Active sensing: head and vibrissal velocity during exploratory behaviors of the rat

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Abstract

The vibrissal-trigeminal pathway of the rat has become an increasingly important model in neuroscience to study how sensory and motor signals are encoded, processed, and integrated in the nervous system, ultimately yielding "perception" of an object. In this chapter, we focus specifically on the role of head and vibrissa (whisker) velocity during exploratory movements. The chapter begins by describing basic vibrissal anatomy and mechanics, and shows that different studies measure "vibrissa velocity" under very different mechanical conditions, which will give rise to very different types of mechanoreceptor activation. It is thus critical to consider forces and bending moments at the whisker base in addition to vibrissa velocity when quantifying vibrissa-object contact during natural behavior. To illustrate this point, we summarize recent results demonstrating that whisking velocity at the time of collision with an object may influence the rat's ability to determine the radial distance to the object as well as the horizontal angle of contact. Further, we present evidence suggesting that the rat may actively select velocities at different points in the whisking trajectory, perhaps to aid localization behavior in these two dimensions. Finally, because the whiskers are always acting in concert with the head, we describe correlations

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between whisking behavior and head velocity. Preliminary data suggest that the position, orientation, and velocity of the head – which moves at a very different spatial and temporal scale than the vibrissae – will have a large effect on the tactile information acquired by the vibrissal system.

1. Introduction

Rats are nocturnal animals with low acuity vision (Dean 1981; Silveira et al. 1987; Keller et al. 2000; Prusky et al. 2000; 2002). They use rhythmic (5–25 Hz) movements of their vibrissae (whiskers) to tactually extract object features, including size (Brecht et al. 1997; Krupa et al. 2001), shape (Brecht et al. 1997; Harvey et al. 2001), orientation (Polley et al. 2005), and texture (Carvell and Simons 1995; Nicolelis et al. 1996; Arabzadeh et al. 2003; 2004; 2006; Neimark et al. 2003; Moore 2004; Hipp et al. 2006; Vaziri et al. 2007). These rhythmic vibrissal movements are known as "whisking," and provide the rat a rich tactile window to its environment.

As shown in Fig. 1A, about 30 vibrissae are arranged in a regular array on each side of the rat's face (Vincent 1913). Although there are no sensors along the length of a vibrissa, each vibrissa base is embedded within a densely innervated follicle (Fig. 1B) (Rice et al. 1986; 1993; 1997; Mosconi et al. 1993; Ebara et al. 2002). Mechanoreceptors in the follicle transduce deformations into electrical signals and provide input to primary sensory neurons in the trigeminal ganglion. (Zucker and Welker 1969; Gibson and Welker 1983a; b; Lichtenstein et al. 1990; Stüttgen et al. 2006; 2008; Szwed et al. 2006; Leiser and Moxon 2007; Khatri et al. 2009). Within nearly every brain structure of the ascending vibrissal-trigeminal system, neurons are grouped so as to directly reflect the regular peripheral topography (Woolsey et al. 1975; Van der Loos 1976; Belford and Killackey 1979; Killackey 1980; Arvidsson and Rice 1991). The presence of these neural maps allows researchers to record from neurons

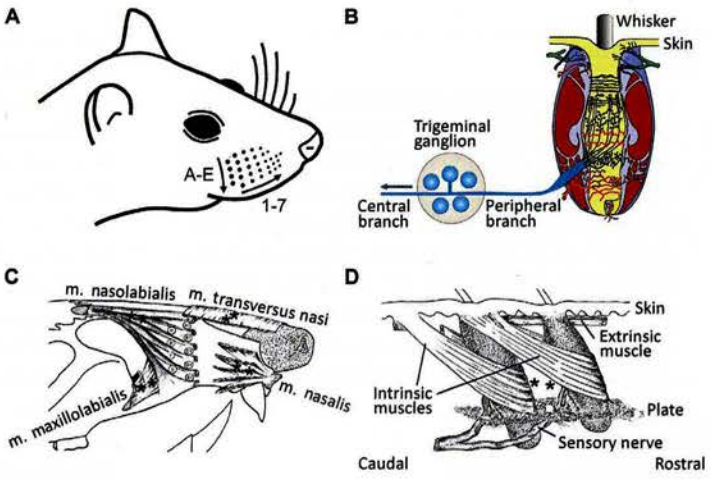

Fig. 1 Vibrissa anatomy and mechanics. **A** Vibrissae are arranged in rows and columns on the rat's face. **B** Peripheral branches of trigeminal ganglion neurons receive input from mechanoreceptors in the vibrissa follicle. Drawing adapted from Diamond et al. (2008), and Rice et al. (1997). **C** Four extrinsic muscles attach the mystacial pad to the skull. **D** The intrinsic muscles form "slings" around the follicles, and join adjacent follicles of a single row. Drawings in C and D were adapted from Hill et al. (2008), which were in turn adapted from Fig. 1 and 3 of Dörfl (1982; 1985)

responsive to particular groups of vibrissae, and to study how tactile information is integrated with motor signals (Ahissar and Arieli 2001; Kleinfeld et al. 2006; Diamond et al. 2008). This makes the rat vibrissal system an excellent model to explore active sensing behaviors and the structure of movements that subserve sensing.

