Using hardware models to quantify sensory data acquisition across the rat vibrissal array

Venkatesh Gopal[1] and Mitra J Z Hartmann[1,2]

[1] Department of Biomedical Engineering, 2145 Sheridan Road, Northwestern University, Evanston, IL 60208, USA
[2] Department of Mechanical Engineering, 2145 Sheridan Road, Northwestern University, Evanston, IL 60208, USA

E-mail: vgopal@northwestern.edu and m-hartmann@northwestern.edu

Abstract

Our laboratory investigates how animals acquire sensory data to understand the neural computations that permit complex sensorimotor behaviors. We use the rat whisker system as a model to study active tactile sensing; our aim is to quantitatively describe the spatiotemporal structure of incoming sensory information to place constraints on subsequent neural encoding and processing. In the first part of this paper we describe the steps in the development of a hardware model (a 'sensobot') of the rat whisker array that can perform object feature extraction. We show how this model provides insights into the neurophysiology and behavior of the real animal. In the second part of this paper, we suggest that sensory data acquisition across the whisker array can be quantified using the complete derivative. We use the example of wall-following behavior to illustrate that computing the appropriate spatial gradients across a sensor array would enable an animal or mobile robot to predict the sensory data that will be acquired at the next time step.

(Some figures in this article are in colour only in the electronic version)

1. Introduction

No robot yet constructed, no matter how lifelike in appearance, can match the agility and grace of a vertebrate animal, can replicate its autonomous, goal-directed movements, or rival its ability to extract salient information from a complex environment. These vertebrate behaviors rely on multiple interconnected stages of neural processing which have as yet no engineering equivalent. Our laboratory studies how animals acquire sensory data in order to gain insight into the neural computations that permit complex sensorimotor behaviors. Our aim is to provide a quantitative description of the structure of incoming sensory information, so as to place constraints on the computations that must occur at higher stages of the nervous system. Our approach emphasizes three important characteristics of the neural control of sensory data acquisition.

First, because the dynamics of sensory surfaces are difficult to model in software, hardware models (robots) are increasingly useful in understanding neural processing in sensory systems. Sensory data acquisition depends directly on the mechanics of the body surface doing the sensing, and these mechanics can be difficult or impossible to simulate. Robotic models that capture the essential features of the sensing process can be used to explore biological sensing mechanisms in the presence of real world dynamics and noise. Iteration between the analysis of biological sensory systems and the construction of hardware models can thus lend neurobiological insight as well as aid in the development of novel engineering devices [1–11].

Second, perception during natural behaviors typically relies on the tight integration of movement and sensing. In this view, a visual percept is induced not merely by the passive formation of an image on the retina, but by the active

exploration of that image through eye movements [12–18]. Similarly, olfactory perception relies on sniffing and on head movements [19–23], and touch is not merely the activation of mechanoreceptors, but includes the cues obtained through movement that indicate how the environment is sampled.

Third, an animal's movements impose a spatiotemporal structure on the incoming sensory data it receives [24, 25]. An animal's nervous system cannot afford to be indiscriminately sensitive to the continuous barrage of sensory data impinging upon its receptors. Instead, the animal must sample the environment so as to select out the information most important to the current behavioral task. One effect of sampling through movement is to reduce the rate at which sensory information is made available to the animal. For example, tapping a finger against a table provides tactile information at the tapping frequency; sniffing provides olfactory information at the sniffing frequency. Movements of sensory surfaces thus regulate the timing and the locations of sensory input, which in turn constrain how the nervous system might be organized to make use of that incoming data.

Our laboratory's research on sensory data acquisition uses the rat vibrissal (whisker) system as a model. Rats are nocturnal, burrowing animals that rely strongly on tactile information from their whiskers for information about the environment. The rat moves its whiskers between 5 and 25 Hz to extract tactile information about an object's three-dimensional spatial properties, including size, shape, orientation and texture. The strong periodicity of rat whisking behavior means that it is one of the 'simplest' mammalian systems in which to quantitatively analyze the relationship between movement and sensing.

In section 2 of this paper we describe our approach—which iterates between experiment and modeling—towards constructing an array of artificial whiskers for object feature extraction. In section 3, we discuss the complexities likely to arise when an artificial whisker array is used on a mobile robot. We use the example of wall-following behavior to illustrate that the complete derivative quantitatively describes the flow of sensory data across the array, and that computation of appropriate spatial gradients would enable a mobile robot (or an animal) to predict the sensory data that will be acquired at the next time step.

