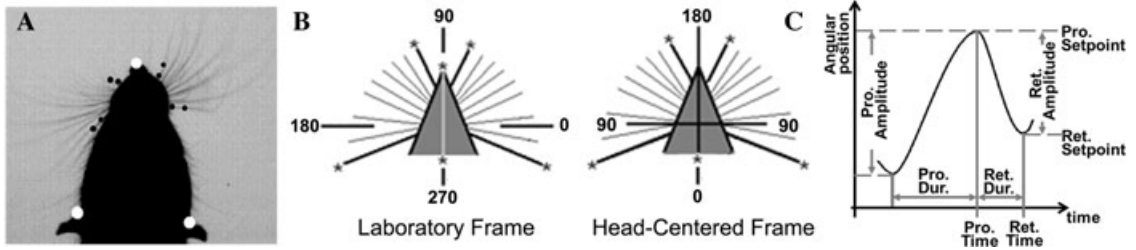
Figure 1. Quantification of whisking kinematics. (A) Representative frame from high-speed (250 fps) video of rat whisking behavior. The initial linear portions of the rostral-most and caudal-most whiskers are tracked (black dots) as well as the head angle (white dots). (B) Coordinate systems to measure whisker angles. The laboratory frame is in fixed Cartesian coordinates. Head coordinates are fixed to the head of the rat. Asterisks indicate the whiskers that were tracked in both coordinate frames. (C) Schematic of a typical whisk representing the kinematic whisk parameters. Pro, protraction; Ret, retraction.

coordinates, the angle of the whiskers is defined to increase during protraction on both sides of the face, regardless of the position or orientation of the head. Finally, whisk parameters are quantified as shown in Figure 1C.

The data described here complement results obtained from studies of the head-fixed animal, which have provided detailed descriptions of whisking kinematics using opto-electronic tracking techniques.[8–12] Although data obtained during the rat's free exploration are more difficult to analyze, the advantage of the approach is that it specifically allows examination of relationships between whisker, head, and body movements.

Leaving the burrow: whisking with and without object contact

Dusk is falling as the rat leaves its central nest or "den," located near the middle of its burrow. The den is roughly spherical in shape, about 6–7 inches in diameter, and connected to the surface through several narrow tunnels with diameters between 2–2.5 inches.[1] We imagine that, as the rat approaches one of the many tunnels from the den, the whiskers on one side of its face, but not the other, make contact with the den wall. These two conditions will cause important mechanical differences at the base of the whisker, illustrated in Figure 2.

During noncontact whisking, the whisker and the follicle move closely as a unit, resulting in the type of motion schematized in Figure 2A.[3,7,13–15] Muscles surrounding the follicle rotate the follicle forward, and there is minimal relative motion between the whisker and follicle. If there is little or no relative motion, mechanoreceptors in the follicle will deform only slightly, and relatively weak forces and

moments will be generated in the follicle. Given these small deformations, one might also expect responses of primary sensory neurons in the trigeminal ganglion (Vg) to be relatively weak. Surprisingly, however, two recent studies have found Vg responses to be remarkably robust during noncontact whisking.[16,17] Although responses were clearly weaker than during contact with an object, most ganglion neurons were found to respond at a preferred whisker position during noncontact whisking,[16,17] and at least two thirds showed significant correlation with one or more kinematic parameters over the duration of a protraction or retraction.[16] These responses may also be enhanced by muscles squeezing down on the follicle, skin stretch deforming the mechanoreceptors in the follicle, and inertial effects deforming the whisker within the follicle.