Given the importance of this model system to neuroscience, it is somewhat remarkable that we have not yet fully identified the mechanical parameters at the vibrissa base relevant to behavior, and how these parameters are encoded in the earliest stages of the vibrissal-trigeminal pathway. Until the mechanical input to the vibrissal pathway is quantified, our ability to interpret the functional and computational characteristics of higher-level neural processing stages will remain severely limited.

One reason that it has historically been difficult to quantify the mechanical variables important to whisking behavior is that whisking is fundamentally a process of "active sensing," in other words, the mechanical signals obtained by the vibrissae depend on how they are moved. In principle, the rat could – and probably does – use any number of control strategies for exploration with vibrissae. For example, it could control the angle of its vibrissae, the velocity of protractions and retractions, or the force required to move its vibrissae through a particular angle. In this chapter, we focus specifically on the role of head and whisking velocity during exploratory movements.

This chapter consists of three main parts. First, we describe basic vibrissa anatomy and mechanics. An important point in this section is that different studies measure "vibrissa velocity" under very different mechanical conditions. Second, we show that whisking velocity at the time of collision with an object will influence the rat's ability to determine both radial contact distance as well horizontal contact angle. We present evidence suggesting that the rat may tune or select velocities at different points in the whisking trajectory, perhaps to aid in localization behavior. Finally, we describe correlations between whisking behavior and head velocity, and suggest some ways in which coordinated head and vibrissa movements may enhance sensing.

2. Vibrissa mechanics: active movements vs. passive stimulation

2.1 Vibrissa and follicle anatomy and muscle mechanics

Rat vibrissae have an intrinsic curvature (Knutsen et al. 2008; Towal et al. 2011) and taper approximately linearly to a diameter of a few micrometers at the tip (Williams and Kramer 2010). The proximal portion of the vibrissa (~60–70%) typically lies in a plane (Knutsen et al. 2008; Towal et al. 2011). That is, if one were to pluck the vibrissa out and place it on a table, the proximal portion would lie flat, in the plane of the table. The remaining fraction of the vibrissa generally curves out of the plane.

The base of each vibrissa inserts into a follicle replete with mechanoreceptors. The responses of these mechanoreceptors to a particular mechanical input will be determined in part by the stiffness of the surrounding tissue. In addition, a large blood sinus occupies much of the follicle, and its degree of engorgement with blood may modulate the stiffness with which the vibrissa is held. Finally, the musculature surrounding the follicle is also likely to alter the stiffness with which the vibrissa is held at its base and with which it resists deflection.

The vibrissae are actuated by two dis-

tinct groups of muscles: extrinsic muscles connect the mystacial pad directly to the skull, while intrinsic muscles form a "sling" around each of the follicles (Dörfl 1982; 1985, see Fig. 1C–D). The intrinsic and extrinsic muscles act in a three-step sequence during the whisk cycle (Dörfl 1982; 1985; Wineski et al. 1988; Berg and Kleinfeld 2003; Hill et al. 2008). First, a rostral extrinsic muscle (*m. nasalis*) initiates protraction by pulling the mystacial pad forward. Second, the intrinsic sling muscles contract around each follicle to rotate the vibrissa farther forward. Finally, two large caudal muscles (*m. nasolabialis* and *m. maxiolabialis*) contract to pull the mystacial pad and vibrissae back to their initial state, aided by the elasticity of the skin.

In the head-restrained or over-trained animal, whisking trajectories can appear quite stereotyped (Bermejo et al. 2002; Mehta et al. 2007). Under more natural conditions, however, involving head movements or contact with objects, the vibrissae can exhibit considerable variability in their kinematic profiles (Wineski 1983; Sachdev et al. 2003; Towal and Hartmann 2006; 2008; Mitchinson et al. 2007; Grant et al. 2009). The trajectories are even more complex if the very tip of the vibrissa is considered. Because the vibrissae are flexible and actuated from the base, tip velocities involve substantial dynamics. Accordingly, vibrissa "velocity" is typically used to refer only to movements of the proximal portion of the vibrissa as it emerges from the mystacial pad. To first approximation, this portion of the vibrissa can be taken to move as a rigid body during free-air whisking (Knutsen et al. 2008), but not during collisions or periods of contact with an object.

A recent study showed that as the vibrissa protracts forward, it exhibits substantial "roll" about its long axis (Knutsen et al. 2008). This same study also showed that over the course of the whisking cycle, the roll angle, ζ, correlates strongly with horizontal angle, θ, (Knutsen et al. 2008). When the head is static, the orientation of the vibrissa's intrinsic curvature relative to an object is determined by the roll angle. Because the roll angle varies with the horizontal angle, the vibrissa will collide with an object at different orientations, depending on the horizontal angle at which the collision occurs. When the head is in motion, both the roll angle and the orientation of the head relative to the object will determine the orientation at which the vibrissa collides with the object. Thus, at the time of a collision, the vibrissa may have its concave side facing the object, its convex side facing the object, or anything in between.