2. Steps in developing a bio-inspired whisking robot

2.1. Observe the biology: three complementary methods for studying trigeminal neurophysiology leave a critical question unanswered

Scavenging animals such as the rat must locate resources in an unpredictable environment, and therefore rely on superior exploratory, navigational and discriminatory capabilities for their survival. Tactile information obtained through the whiskers is an important component of these capabilities. Approximately 30 whiskers emerge from follicles arranged in a lattice on each side of the rat's face, with longer whiskers located caudally and shorter whiskers rostrally [31]. Whiskers have no receptors along their length, instead, all
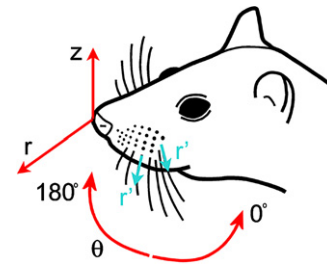

Figure 1. *Peripheral arrangement of whiskers.* Whiskers are arranged in an orderly 'matrix-like' pattern on the rat's face, and the rat is typically represented in a cylindrical coordinate system. The r and z coordinates have their origin at the whisker snout. The horizontal angle θ is defined with zero directed backwards towards the tail and $180°$ directed towards the snout. This choice of horizontal angle means that protraction of the whiskers is associated with an increase in θ and a retraction associated with a decrease. Two examples of 'whisker-specific' coordinates are indicated in light blue as r' (r-prime).

sensory information must be mechanically transduced back to receptors in the follicle at the whisker base [38–40]. Receptor responses are transmitted to the primary sensory neurons of the trigeminal ganglion, then to the trigeminal nuclei, and then through the thalamus to primary somatosensory cortex (reviewed in [41]). At each stage of neural processing in this 'trigeminal pathway', groups of neurons are arranged into somatotopic maps that reflect the peripheral lattice-like topography.

Figure 1 depicts the three-dimensional cylindrical coordinate system in which the rat is typically represented, with θ representing rostral–caudal ('horizontal') angle, z representing height and r representing the radial distance outwards [42]. Within this snout-centered cylindrical coordinate system, it is also useful to identify an r' ('r-prime') coordinate for each individual whisker, indicating the radial distance outwards from that whisker's base.

Electrophysiological investigations of whisker-responsive neurons in the trigeminal pathway have included three complementary types of experiments. In passive stimulation, a single whisker of the anesthetized rat is displaced back and forth [43–55], providing measurements of neural responses to kinematic variables. A second experimental technique, called 'artificial whisking', uses electrical stimulation of the facial motor nerve to induce whisker movements, either in free air or against obstacles. However, artificial whisking induces a highly unnatural pattern of muscle activation that involves the simultaneous contraction of both intrinsic and extrinsic muscles, which does not occur in natural whisking behavior [56, 57]. The third experimental preparation involves recording from the awake animal, either in a head-fixed preparation [58, 59] or during active behaviors [60–70]. Aside from the marked technical complexity of these experiments, it is often difficult to ensure that the animal behaves in a repeatable fashion, and neural responses can vary depending on the motivational, cognitive, or emotional state of the animal. Taken together, these three experimental techniques have provided useful descriptions of many features of neural responses in the trigeminal pathway, but have left unanswered a

critical question: what are the mechanical variables transduced by the whiskers that permit the rat to extract three-dimensional information about objects?

2.2. Construct a theoretical model to help answer the open question: what are the mechanical variables that permit three-dimensional feature extraction?

We asked how the rat could obtain accurate estimates of each of the three coordinates (r', θ and z) identified in figure 1. Note that r' specifically refers to the radial distance from the base of each whisker. Previous studies have suggested that the height z at which a whisker contacted an object could be encoded by whisker identity, because each whisker is at a fixed height relative to the rat's snout, regardless of head or whisker movements [42]. In contrast, the horizontal angle and the radial distance at which a whisker contacts an object cannot be encoded by identity because their values change over the course of a whisk. We first investigated how the rat might obtain estimates of radial object distance r'. Along the way, we also uncovered some clues about how the rat might determine the horizontal object angle θ.