In contrast to noncontact whisking, contact whisking causes the whisker to bend and generate larger forces and moments in the follicle as shown in Figure 2B.[18,19] The mechanical effect of this bending is that the whisker curves slightly to press against a set of mechanoreceptors. Direct activation of mechanoreceptors during object contact produces a strong response in trigeminal ganglion neurons, generally much stronger than that observed during noncontact whisking.[14,17,20–22]

Imagine now that the rat has found a tunnel and begins to scurry upward toward the outdoors. Following the tunnel walls may not be a simple task. Tunnels abruptly change shape, turn, and sometimes dead end.[1] In order to follow the tunnel contours, the rat must determine how far away its head is from the wall and control its locomotion to approximately maintain this distance. In the section entitled "A surprise collision with an object: the
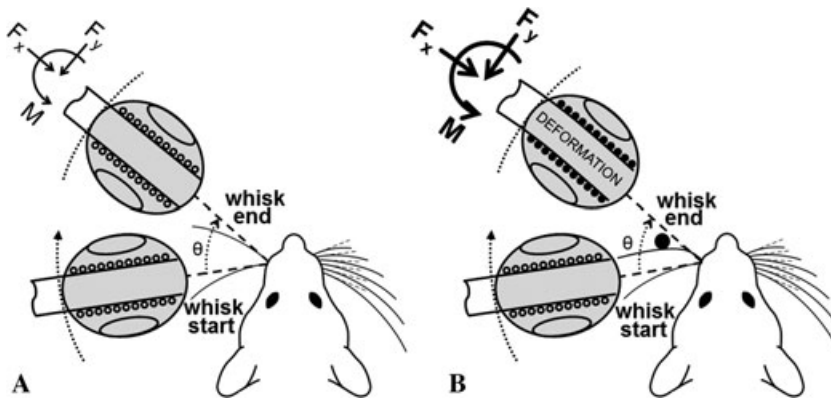
Figure 2. Noncontact versus contact whisking. (A) During noncontact whisking there is little relative motion between the whisker and the follicle, and the forces and moments generated are quite small. Mechanoreceptors in the follicle (open circles) are only weakly deformed. (B) During contact whisking the follicle rotates forward, but the whisker is obstructed by an object. The bending of the whisker induces large forces and moments and causes mechanoreceptors in the follicle to deform substantially (filled circles).

mechanics of contact and object localization," we will suggest a mechanical basis by which the rat could determine head-to-wall distance to enable wall following.

Tactually scanning empty space

Reaching the end of the tunnel, our rat tentatively pokes its nose out, sniffing for the neighborhood cat. The rat's acute sense of smell will likely provide the first cue that another animal may be waiting outside the burrow.[2] Finding the coast clear, the rat pokes its full head out into the cold night air, ceaselessly sniffing and whisking the darkness. Ever cautious, it plants its paws at the edge of the tunnel and cranes its neck, turning its head this way and that to scan the open space immediately around the tunnel entrance.

During this continuous movement, how does the rat maintain a stable perceptual representation of the world? The rat must somehow coordinate the movements of its head and whiskers as it scans. We recently performed an experiment to examine head–whisker coordination and the rat's control over whisking velocity during a behavioral task in which the rat was required to rotate its head in free space to localize a reward.[7,15]

Previous studies in head-fixed rats had suggested that—in the absence of contact with an object—whisker movements tended to remain symmetric around the head and follow relatively stereotyped trajectories.[3,22–27] Observations in the freely behaving animal, however, revealed both a high degree of

right–left whisking asymmetry[6] and considerable variability in movement.[15] Specifically, we found that at every instant during the whisk, the positional asymmetry of the left and right whisker arrays was approximately equal to the distance that the head would rotate during a whisk[7] (Fig. 3A).

In other words, the whiskers "look ahead" of the current position of the head to anticipate where the head will be at the start of the next protraction. If the head is turning to the left, the left whiskers will whisk through a more retracted region of space than the right whiskers; the opposite is true if the head is turning to the right. This "looking ahead" behavior might be seen as analogous to a combined head–eye gaze shift, in which the eyes reach a new fixation point before the head moves to that point.[29,30]

In addition, the majority of whisker protractions did not follow the smooth and monotonic trajectories illustrated in Figure 3B. Instead, the rat tended to reduce the speed of its whisker movements in the middle of the whisking trajectory, performing a "delayed pump." Many whisking trajectories even reversed direction during the course of the protraction, resulting in a "double pump."[15] Examples of these whisking profiles are illustrated in Figure 3C. It is clear that different whisking velocity profiles achieve maximum velocity when the whiskers are at different positions relative to the head.