The intrinsic curvature of the vibrissa as it collides with an object will in turn affect the forces generated during collision. For example, collisions with the concave side of the whisker will generate a larger net force vector and longer duration contacts than collisions with the convex side of the whisker (Quist and Hartmann, submitted). This in turn leads to the behavioral prediction that the rat might sometimes alter its exploratory strategies to ensure collisions with the vibrissa's concave side.

The forces generated by a collision are mechanically transmitted by the vibrissa to its base, where, as described above, mechanoreceptors in the follicle transduce mechanical deformations to electrical signals. Deformation of a mechanoreceptor could result if the vibrissa moves relative to the follicle; it could result from muscles (either intrinsic or extrinsic) squeezing on the outside of the follicle; or it could result from the blood sinus distending or relaxing. These complex features of mechanical transduction in the follicle mean that boundary conditions and the shape of the vibrissa at contact will clearly have a large effect on the incoming sensory information.

2.2 Different studies measure "vibrissa velocity" under very different mechanical conditions

All studies to date have measured "vibrissa velocity" in essentially the same way, but, as will be shown, under very different mechanical conditions. Vibrissa angle is measured near the base, along the initial linear portion of the vibrissa (θ in Fig. 2A). The first time derivative of the angle is then taken as the velocity. The apparent uniformity across studies in the method for measuring "vibrissa velocity," however, belies the very different mechanical conditions under which this quantity is measured.

Many studies of whisking behavior in the awake animal measure kinematics during

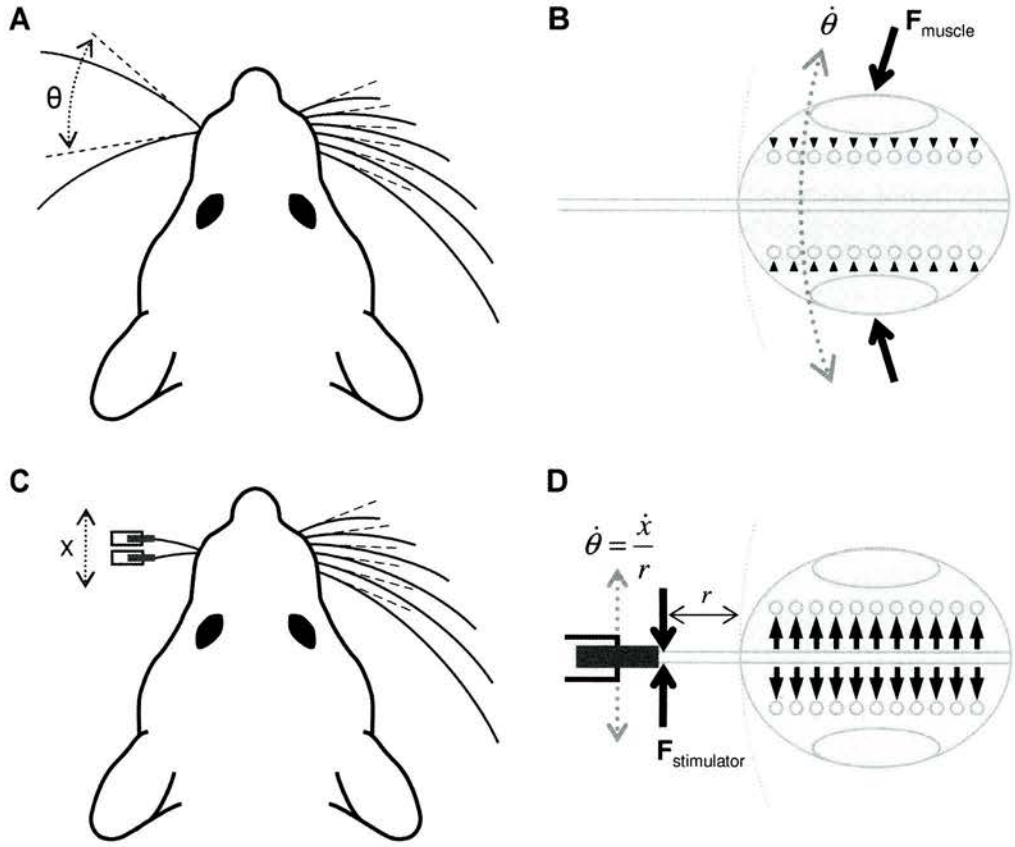

Fig. 2 Vibrissa velocity measured during free-air whisking and during passive vibrissa displacements. **A** Overhead view of rat whisking in free air. A single vibrissa on the left mystacial pad is shown to sweep through the angle θ. **B** Overhead view of passive deflection of a vibrissa by a stimulator. Because displacements are typically small, they are measured linearly (x). **C** During free-air whisking behavior, forces (large solid black arrows) from the surrounding musculature act on the follicle-sinus-complex as a unit. Forces acting on the mechanoreceptors (stylized as gray circles) are likely to be small. **D** During passive stimulation, an external force is imposed directly on the vibrissa shaft and transmitted into the follicle. The vibrissa will exert forces (solid black arrows) directly on the mechanoreceptors (stylized as gray circles) and a large response will be generated

free-air whisking (Sachdev et al. 2002; Berg and Kleinfeld 2003; Jin et al. 2004; Towal and Hartmann 2006; 2008; Khatri et al., 2009). During free-air whisking, the intrinsic and extrinsic muscles move the follicle and mystacial pad as described earlier, resulting in the type of motion schematized in Fig. 2A. Protraction velocities in these studies typically range from 250°/sec to 1000°/sec; retraction velocities typically have a higher upper bound, near 1500°/sec. Slightly lower values (~700°/sec and ~1100°/sec for retraction) were found for protractions and retractions over a textured surface (Carvell and Simons 1990).