We modeled the whisker as a cylindrical elastic beam [28, 71, 72] and used classical elasticity theory to obtain a unique relationship between the radial object distance R (in the r' direction) and the moment (often called 'torque') at the base of the whisker. The relationship depends on the angle θ, which means that the radial contact distance can be computed by keeping track of the absolute moment M at the base of the whisker along with the whisker's angular position (equation (1)). Alternatively, the radial contact distance can be obtained by dividing the rate of change of moment at the whisker base by the whisker's angular velocity (the dots above θ and M indicate temporal derivatives). This second possibility is more biologically plausible, as nervous systems are typically poor at determining absolute quantities, but good at assessing relative values:

$$R = C\frac{\theta}{M} \quad \text{or} \quad R = C\frac{\dot{\theta}}{\dot{M}}. \tag{1}$$

In equation (1), C is a constant stiffness factor that depends on the material and geometrical properties of the whisker. Specifically, $C = 3EI_{\text{base}}$, where E is the elastic modulus and I_{base} is the area moment of inertia at the base of the whisker. The accuracy of the equation depends on the small angle approximation, in which $\sin(x) \approx x$ and θ is less than $\sim 14°$. Within these constraints, the rat can in theory determine the radial distance to all the points of whisker contact with a three-dimensional object. Equation (1) also underscores the tight relationship between sensing and movement: for the vibrissal system, the *dynamics is the sensing*, because $\dot{M}$ and $\dot{\theta}$ do not exist without motion of the whisker.

2.3. Develop a hardware model to test the plausibility of the proposed theoretical explanation. Construct an artificial whisker array to determine the radial object distance

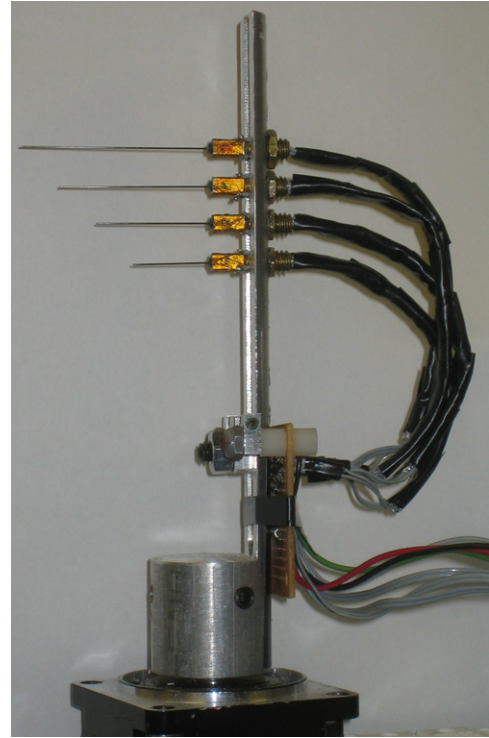Equation (1) provides an analytic description of the consequences of whisker bending, but it can never simulate

Figure 2. *A vibrissal sensobot for radial distance extraction.* A single motor rotates four nitinol whiskers. Each whisker is inserted into a set screw with two opposing pairs of strain gages to measure moment at the whisker base.

the complexities that whiskers would encounter in a real-world environment. To test whether some version of this computation is used by the real animal would require training rats to perform a discrimination task (similar to [65]), and then correlating very tiny deformations of the whiskers with task performance. This type of high-resolution behavioral experiment is extremely difficult to perform and often yields ambiguous results.

Instead, to test the plausibility of the proposed radial-distance encoding mechanism, we constructed an artificial whisker array that relied on sensing moment at the whisker base to determine the radial object distance [73]. The idea of developing artificial whiskers is not itself new. Work on the AMOUSE project has focused on developing robotic arrays of whiskers that can determine surface texture [4, 5, 8, 9, 74, 75]. The Whiskerbot project in Sheffield, England, has focused on using whiskers for navigation and spatial mapping tasks [6, 76–79]. Other research teams in the US, Japan and Australia have constructed whiskers that extract some aspects of object shape, but have been limited by bulky sensors and complex movement strategies, making the transition to multi-whisker arrays problematic [80–85].

A picture of our laboratory's artificial whisker array is shown in figure 2. The array has only a single actuator, but several sensors at the base of each whisker. We call this array a 'sensobot' (for SENSOry roBOT) because its purpose is not to move, *per se*, but rather to sense properties of its environment. In distinct contrast to traditional robots, which must execute the same motor task accurately and repetitively, the sensobot
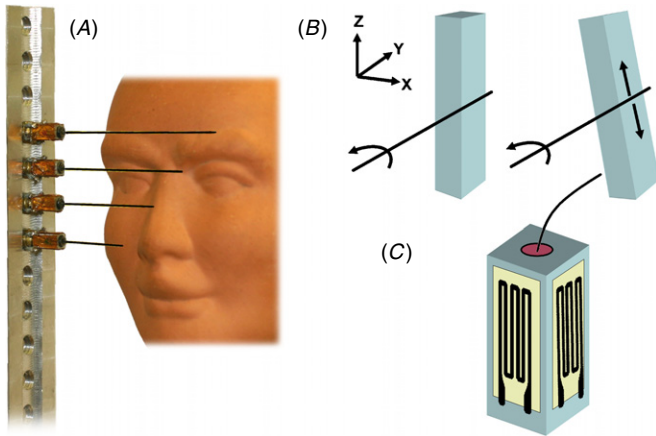
Figure 3. *Solving the problem of lateral slip.* (*A*) The sensobot was brushed against a small sculpted head. Figure reproduced from Solomon and Hartmann (2006) [73]. (*B*) If the whiskers encountered a surface normal to their plane of rotation, they tended to bend within the plane, and equation (1) could be used to calculate contact distance (left). If instead, the surface was slanted relative to the whisker's plane of rotation, the whisker slipped either up or down out of the plane (right). (*C*) Inserting each whisker into a 'follicle' that could sense moment in two dimensions allowed us to measure and compensate for lateral slip. Differential voltage measurements are taken from strain gages on opposite sides of the follicle to improve signal to noise.