Importantly, however, despite the high variability in instantaneous whisking velocity, the average whisking velocity was found to remain remarkably constant from whisk to whisk.[15] This constancy was
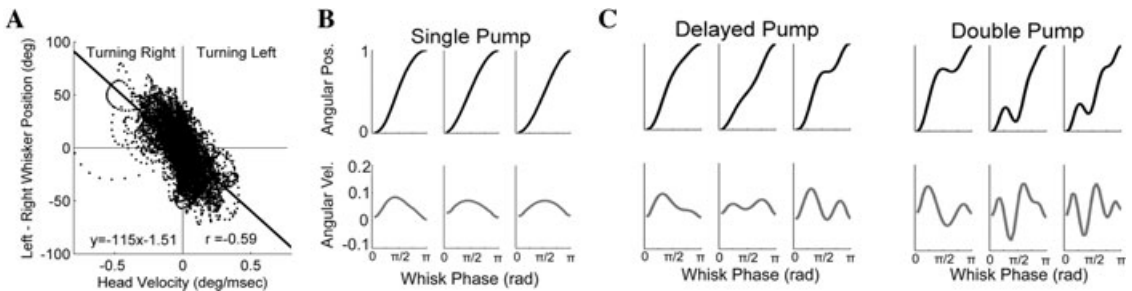
Figure 3. Variable whisking kinematics. (A) Spatial asymmetry between left and right whisker arrays is proportional to head velocity. The slope is −115 ms, approximately the duration of a whisk. Negative head velocity indicates that the rat is turning to the right, positive to the left. (B) Three examples of smooth protractions monotonic in position ("single pumps"). (C) Three examples of delayed and double pumps. In B and C, the top row illustrates angular position of the whisker, and the bottom row is angular velocity.

possible because the rat appeared to adjust for the initial velocity of the protraction. If a protraction started faster than average, then the rat tended to execute a delayed or double pump to slow it down (Fig. 3B,C). If a protraction started more slowly than average, then the rat tended not to perform a double or delayed pump, but rather a single pump that increased in speed over the course of the protraction (Fig. 3B). In summary, protractions exhibit a large variability in instantaneous velocity but—across all whisks—a low variability in average velocity. This result suggests that the rat may actively adjust its whisking velocity at every time point during the whisk. The potential importance of this ability will become apparent in the next section.

A surprise collision with an object: the mechanics of contact and object localization

As our rat scans the space around its tunnel exit, one of its whiskers unexpectedly makes contact with an object. As was shown in Figure 1B, once contact occurs, the whisker will bend, and forces and moments will be transduced via the whisker shaft to mechanoreceptors in the follicle. Contact between the whiskers and an object during tactile exploration generally leads to dramatic changes in whisking movements[28,31–33] coupled with an orienting motion of the head toward the object. Some recent studies[31,32] have observed that the rat rapidly ceases protraction immediately upon object contact, and, on the subsequent whisk, controls left and right arrays so that the maximum protraction on each side is just sufficient to make contact with the object. This overall control strategy has been termed "minimal-

impingement, maximal-contact," as the rat tries to ensure that the whiskers bend as little as possible during contact, while maximizing the number of whiskers in contact.[31,32]

In particular, if the initial whisker–object contact happens to occur only unilaterally, then the rat will control the subsequent whisk to ensure that both sides make contact.[31] This would have the effect of making the whisking more right–left symmetric about the object, consistent with the orienting response. A complementary hypothesis, as yet untested, is that immediately after object contact whisker movements may compensate for head rotations in a manner similar to the vestibulo-ocular reflex (VOR).[7] According to this hypothesis, both right and left whiskers should move "equal and opposite" to the head. For example, during a head rotation to the left, the left whiskers would have to slow down in world coordinates by an amount exactly equal to the head velocity, whereas the right whiskers would have to speed up by the same amount. Further studies are necessary to fully determine how whisking movements are altered by the presence of an object. Interestingly, it has been informally observed[32] (though not quantified) that the changes in whisker movement appear to depend on attention; when the orienting response is absent (taken to indicate absence of attention), the changes in whisker movements are as well. It has, therefore, been suggested that both behaviors are expressed only toward attended stimuli, consistent with the expression of changes in whisker movements toward anticipated stimuli.[28]