In contrast, studies describing neural recordings from the anesthetized animal generally measure velocity of the vibrissa when it is rigidly attached to a stimulator and passively displaced (Pinto et al. 2000; Shoykhet et al. 2000; Jones et al. 2004). The stimulator is often a piezoelectric crystal, a stepper motor, or a solenoid, and is moved either in a "ramp-and-hold" paradigm or oscillated at known frequencies. Because these passive displacements are typically small, and the stimulator is often translated instead of rotated, velocities are often expressed as linear measures (mm/sec). This results in the type of motion shown in Fig. 2B. When converted to angular velocities, the linear velocities in these studies typically range from 700°/sec to 2000°/sec.

These two types of experimental conditions could produce *identical* "velocities," but they are mechanically very different, and will generate very different deformations of mechanoreceptors in the follicle. The differences become apparent when considering the anatomy of the vibrissa/follicle complex together with the locations of the receptors, as shown in Fig. 2C–D.

In the case of free air whisking, the vibrissa and the follicle are actuated together, as a unit, by the muscles surrounding the follicle. This is the situation depicted in Fig. 2C, in which two black solid arrows illustrate the force of the surrounding muscles and skin tissue on the follicle. In this case, there is likely to be minimal relative motion between the vibrissa and follicle. If there is little or no relative motion, mechanoreceptors in the follicle will deform only slightly, and only a very weak signal will be transmitted to primary sensory neurons. This is consistent with recent findings that kinematic variables (deflection amplitude, velocity, position) are poorly coded by primary sensory neurons during free-air whisking behavior (Khatri et al. 2009). The small correlation that does exist may be due to the muscles squeezing down on the follicle or inertial effects deforming the vibrissa within the follicle (small black arrowheads in figure).

If instead a stimulator is used to passively displace the vibrissa, as during experiments with anesthetized animals, the applied force will generate forces and moments via the vibrissa shaft *in* the follicle (Pinto et al. 2000; Shoykhet et al. 2000; Jones et al. 2004). This is illustrated in Fig. 2D by the solid black arrows, now on the *inside* of the follicle, depicting the vibrissa pressing against a set of mechanoreceptors. Direct activation of mechanoreceptors during passive stimulation is consistent with the strong responses of primary ganglion neurons in these experiments (Gibson and Welker 1983a; b; Lichtenstein et al. 1990; Leiser and Moxon 2006; Szwed et al. 2006).

It is important to note that we cannot determine the precise distribution of forces on mechanoreceptors in the follicle, because we do not yet know exactly how stiffly (or loosely) the vibrissa is held at every point within the follicle. Regardless of the precise distribution of forces, however, it is clear that during free-air whisking the driving force originates in the muscles outside of the follicle, while during passive stimulation, the driving force originates from the vibrissa shaft inside of the follicle.

2.3 Interpretation of studies using ramp-and-hold stimuli and oscillatory stimuli

To summarize so far, the velocity of a vibrissa does not uniquely determine the forces and moments generated at its base. Muscles may pull on the vibrissa-follicle complex to generate a velocity of 1000°/second, but if there is no relative motion between vibrissa and follicle, mechanoreceptors will not deform. A situation similar to this may arise as the rat whisks freely in air. Conversely, if an object near the vibrissa base obstructs the vibrissa's movement, its velocity might approach zero, but generate forces and moments that cause substantial mechanoreceptor deformation.

Comparing "vibrissa velocity" during passive stimulation to "vibrissa velocity" during free air whisking is like comparing apples and oranges. Studies that employ passive ramp-and-hold stimuli in anesthetized animals are most likely examining how neurons respond to rates of change of forces and moments, as might occur during collision with an object.

For example, previous studies using ramp-and-hold stimuli have shown that rat barrel cortical neurons respond preferentially to "high-velocity" ramp stimuli. These stimuli were found to produce highly synchronized responses in the ventral posterior medial thalamus (VPm), which in turn produced strong responses in layer 4 barrel cortex (Pinto et al. 1996; 2000; Temereanca and Simons 2003). In contrast, large amplitude movements at low velocities did not evoke strong responses in the cortex despite causing high thalamic discharge rates (Pinto et al. 2000). These studies concluded that the strength of cortical responses (in number of action potentials and duration of response) was directly proportional to vibrissa velocity. But from a behavioral point of view, these neurons would respond most strongly to rapid force and moment changes associated with collisions with objects. The neurons would be unlikely to respond to high velocities during free-air whisking behavior.