does not need to move the same way every time, as long as it obtains the desired sensory information. The purpose of the array is to sense its surroundings, not to move in a particular manner, or to move itself from one position to another.

Our sensobot [73] differs from previous hardware vibrissal technologies [80–85] in two important respects. First, our method requires only that the whisker be equipped with a two-axis moment sensor at the base (see problem 2.4A), and does not need to independently sense force and moment. Second, the method does not require each whisker to independently adjust its plane of rotation, and is therefore very amenable to implementation on a large-scale array.

2.4. Use the hardware model to expose problems with the theoretical explanation. How does the rat whisker array solve the problems exposed by the artificial whisker array?

We next attempted to test the radial-distance extraction capabilities of the array on a more complex object. A sculpted face was chosen as the object because it had particularly intricate convexities and concavities (figure 3(*A*)). We planned to sweep the whisker array across the sculpture, measure θ with the motor encoder, compute the radial distance R by inserting measurements of M and θ into equation (1), and to fix z as the whisker height. In principle, this strategy should have provided us with the coordinates of every point of contact for each whisker in 3D space. This would then have allowed us to build up multiple contact points over multiple whisks to perform 3D feature extraction. Before we could put this plan into execution, however, we encountered several problems.

Problem 2.4A. Whisker slip suggests why trigeminal ganglion neurons have strong directional tuning. As illustrated in figure 3(*B*), the artificial whiskers tended to slip out of the plane of rotation whenever they encountered a non-vertical surface. This problem had been solved in previous studies either by forcibly constraining movement to a single dimension (e.g., [83]) or by repositioning the whisker so that its plane of rotation was always perpendicular to the surface [81]. Our solution was to develop a 'follicle' for the whisker that could sense in two dimensions (figure 3(*C*)). Two-dimensional sensing then allowed us to multiply by a factor β related to the slope of the surface. If we assume that the surface being contacted is flat (true over a small local region) and frictionless, equation (1) becomes

$$R = C\frac{\theta}{|M|} \cdot \cos\beta, \tag{2}$$

where $|M| = \sqrt{M_x^2 + M_y^2}$, M_x is the component of the moment in the direction of the axis of rotation, M_y is the component of the moment in the lateral plane $\beta = \tan^{-1}(M_y/M_x)$, and C is the same constant as in equation (1). The ability to sense in two dimensions and compensate for lateral slip of the whiskers using equation (2) was an important component of this research, as it permitted 'whisking' in any direction across the object, similar to the real animal.

Instantiating equation (2) in hardware suggested a reason for the strong directional tuning of trigeminal ganglion neurons [45]. These neurons tend to respond most strongly to whisker deflection in one direction, with smaller subsidiary responses in alternate directions. We suggest that one reason for this strong directional tuning is to permit the rat to perform a computation similar to equation (2).

Problem 2.4B. Longitudinal forces suggest a method for the rat to compute the horizontal angle θ. Rotating the artificial whiskers into objects immediately revealed the presence of significant longitudinal forces, that is, forces tangential to the whisker near its base. To quantify these forces, we plucked a real whisker from a rat, and rotated it against a point object with force-sensing capabilities (figure 4(*A*)). Careful measurement of the ratio of normal to longitudinal forces demonstrated that this quantity provided information about horizontal angle θ measured from the angle of object contact (figure 4(*B*)). *This was an unexpected result that we would not have found without a hardware implementation.*