The rat's ability to orient toward an object implies that it can make use of the mechanical information
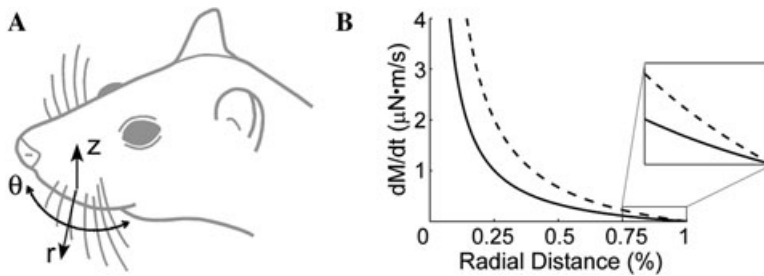
Figure 4. (A) A cylindrical coordinate system (r, θ, z) can describe the 3D locations of whisker–object contact. (B) For any given whisking velocity, there exists a monotonic relationship between dM/dt and r. The two curves illustrate this relationship for two whisking speeds: 180 deg/s (solid line) and 360 deg/s (dashed line). Radial distance is normalized to a fraction of the whisker length (tip of the whisker is 1). The whisker is assumed to have a base radius of 60 μm and an elastic modulus of 3.5 GPa.

obtained during contact to localize the object. One important component of the localization problem is for the rat to determine the radial distance to the object—that is, how far away the object is from the base of the whisker that touched it (Fig. 4A). Our laboratory recently demonstrated that the rat could make use of bending near the whisker base to determine the radial distance to an object.[18,19]

Our method was based on an approach first described by Kaneko.[34] When a whisker collides with an object, there is a monotonic relationship between the radial distance of object contact and the rate of change of moment (dM/dt) for any given whisker velocity (dθ/dt), as shown in Figure 4B. Importantly, this means if the rat can keep track of dM/dt and dθ/dt upon object contact, enough information will be present to uniquely determine radial object distance r.

One possible problem with this scheme for radial distance determination is that dM/dt approaches zero when the whisker contacts the object at its tip. Fortunately, there is a simple solution: the rat can simply increase the rate of change of M. Figure 4B shows that by doubling whisker velocity from, say, 180°/s (solid line) to, say, 360°/s (dashed line), dM/dt will also double.

Imagine, then, that the rat happened to be moving its whiskers very slowly at the instant it made unexpected contact with an object. In this case, it may not be able to obtain accurate information about the distance to the object. On the next whisk, however, the rat could potentially choose to ensure that object contact occurred during a fast region of the whisk, perhaps using the "double-pump" strategy described earlier. In other words, the rat could choose to "tune" its whisking velocity to in-

crease the magnitude of dM/dt to a more perceptible level.

It is by these mechanisms, we imagine, that the rat could obtain the sensory information required to follow the twists and turns of a tunnel. Specifically, the rat could tap its whiskers against the tunnel walls, and monitor changes in whisker bending (moment) to determine the distance to the wall. The rat could then control its locomotion to approximately maintain this approximate head-to-wall distance.

Finally, we note that our analysis has focused on how the rat might determine the radial distance to the object but has not considered how it might determine the other two dimensions illustrated in Figure 4A, namely, the height of the object (z) or its angular position in the horizontal plane (θ). Earlier studies have suggested that the vertical location (height) of each point on an object may be coded by the identity of activated whiskers along each column.[35,36] This identity-based coding scheme is consistent with the central neural representation of vibrissae in a manner that reflects the regular topographical arrangement of whiskers on the face.