Similarly, studies that rapidly oscillate the vibrissa back and forth about its rest point are inducing rapid changes in forces and moment that do not resemble those that would be generated either by free-air whisking, or by collision with an object. It is difficult to say what behavioral condition these experiments replicate. The oscillations generated may be similar to the rapid vibrations that could be induced as a rat swept its vibrissae over a texture, but they are not quite the same, because the vibrissa is being driven quite differently than would occur during natural texture exploration (Hartmann et al. 2003; Neimark et al. 2003).

In the next section, we discuss how vibrissa velocity influences the forces and moments that will be generated at the vibrissa base, and the roles that velocity may play in the rat's exploratory strategies.

3. The importance of velocity in object localization

The natural exploratory behavior of the rat is characterized by "bouts" of whisking that last between a few hundred milliseconds up to a few seconds (Welker 1964; Berg and Kleinfeld 2003). During tactual exploration of the environment, the rat moves its body and head so that its vibrissae are sometimes moving in free air, but at other times colliding with various objects in the environment.

When the vibrissa collides with an object, any one of several behavioral events can occur. One possibility is that the rat may bring

its vibrissa to a very quick halt and then reverse its direction of motion (Grant et al. 2009). On the opposite extreme, the rat may continue to brush the vibrissa along the object, so that at some point the vibrissa may ultimately slip past it and lose contact during protraction (Hartmann et al. 2003). Regardless of which behavior occurs, there are three important points to be made about the collision process in the context of object localization.

First, contact with an object can occur at any location along the length of the vibrissa. Contact does not need to occur at the vibrissa tip. This leaves the rat with the problem of determining both the radial distance to the object and the angle of contact. Somehow, the forces and moments induced by the collision must be interpreted by the nervous system to yield an impression of a spatial coordinate in (r, θ, and z). This problem is illustrated in Fig. 3A. Note that the height (z) of a given vibrissa is thought to be coded by a labeled line strategy (Diamond et al. 2008)

Second, mechanoreceptor deformation is the only event that can let the animal know that contact with an object has occurred. Receptor deformation will be induced by the forces and moments (including vibrations) generated by collisions. This is because the collision generates reaction-forces and reaction-moments at the vibrissa base, as shown in the free-body diagram of Fig. 3B. Ultimately, forces and moments are the physical variables corresponding to "touch." Work from multiple laboratories has convincingly demonstrated that position or phase information must be combined with "touch" information in order for the rat to determine the horizontal angle of contact (Szwed et al. 2006; Mehta et al. 2007; Diamond et al. 2008).

Third, the particular forces and moments generated by the collision will depend on the vibrissa velocity at the time of collision. In the next section we describe how the velocity at the time of collision may affect how the rat localizes the horizontal angle of the object. We then present evidence to suggest that the rat may control or "tune" the instantaneous whisking velocity during the whisk cycle, perhaps to aid in this process of localization.

3.1 Role of velocity in determining object coordinates: radial distance and horizontal angle

Our laboratory recently described a mechanism through which the rat could determine the radial distance from the vibrissa base to an object. (Solomon and Hartmann 2006;

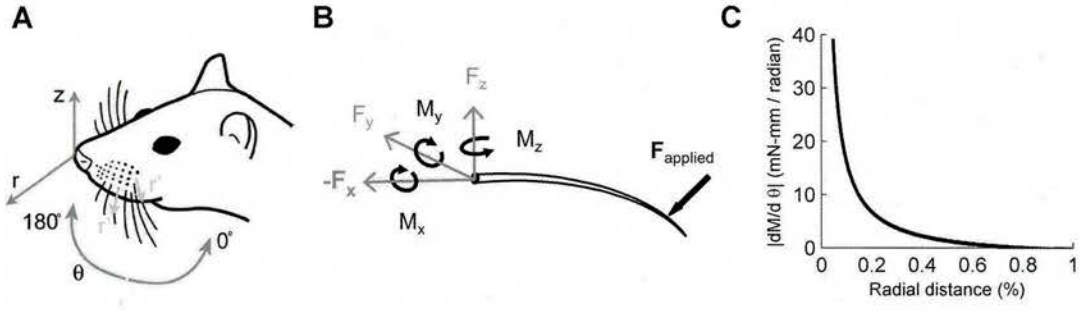

Fig. 3 **A** The rat must localize an object in 3-dimensions relative to the snout: r, θ, and z. Fig. adapted from Gopal and Hartmann (2007). **B** Free-body diagram of vibrissa. **C** $dM/d\theta$ as a function of normalized contact distance. The plot shows simulation results for a straight, linearly tapered vibrissa deflecting against a frictionless peg

Birdwell et al. 2007). Our method was based on an approach first described by Kaneko in 1998 (Kaneko et al. 1998). When the vibrissa collides with an object, the resulting force causes the vibrissa to bend. The amount of bending is proportional to the moment M generated at the base, and the quantity $dM/d\theta$ can be shown to be monotonically related to the radial object distance, r, as shown in Fig. 3C (Kaneko et al. 1998; Birdwell et al. 2007). This means that if the rat can keep track of the rate of change of moment (dM/dt) and the velocity ($d\theta/dt$) with which it is "pushing" its vibrissa against the object, enough information will be present to determine $dM/d\theta$ and thus the radial object distance *r.* In the same set of papers, we also noted that the rat could choose to "tune" the particular value of dM/dt associated with a particular value of *r,* simply by changing the velocity of its whisk. If the rat whisks at a higher velocity, the rate of moment change dM/dt will also be higher; the rat could potentially tune its whisking velocity to bring dM/dt into the most sensitive (highest resolution) region.