Problem 2.4C. Variations in the estimated distance suggest two distinct exploratory strategies for the rat. The radial object distance R estimated from the application of equation (2) was found to change slightly over the course of a single whisk. Although outside the scope of the current paper, it is possible to show that this effect is due to the changing local object curvature. An estimate of the local object curvature can be obtained by looking at the second derivative of moment with respect to time as the whisker is increasingly deflected into an object. Thus, the results from the sensobot suggest that combining two strategies might help maximize the acquired sensory information. First, rats may be able to build up a
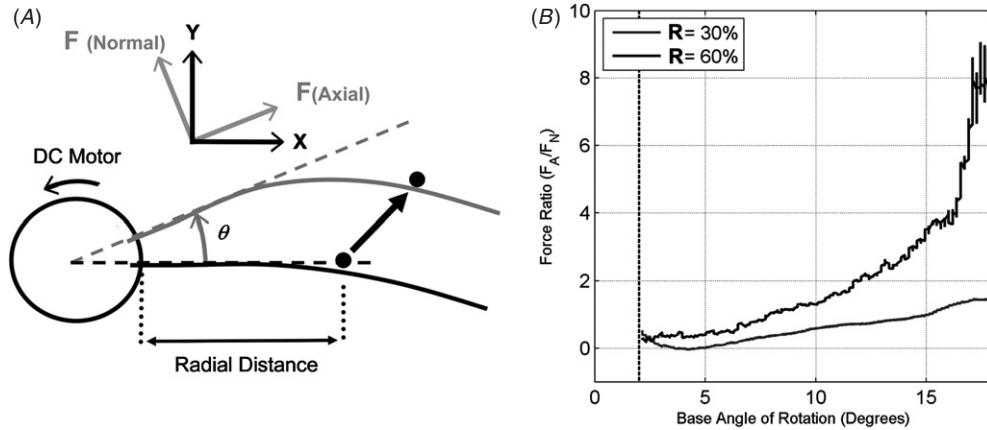
Figure 4. *Axial and normal forces on a whisker generated by object contact* (*A*) Setup for measuring forces on the whisker. A DC motor rotates a plucked whisker into a point object fitted with force-sensing capabilities. Forces are measured in an *x–y* world coordinate system and then rotated to find axial and normal forces. (*B*) The ratio of axial to normal forces is monotonic with angle of rotation θ. The two curves show results for the point object placed at two different radial distances ($R = 30\%$ and 60% out along the whisker).

representation of the object point-by-point if they 'tap' their whiskers against an object. Second, rats might be able to make use of local curvature information in determining the object shape if they 'sweep' their whiskers against an object.

Problem 2.4D. Whisker taper suggests a specific role for contact near the whisker tip. In comparing the whisking dynamics of the sensobot with that of the real rat, we observed that the cylindrical whiskers of the sensobot did not deflect as much as the tapered whiskers of the real animal. It is intuitively obvious, and easy to show analytically, that a tapered whisker with a particular base radius will deflect more than a cylindrical whisker of the same radius for the same imposed force. However, although the whisker's taper makes it bend more, it also reduces the moment ultimately transmitted to the base, as shown in equation (3):

$$M = C\theta \left(\frac{1}{R} - \frac{1}{L} \right) \quad \text{or} \quad \dot{M} = C\dot{\theta} \left(\frac{1}{R} - \frac{1}{L} \right) \quad (3)$$

In equation (3), C is the same constant as in equations (1) and (2), L is the length of the whisker, and R is the location of radial object contact as before [73]. Notably, the moment transmitted to the base is exactly zero at the very tip of the whisker, where $R = L$. This suggests that contact near the tip would be most useful if the moment could somehow be amplified. It is possible that the whisker's natural resonance frequency may serve as a mechanism to amplify vibrations that occur near the whisker tip [28, 71, 86].

2.5. Return to the question posed in step 2: Has the hardware model helped to identify the mechanical variables that permit three-dimensional feature extraction?

We successfully used the vibrissal sensobot to extract the 3D features of the sculpted head (figure 5). The sensobot required information about angular position, angular velocity, and either moment or rate of change of moment to extract these features. This suggests that these four mechanical variables should be encoded in responses of primary sensory
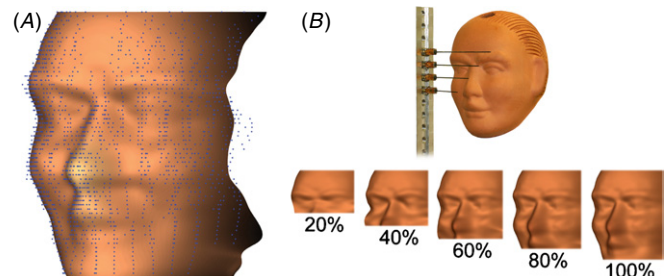