The determination of angular position θ is more problematic, because the rat has no proprioceptors in the muscles that control the whiskers.[6] One recent study demonstrated that neurons in barrel cortex preferentially respond to the combination of a whisker making contact with an object and a particular phase of the whisk.[37] In other words, different neurons responded more strongly to contact that occurs during different phases (but not positions) of the whisk.

In principle, the rat could use information about the phase of the whisk to infer the angular position (θ) of contact with an object, provided it also had
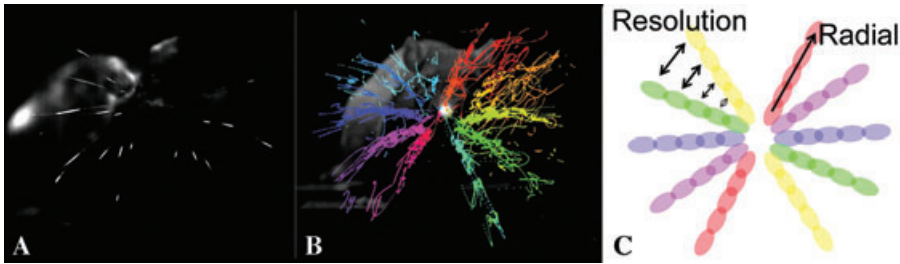
Figure 5. Rat exploratory behavior measured with a laser light sheet. (A) Representative video frame as the rat explored a flat glass sheet. (B) Contact patterns of the whiskers on the glass after the effect of head translation has been removed. Each color represents a different whisker. (C) The morphology of the array ensures that more rostral whiskers sample the object with a higher spatial resolution than whiskers in more caudal columns.

information about the initial positional "set-point" from which the whisk started.[35,37,38] For example, in Figure 4C, if the rat knew that its whisk started from a set point of π/4, it could infer the position of its whisker in head-centered coordinates at every time point during the whisk. As yet, however, we understand neither how this positional information is obtained by the nervous system[16] nor the mechanism by which phase information could be converted into rat-centered coordinates. Importantly, at least one study in the awake animal[17] has suggested that the responses of ganglion neurons may contain some information about whisker position; this is likely to be a fruitful avenue for future research.

Detailed object exploration and feature extraction

The video and mechanical analysis methods we have used in the first part of this narrative can be used to clarify how the rat localizes an object with a single whisker. More complex perceptions, however, require the rat to scan the object with its full whisker array. For example, returning to our rat near the tunnel exit, we find that it has now oriented toward the strange object and is exploring it intensely. What are the patterns of contact that the whiskers make with the object? How might the rat determine the object's shape or size? Quantifying the rat's exploratory strategies during natural behavior has historically been quite difficult because the small size and rapid speed of whisker movements has limited our ability to monitor patterns of whisker–object contact.

To address this problem, our laboratory recently developed a sensor to visualize the contact patterns that the whiskers make with an object during the rat's natural exploratory behavior. Light from a laser diode is passed through a set of lenses to create a thin, planar light sheet. The light sheet cascades vertically down immediately in front of a flat glass wall. Figure 5A shows one frame from a high-speed video camera (1,000 fps) obtained as a rat explored the flat glass surface. Whiskers in contact with the glass are clearly seen as white dashes.

We have used this technology to characterize several features of the whisker–object contact patterns generated during active exploration of the glass plane. One feature to emerge is that within a single whisk, the rat samples a region of an object at multiple spatial scales simultaneously. This may permit the rat to extract quite complicated object features in a single whisk. For example, suppose that the rat encounters a box made of corrugated cardboard. The box may be 10 cm on a side, with corrugations spaced 1 cm apart. Defects in the texture of the cardboard may occur on spatial scales 1 mm or smaller. With a single whisk, the rat could determine the overall shape of the box, while simultaneously sensing the corrugations and texture defects by comparing information obtained from whiskers spaced more or less closely together.