Velocity may be similarly important in determining the horizontal angular location of an object, the variable θ in Fig. 3A. As discussed above, in order to determine the angular location of an object in the horizontal plane, the rat must combine kinematic information with information about the time or location of object collision. There are currently two hypotheses for the computation of horizontal location.

One hypothesis predicts that the nervous system performs coincidence detection between the responses of *position*-sensitive neurons and contact-sensitive neurons (Szwed et al. 2003; Mehta et al. 2007) to determine the horizontal angle of an object. A second hypothesis, however, predicts that the nervous system performs coincidence detection between the responses of *phase*-sensitive neurons and contact-sensitive neurons to determine the horizontal angle of an object (Ahissar 1998; Ahissar and Arieli 2001; Szwed et al. 2003; Curtis and Kleinfeld 2009). Notice that the definition of phase used in these studies is a *temporal* phase, found by dividing each whisk cycle evenly between 0 and 2π radians. This hypothesis requires that the velocity of the protraction always have the same sign (i. e., that the vibrissa does not reverse direction during a protraction). Otherwise, the relationship between temporal phase and position is not unique, and horizontal location cannot be determined. Velocity is thus likely to play a critical role in spatial localization in both the radial and horizontal dimensions. In the next section, we present evidence that the rat may tune instantaneous whisking velocity during the whisk cycle, perhaps to aid in this process of localization.

3.2 Variations in whisking velocity during the whisk cycle

We recently quantified variability in the velocity profiles of whisking during natural exploratory behavior (Towal and Hartmann 2008). The results showed that although most retractions consisted of smooth, monotonic velocity profiles, the majority of protractions were not smooth or monotonic. Most notably, a significant number of the protractions showed a slowing mid-trajectory, and many actually reversed direction during the course of the protraction. Examples of these three types of whisking profiles are illustrated for protractions in Fig. 4. It is clear from the figure that different whisking velocity profiles achieve maximum velocity at different temporal phases of the whisk.

Importantly, however, the results also indicated that despite the high degree of variability in the instantaneous whisking

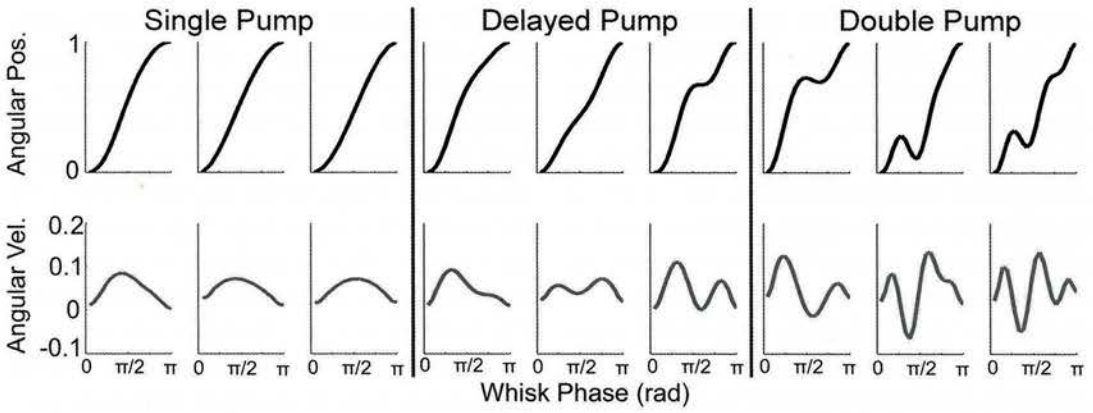

Fig. 4 Nine exemplary protraction segments illustrate the continuum of position and velocity profiles. Angular position has been normalized between zero and one. Angular velocity was calculated as the derivative of the normalized angular position. Both velocity and position are plotted as a function of temporal phase, with π indicating full protraction. Thick black vertical lines indicate the separation of the continuum into the three profile types: single, delayed, and double

velocity, the average whisking velocity remained remarkably constant from whisk to whisk. This constancy was possible because different whisking profiles appeared to compensate for any initial "error" in the velocity of the whisk segment. If a whisk segment started faster than average, then a delayed or double pump whisk profile subsequently slowed it down. If a whisk started more slowly than average, then the rat tended not to execute a double or delayed pump, but rather to execute a single pump that increased in speed.