Figure 5. *Complex feature extraction with the vibrissal sensobot.* Figure adapted from Solomon and Hartmann (2006) [73]. (*A*) To extract features of the sculpted head, the sensobot was positioned at regular intervals of height z and angle θ and a single whisk was performed at each position. Each blue dot represents a point (r, θ, z) contacted by one of the sensobot's whiskers. These points were splined together in MATLAB to reconstruct the face. (*B*) As the sensobot swept over the face at different heights and angles, the full shape of the sculpted head was extracted. See [73] for details.

neurons of the rat trigeminal ganglion. To test this prediction, we constructed a leaky integrate-and-fire model of trigeminal ganglion neurons that responded to combinations of the four variables, and compared the model's output with published neurophysiological data [29, 45]. Figure 6(*A*) illustrates that the modeled neural responses were an excellent qualitative match to actual neural responses observed in two different laboratories [29, 45]. The top row shows that neurons typically categorized as rapidly adapting can be modeled as responding mostly to velocity. In contrast, ganglion neurons typically categorized as slowly adapting required a combination of position and velocity (data not shown). Combinations of M, $\dot{M}$ and direction sensitivity are necessary to model ganglion responses during whisker/object contact (the bottom row of figure 6(*A*)).

We have recently suggested that this method of modeling trigeminal ganglion responses naturally lends itself to a state-encoding scheme in which mechanical variables form the axes of a state space [72] (also cf [88–95]). In this scheme, illustrated in figure 6(*B*), neurons have a certain probability
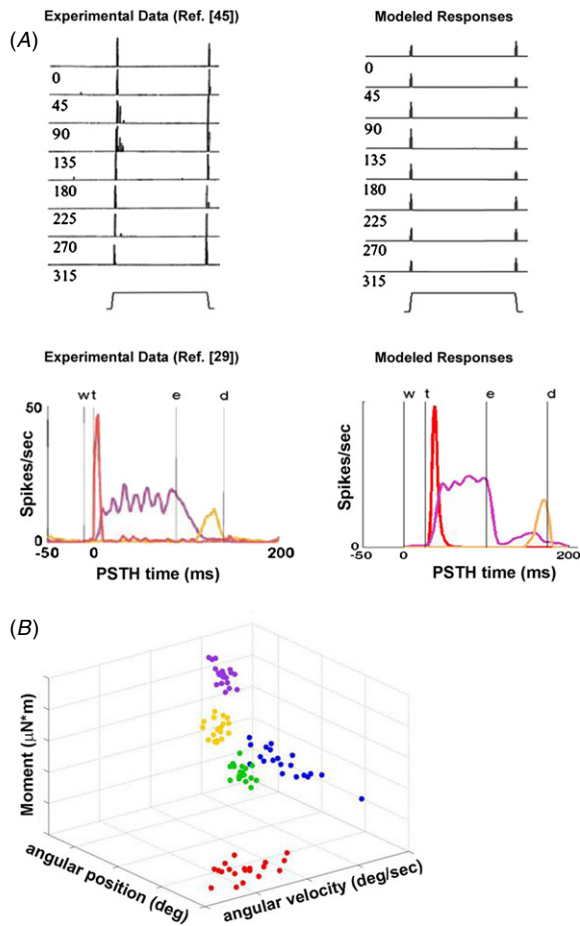
Figure 6. *Modeling responses of neurons in the trigeminal ganglion* (A) Modeled neural responses compared to actual neural responses. Top: neurons typically categorized as rapidly adapting can be modeled as responding to a current proportional to whisker velocity (including direction) and an adaptation current. The bottom trace in each column represents the ramp-and-hold stimulus with which the whisker was deflected. Each subsequent trace represents the neural response to deflection in the indicated angular direction. Experimental data are from Lichtenstein *et al* [45]; figure adapted with permission. Bottom: to model the responses of contact, detach, and pressure neurons during an artificial whisking experiment requires combinations of M and $\dot{M}$ (including direction sensitivity), and an adaptation current. Contact cells (red traces) respond transiently when the whisker contacts an object, and detach cells (yellow traces) respond transiently when the whisker detaches from an object. Pressure cells (purple traces) respond continuously as the whisker presses into an object. Experimental data are from Szwed *et al* [29]; figure adapted with permission. (B) A cartoon that illustrates the representation of trigeminal ganglion responses in a state-encoding scheme. The responses of five different idealized neurons are each indicated in a different color. Each data point represents a spike from a neuron, and each data point is placed at the location in the state space that corresponds to the state of the whisker when the neuron fired. For example, the 'red' neuron responds to combinations of angular velocity and position, while the 'blue' neuron responds to combinations of moment and position. The neurons represented by the green, yellow and purple data points respond to combinations of all three state variables.

of producing a spike when the whisker is in a particular 'state'. In the example of figure 6(B), the whisker's state is uniquely defined by whisker position, velocity and moment.