These multiple sensing scales are seen clearly in Figure 5B and C. In Figure 5B, the contact locations of each whisker (color indicates whisker identity) relative to the nose of the rat are plotted on a representative image of the rat. A clear radial pattern emerges in which whiskers within a row are aligned like spokes on a wheel centered at the rat's nose. This radial "footprint" of the sensor array ensures that whiskers in different columns sample the object with different resolutions in the angular dimension (Fig. 5C). Specifically, the whiskers

in columns closer to the rat's nose sample the object with a higher spatial resolution than whiskers in columns further from the rat's nose. This is consistent with the possibility that the rostral whiskers immediately surrounding the snout may serve as a high-acuity "fovea" during tactual exploratory behavior.[3,39] Sensitivity across multiple spatial scales ensures that the rat will be able to extract object features at these scales simultaneously.

Conclusions and open questions

Our rat is delighted to find that the unexpected object is a half-empty cereal box, and returns to its burrow well fed. What have we learned from watching our friend through the night, and what questions remain? Above all, it is clear that mechanics are critical to an understanding of sensory systems—sensors cannot simply be studied as arrays of passive receiving elements. However, we can also draw some more specific conclusions and provide suggestions for future studies.

First, kinematic variables (i.e., position, velocity) are not sufficient to completely describe the mechanical state of the whisker. Figure 2 demonstrates that quantifying differences between contact and noncontact whisking requires consideration of forces and bending moments at the whisker base. Future studies will also need to carefully identify the variables that describe the deformation of the mystacial pad; this will be particularly important if skin stretch is found to provide information about the horizontal angular position of the whisker (θ in Fig. 4).

Second, whisking movements are tightly coordinated with head movements, both during noncontact whisking (Fig. 3A) as well as during contact with an object (Fig. 5B). Thus, the vibrissal system cannot be studied in isolation; vibrisso–tactile behaviors must be interpreted in the context of head movements. In particular, the sequences with which the whiskers will make contact with an object will depend strongly on head position and orientation.

Third, during the tactual exploratory process, the rat transitions seamlessly between scanning, in which whiskers are swept rhythmically through empty space until an object is detected; orientation toward the object; and detailed object exploration. These behaviors clearly require the close integration of whisker, head, and body movements. Future research may not only examine the neural basis for

these transitions, but also quantify how movements performed during detection and orientation are different from those performed during more detailed exploration. How do whisker–object contact patterns and the sequences of head movements vary with the object being explored, and with the kind of information that is desired?

Fourth, the information acquired during sensing behavior depends directly on the "embodiment" of the peripheral sensors, that is, on the details of their morphology and mechanics. In the case of the vibrissal system, if the whiskers were curved or tapered differently, had different lengths, or were actuated differently, the spatiotemporal patterns of whisker–object contact would be entirely different. These patterns in turn place direct constraints on the neural computations that can successfully extract particular object features, for example, local object curvature.

Fifth, the close relationship between sensor mechanics and neural coding leads directly to the question of how whisker deflection is represented in the spiking activity of individual Vg neurons. Although multiple studies have shown that Vg neurons greatly increase their firing rate during whisker–object contact compared to noncontact whisking,[14,17,21] it is not clear how these changes in spiking activity are related to the mechanical variables at the whisker base. Future studies may specifically aim to characterize the relative contributions of neurons classified as rapidly and slowly adapting. These two cell classes have generally been thought to be distinct, but recent studies have demonstrated that under some conditions of object contact, they can produce very similar responses.[17,22] It will be particularly important for future studies to record from the same Vg neuron under conditions of both contact and noncontact whisking, while performing precise high-speed videography of vibrissal movement and bending.

Finally, a more general question is how animals ensure that their perception of object qualities remains independent from the temporal components of the movements executed to extract them. The animal must either cancel out the temporal characteristics of the movement with an efference copy or ensure that information is parsed the same way regardless of speed. Future studies may examine how a sampling strategy—implemented through periodic whisking movements and/or through

central oscillations—could accomplish this second mechanism.