Thus, the primary result of the study was that each protraction and retraction may exhibit a large variability in instantaneous velocity but – across whisks – demonstrate a low variability in average whisking velocity. This suggests that the rat may be exploiting the tri-phasic muscle activation pattern to actively adjust its whisking velocity in real time. In principle, these velocity adjustments may alter the rate of moment change so as to improve the extraction of radial distance. For example, the rat may want to increase the rate of moment change for contact with objects near the tip to increase signal size.

In addition, these results argue against the temporal-phase hypothesis for horizontal object localization, because the relationship between whisk phase and external space is unique only when the vibrissa position monotonically increases through the whisk. If a double pump is generated by a single triphasic pattern of muscle activity, then a reversal in direction occurs during the whisk. This means that the relationship between temporal phase and external space is non-unique, as the same spatial location is achieved at three distinct times (temporal phases) during the whisk. Instead, our data favor the position-hypothesis for determination of the horizontal contact angle, consistent with recent findings from the Kleinfeld laboratory (Mehta et al. 2007). By directly measuring vibrissa position, the delayed and double pumps no longer pose a problem for calculating the spatial position of contact.

4. The relation between head velocity and whisking movements

As described in section 2.1, the velocity of the vibrissa as it makes contact with an object will determine the changes in the forces and moments at the vibrissa base. When the head is static, the rat can control vibrissa velocity via its intrinsic and extrinsic muscles (Fig. 1). If the head is free to move, however, then the velocity of the vibrissa relative to the object also depends on the head velocity, because the vibrissa is attached to the head. In this section we describe the coupling that exists between head and vibrissa movements.

4.1 Right-left positional asymmetries are correlated with rotational head velocity

We recently performed a study to examine the extent to which bilateral free-air whisking movements were influenced by head rotations in the horizontal plane. We initially hypothesized that the rat might want to maintain spatial and temporal symmetry in world coordinates. That is to say, the vibrissae should maintain their velocity in the world reference frame *regardless* of the head velocity. For example, suppose that the rat is turning its head to the right with a velocity ω_{head}. In this case, the right vibrissae would need to speed up by a velocity exactly equal to ω_{head} and the left vibrissae would need to slow down by a velocity ω_{head}. This would mean, in turn, that the difference of left and right vibrissa velocities should be proportional to twice the head velocity. (In practice, this difference becomes a sum because left vibrissa velocities are neg-

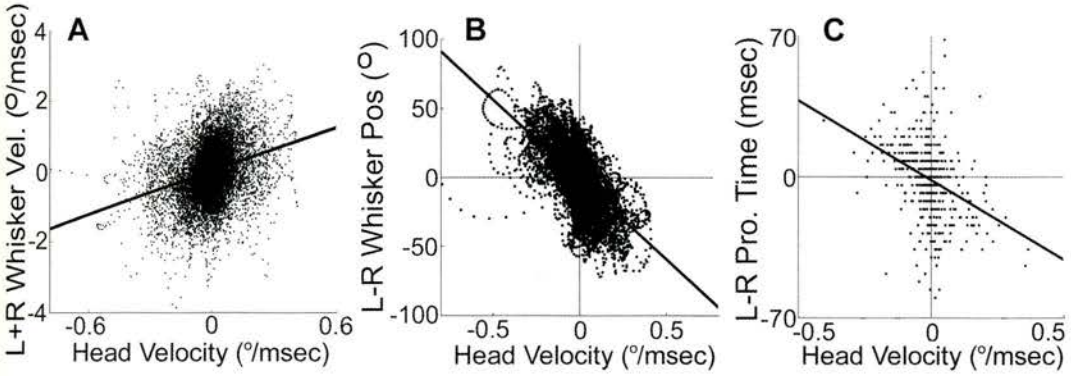

Fig. 5 Relationships between whisking parameters and head velocity. In all graphs, head velocities are represented in world coordinates, with negative velocity indicating that the head is turning to the right. **A** Velocity asymmetry does not strongly depend on head velocity. In world coordinates, the sum of whisking velocities correlates weakly with head velocity with a slope of 2.06. This slope is statistically indistinguishable from the slope of 2.00 that would occur if one side sped up by the head velocity, while the other side slowed down by the head velocity ($p = 0.30$). **B** Spatial asymmetry does depend on head velocity. Instantaneous left–right vibrissa position difference versus instantaneous head velocity plotted continuously over 373 whisks. The slope of the best linear fit is 115 msec, which approximately equals the average duration of a single whisk (121 msec). The r-value is 0.58. **C** Temporal asynchrony is not well correlated with head velocity The largest correlation ($r = 0.34$) between left–right vibrissa time differences and head velocity was found for protractions, with the head velocity averaged over 52 msec following the protraction

ative when measured in world coordinates.) The results of this analysis are shown in Fig. 5A. Although the slope is very close to 2, as predicted, the correlation is weak, with an r-value of 0.28. This led us to reject our initial hypothesis.

Instead, as shown Fig. 5B, left-right whisking asymmetry was found to be strongly correlated with rotational head velocity. Specifically, the positional asymmetry of the left and right vibrissae arrays was equal to the distance that the head would rotate during a whisk. In other words, the vibrissae "look ahead" of the current position of the head to anticipate head movement that would occur, were the rat to continue to rotate its head at that velocity. The rat thus appears to use its vibrissae to search in advance of the head, presumably to avoid running into unexpected obstacles.