The activity of a neuron can be represented by placing a data point at the correct place in the state space every time that neuron fires. Velocity could be defined to have two dimensions (rostral–caudal and dorsal–ventral) to account for the directional sensitivity of the cells [53]. Another axis may be required to represent the rate of change of moment. These added dimensions would result in a higher dimensional space but would otherwise leave the state-encoding representation unchanged.

The state-encoding scheme shown in figure 6(B) is intended as a conceptual tool for grappling with the real-world complexity of trigeminal ganglion response types. State encoding inherently permits a spectrum of response types, and allows us to examine how the ganglion neurons 'cover' the relevant behavioral space of the rat. The scheme can quantify the flow of data into the array in mechanical terms, and thus real rat behaviors can be characterized in terms of the quantifiable mechanical variables they generate.

3. Anticipated complexities in using the array on a mobile robot in a dynamic environment

As we have shown in section 2, an iterative approach between hardware modeling and biological studies can be a powerful method to investigate sensory acquisition strategies. The five steps described earlier resulted in the construction of a hardware model of rat whisking that provided considerable insight into possible mechanisms of sensory acquisition that the rat could be using during whisking behavior. We found three major advantages of making this model. First, the model clearly confirmed that the sensing moment at the whisker base could provide information about the radial object distance. Second, the technical difficulties encountered when using the hardware model highlighted problems that the rat must also overcome, if indeed it is measuring (sensing) moment at the whisker base. This also suggested roles for directional sensitivity, longitudinal forces and whisker taper. Third, comparison with physiological data from the trigeminal ganglion of the rat suggests that the mechanical variables identified and used by the model might be the same ones that the rat uses as well.

We now consider the complexities likely to result from using such an array on a mobile robot during navigational and exploratory tasks. In mobile robotics applications, not only will the whisker array be in motion relative to the rover, but the rover will be in motion relative to the world, and the world may contain inherent motions of its own.

3.1. Using the complete derivative to quantify the flow of sensory data across the vibrissal array

The complete derivative (equation (4)) provides a mathematical description of the structure of incoming data across an active sensor array operating in a dynamic environment:

$$\frac{dA_{sensor}}{dt} = \frac{\partial A_{environment}}{\partial t} + (V_{sensor} - V_{environment}) \bullet \nabla A_{sensor}.$$

(4)

In this equation, A is any property of the world, ∇ is the gradient operator and $V_{\text{sensor}} - V_{\text{environment}}$ is the relative velocity between the sensor array and the environment. In the case of a vibrissal array on a rat or mobile robot, evolution of the sensory flow field may be found by replacing the variable A in equation (4) with the radial distance to an object (R). In this case, the term on the left side of the equation represents changes in R that are sensed by receptors (strain gages) at the base of the whisker. The first term on the right describes any local deformations of the object in time. The second term on the right represents the relative velocity between the object as a whole and the whisker array, multiplied by the spatial gradient of R across the array.

The complete derivative can be thought of as a more general form of the 'optic flow' equation [96–111], which is thought to provide cues about time to object collision during locomotion [97, 99, 109]. It has been argued, however, that optic flow may be of limited use because eye and head movements distort the flow field. Space constraints prohibit an extensive comparison between vibrissal and visual systems, but we note briefly that rather than distorting perception, eye and head movements may themselves generate useful optic flow, albeit on a different spatiotemporal scale than locomotor movements.

3.2. Exploration of a static object: wall following

If a vibrissal array on a mobile robot is used to explore a static object, such as during wall following, then equation (4) simplifies to

$$\frac{\mathrm{d}R_{\text{sensor}}}{\mathrm{d}t} = V_{\text{sensor}} \bullet \nabla R_{\text{sensor}}. \tag{5}$$

Equation (5) demonstrates that computing local spatial derivatives provides a mechanism to predict the sensory data that will be acquired in the next sensory instant. In other words, the progression of spatial gradients is almost completely deterministic. New information flows over the edges of the sensory surface, but thereafter, values may be computed by calculating the spatial gradients of A across the sensor. The rate at which new information flows over the edges of the array depends on how fast the robot is moving.

It would be advantageous for a mobile robot (or an animal nervous system) to make use of the correlations in equation (5) to enable sensory prediction. The equation allows the system to form a *quantitative* expectation value of the future against which it can match its sensory input. It is critical to note however, that in order for the computation to be of value, gradients will almost certainly need to be computed across different length scales, and across different directions. In addition, sensory surfaces can move with different velocities, so computing the total derivative is likely to involve computing many local velocities.