Improved tools for monitoring and modeling vibrissal mechanics make this a particularly exciting time for research in this extraordinarily rich sensory system. When combined with neurophysiological recordings, the analysis of vibrisso–tactile exploratory behaviors is likely to provide new insights into the neural circuitry underlying sensorimotor integration.

Acknowledgments

Conflicts of interest

The author declares no conflicts of interest.

References

1. Pisano, R. & S. Storer. 1948. Burrows and feeding of the Norway rat. *J. Mammal.* **29:** 374–383.
2. Burn, C.C. 2008. What is it like to be a rat? Rat sensory perception and its implications for experimental design and rat welfare. *Appl. Anim. Behav. Sci.* **112:** 1–32.
3. Berg, R. & D. Kleinfeld. 2003. Rhythmic whisking in rat: retraction as well as protraction is under active muscular control. *J. Neurophysiol.* **89:** 104–117.
4. Welker, W.I. 1964. Analysis of sniffing of the albino rat. *Behaviour* **22:** 223–244.
5. Brecht, M., B. Preilowski, M.M. Merzenich, *et al.* 1997. Functional architecture of the mystacial vibrissae. *Behav. Brain Res.* **84:** 81–97.
6. Ebara, S., K. Kumamoto, T. Matsuura, *et al.* 2002. Similarities and differences in the innervation of mystacial vibrissal follicle-sinus complexes in the rat and cat: a confocal microscopic study. *J. Comp. Neurol.* **449:** 103–119.
7. Towal, R. & M. Hartmann. 2006. Right–left asymmetries in the whisking behavior of rats anticipate head movements. *J. Neurosci.* **26:** 8838–8846.
8. Bermejo, R., M. Harvey, P. Gao & H.P. Zeigler. 1996. Conditioned whisking in the rat. *Somatosens. Mot. Res.* **13:** 225–233.
9. Bermejo, R., D. Houben & H.P. Zeigler. 1998. Optoelectronic monitoring of individual whisker movements in rats. *J. Neurosci. Methods* **83:** 89–96.
10. Bermejo, R. & H.P. Zeigler. 2000. "Real-time" monitoring of vibrissa contacts during rodent whisking. *Somatosens. Mot. Res.* **17:** 373–377.
11. Bermejo, R., A. Vyas & H.P. Zeigler. 2002. Topography of rodent whisking—I. Two-dimensional monitoring of whisker movements. *Somatosens. Mot. Res.* **19:** 341–346.
12. Bermejo, R., W. Friedman & H.P. Zeigler. 2005. Topography of whisking II: interaction of whisker and pad. *Somatosens. Mot. Res.* **22:** 213–220.
13. Jin, T.-E., V. Witzemann & M. Brecht. 2004. Fiber types of the intrinsic whisker muscle and whisking behavior. *J. Neurosci.* **24:** 3386–3393.
14. Szwed, M., K. Bagdasarian & E. Ahissar. 2003. Encoding of vibrissal active touch. *Neuron* **40:** 621–630.
15. Towal, R. & M. Hartmann. 2008. Variability in velocity profiles during the free-air whisking behavior of unrestrained rats. *J. Neurophysiol.* **100:** 740–752.
16. Khatri, V., R. Bermejo, J.C. Brumberg, *et al.* 2009. Whisking in air: encoding of kinematics by trigeminal ganglion neurons in awake rats. *J. Neurophysiol.* **101:** 1836–1846.
17. Leiser, S.C. & K.A. Moxon. 2007. Responses of trigeminal ganglion neurons during natural whisking behaviors in the awake rat. *Neuron* **53:** 117–133.
18. Birdwell, J.A., J.H. Solomon, M. Thajchayapong, *et al.* 2007. Biomechanical models for radial distance determination by the rat vibrissal system. *J. Neurophysiol.* **98:** 2439–2455.
19. Solomon, J.H. & M.J. Hartmann. 2006. Robotic whiskers used to sense features. *Nature* **443:** 525–525.
20. Szwed, M., K. Bagdasarian, B. Blumenfeld, *et al.* 2006. Responses of trigeminal ganglion neurons to the radial distance of contact during active vibrissal touch. *J. Neurophysiol.* **95:** 791–802.
21. Zucker, E. & W.I. Welker. 1969. Coding of somatic sensory input by vibrissae neurons in the rat's trigeminal ganglion. *Brain Res.* **12:** 138–156.
22. Jones, L.M., D.A. Depireux, D.J. Simons & A. Keller. 2004. Robust temporal coding in the trigeminal system. *Science* **304:** 1986–1989.
23. Carvell, G.E. & D.J. Simons. 1990. Biometric analyses of vibrissal tactile discrimination in the rat. *J. Neurosci.* **10:** 2638–2648.
24. Fee, M.S., P.P. Mitra & D. Kleinfeld 1997. Central versus peripheral determinants of patterned spike activity in rat vibrissa cortex during whisking. *J. Neurophysiol.* **78:** 1144–1149.
25. Gao, P.H., R. Bermejo & H P. Zeigler. 2001. Whisker deafferentation and rodent whisking patterns: behavioral evidence for a central pattern generator. *J. Neurosci.* **21:** 5374–5380.
26. Harvey, M.A., R. Bermejo & H.P. Zeigler. 2001. Discriminative whisking in the head-fixed rat: optoelectronic monitoring during tactile detection and discrimination tasks. *Somatosens. Mot. Res.* **18:** 211–222.
27. Hattox, A., Y. Li & A. Keller. 2003. Serotonin regulates rhythmic whisking. *Neuron* **39:** 343–352.
28. Sachdev, R.N.S., R.W. Berg, G. Champney, *et al.* 2003. Unilateral vibrissa contact: changes in amplitude but not timing of rhythmic whisking. *Somatosens. Mot. Res.* **20:** 163–169.