Surprisingly, however, there was only a weak relationship between head velocity and right–left time differences of peak protraction and retraction. Fig. 5C shows that although temporal asynchrony is large (up to 70 msec), it is not nearly as well correlated with head velocity as is spatial asymmetry. Temporal asynchronies could, theoretically, be used to differentially search particular regions of space during head rotations. For example, the rat could choose to stop protraction on right and left sides at different points in time, thus selecting whisk amplitudes and the particular (spatial) regions swept out by each side.

In summary, during free air whisking behavior that includes head rotations, the rat is not trying to ensure that right and left vibrissa arrays have the same velocity, or that right and left vibrissae arrays are in the same phase of the whisk. Neither are the protraction and retraction times strongly related to the rotational head velocity. Instead, the angular positions of left and right arrays are strongly correlated with the velocity of the head.

4.2 Future directions: Simultaneous measurement of head and vibrissa velocities during contact with an object

Until recently, the small size and rapid speed of vibrissa movements precluded quanti-

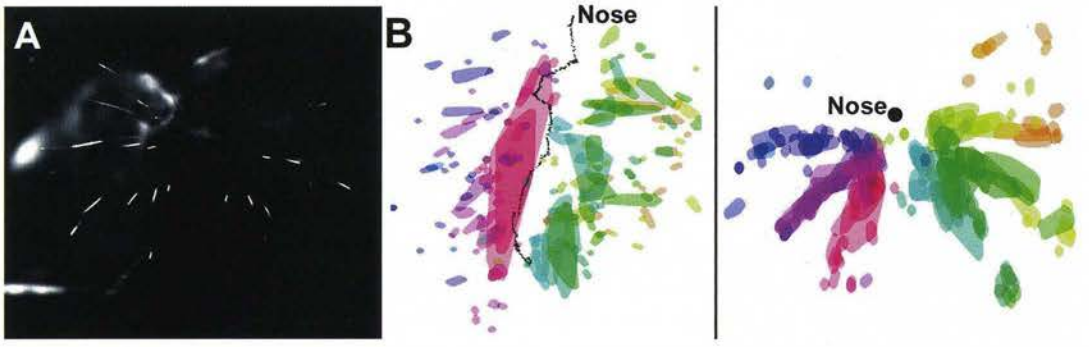

Fig. 6 Vibrissa-object contact patterns measured with a laser light sheet. **A** Image from a high speed camera obtained as the rat explored a flat glass plate with the light sheet in front. The points of contact that the vibrissa makes with the sheet are seen as white dots. **B** Contact patterns of vibrissae on the glass plate over a period of three whisks (~360 msec) *Left:* Spatial distribution of vibrissa contacts as the rat's head moved in an approximately-vertical trajectory (dark line labeled "nose"). The contacts of each vibrissa are represented in a different color. *Right:* The same data as in the left plot, after subtracting out head movement. A high degree of spatial overlap across the three whisks is revealed, demonstrating that head movement accounts for the large spatial coverage in the left plot

fication of the patterns of contact that the vibrissae make with an object, and there was no method to examine how head and vibrissa velocities might change during the exploration process. Our laboratory has recently developed a technique to permit visualization of vibrissa-object contact patterns during the rat's natural exploratory behavior (Towal and Hartmann 2010). Light from a laser 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. Fig. 6A shows one frame from a high speed video camera (1000 fps) obtained as a rat explored the flat glass surface. Vibrissae in contact with the glass are clearly seen as white dashes. As shown in Fig. 6B, we have used this technology to quantify the external space contacted by each vibrissa as the rat explores the glass sheet. It is clear from the figure that head movements account for much of the variability in the spatial locations of vibrissa-object contact. When head movements are removed, the vibrissae remain primarily in narrow "slots," associated with their position in the array. This was confirmed using step-wise regression techniques which indicate that both whisker and head movement variables are required to explain a significant amount of the variability in the whisker-object contact patterns.

Conclusions

This chapter has three main conclusions.

First, and most importantly: different studies measure "vibrissa velocity" under extremely different mechanical conditions. Passively shaking a vibrissa at 8 Hz, for example, does not replicate the mechanical conditions associated with 8 Hz free-air whisking.

Second, the velocity of whisking is likely to be an important control parameter for the rat. The rat could vary whisking velocity to improve the accuracy of radial distance determination.

Third, the position, orientation, and velocity of the head will have a large effect on the tactile information acquired by the vibrissae. Like the eyes and the fingers, the vibrissae are relatively low mass, high resolution sensing structures, whose movements may be controlled nearly kinematically. Eyes, vibrissae and fingers are all located on far more massive structures (the head and the forelimb) whose mass cannot be neglected. Movements of the head and forelimb are generally much slower than those of the vibrissae, eyes, and fingers, and they serve to place these fine-resolution sensory structures on the portion of the surface that the animal will explore next. Future work will aim to quantify the relative contributions of head and vibrissa movements – operating at different spatial and temporal scales – to the acquisition of sensory information as the rat explores an unknown environment.

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