29. Guitton, D., A. Bergeron, W. Choi & S. Matsuo. 2003. On the feedback control of orienting gaze shifts made with eye and head movements. *Progr. Brain Res.* **142:** 55–68.

30. Land, M. 2004. The coordination of rotations of the eyes, head and trunk in saccadic turns produced in natural situations. *Exp. Brain Res.* **159:** 151–160.

31. Grant, R.A., B. Mitchinson, C.W. Fox & T.J. Prescott. 2009. Active touch sensing in the rat: anticipatory and regulatory control of whisker movements during surface exploration. *J. Neurophysiol.* **101:** 862–874.

32. Mitchinson, B., C.J. Martin, R.A. Grant & T.J. Prescott. 2007. Feedback control in active sensing: rat exploratory whisking is modulated by environmental contact. *Proc. R. Soc. B-Biol. Sci.* **274:** 1035–1041.

33. Wineski, L.E. 1983. Movements of the cranial vibrissae in the golden-hamster (mesocricetus-auratus). *J. Zool.* **200:** 261–280.

34. Kaneko, M., N. Kanayama & T. Tsuji. 1998. Active antenna for contact sensing. *IEEE Trans. Robotic. Autom.* **14:** 278–291.

35. Ahissar, E. & A. Arieli. 2001. Figuring space by time. *Neuron* **32:** 185–201.

36. Ahissar, E. & P.M. Knutsen. 2008. Object localization with whiskers. *Bio. Cybernetics* **98:** 449–458.

37. Curtis, J.C. & D. Kleinfeld. 2009. Phase-to-rate transformations encode touch in cortical neurons of a scanning sensorimotor system. *Nat. Neurosci.* **12:** 492–501.

38. Ahissar, E., S. Haidarliu, & M. Zacksenhouse. 1997. Decoding temporally encoded sensory input by cortical oscillations and thalamic phase comparators. *Proc. Nat. Acad. Sci. U. S. A.* **94:** 11633–11638.

39. Catania, K. & F. Remple. 2004. Tactile foveation in the star-nosed mole. *Brain Behav. Evol.* **63:** 1–12.