Finally, deviations from the expectations formed by computing spatial gradients across the array may provide a computational mechanism for the instant detection of motion. A mismatch between expected and actual sensory input via computation of the total derivative instantly permits attention to be directed to the relevant part of the sensory space.
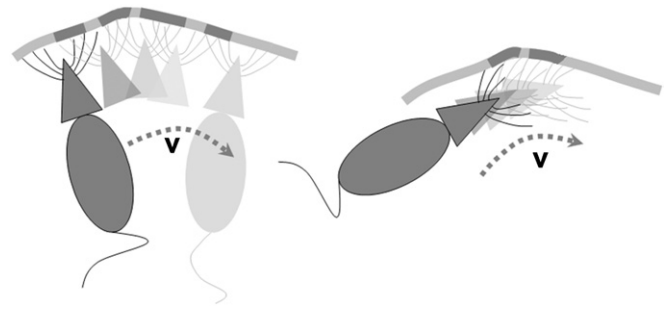

Figure 7. *Head movements permit the rat to obtain overlapping samples of an object.* These schematics illustrate two possible sequences of whisking positions as a rat scans a wall. Dark gray areas indicate the regions where two consecutive whisks overlap. The rat, translating its whisker array at a velocity **v**, can use gradients of the spatial variation of surface curvature to extrapolate and predict the curvature it expects in the next whisk.

Any system that inhabits a changing environment gains a tremendous advantage by accurately predicting the future state of the world that it will sense or perceive.

Returning to biology, it is interesting to note that rats often combine whisking behavior with small, periodic head movements that tend to be temporally synchronized with whisking [19, 31, 112]. The relationship between head movements and whisking is not always one to one; in some instances, more than one whisk occurs at the same head location [112]. The end result of the synchronized head and whisker movements is that the rat often obtains overlapping 'whisked' samples of an object as illustrated in figure 7. This suggests that rats may be implementing a strategy similar to that suggested by equation (5).

4. Discussion

4.1. Iteration between biological investigation and engineering solutions

The field of neuroscience historically has treated sensing systems as arrays of passive receiving elements, but is gradually moving towards the understanding that mechanics plays an essential role in the acquisition of sensory data across modalities. The experimental study of active sensing, though, is rather challenging. Measuring the stimulus field with high accuracy while also accurately tracking movements of the sensory surfaces often is a daunting task. The complexity of these measurements increases as one studies sensory surfaces such as hands and pinnae, whose motion is no longer rhythmic and relatively stereotyped like whisking. As we have demonstrated with the example of whisking, turning to mechanical models can provide great insight. Complex motions and forces can be studied in a simplified form that captures the essentials of the biological system. Yet much of the real-world complexity embedded in noise and other properties of mechanical systems are preserved since these 'experiments' are performed in hardware and not computer simulations. This allows the systematic investigation of many features that usually can be introduced only in a simplified and artificial way in a computer simulation.

The tight relationship between sensing and movement strongly motivates an experimental approach that iterates between biology and the construction of hardware models that elucidate system dynamics. For example, the sensobot demonstrates a sensory task (shape extraction) that is accomplished by the measurement of an intrinsically dynamic variable, namely $\dot{M}$, the rate of change of moment at the base of the whisker. For the sensobot, the dynamics is the sensing, since $\dot{M}$ does not exist without the motion of the sensor array. Although the utility of this approach in the mechanical model does not prove that the rat indeed does measure these variables, the model supplements our intuition in two ways: first, by providing us with a test bed where we can rapidly test the merits and plausibility of competing hypotheses, and second, by drawing our attention to the mechanical variables of interest in the task and how these variables are affected by real-world dynamics and noise.

4.2. Computation of the complete derivative

Although we have presented no direct experimental evidence that the brainstem circuitry of the rat is computing the complete derivative, this idea is compelling for two reasons. First, it is clear that auditory, visual and somatosensory cortices have similar anatomical structures and functional circuits [113–115]; so similar in fact, that they can process data received from other modalities. For example, the visual cortical areas of blind Braille readers respond to tactile stimulation [116, 117]. This observation suggests that there may be a unifying pre-processing of sensory data that ensures a relatively uniform spatiotemporal structure for processing by thalamocortical loops. Understanding this formatting of sensory input would provide us with a powerful framework with which we might unify the study of disparate sensory systems.

Second, in analogy to the 'efficient coding hypothesis' [13, 118–126], we suggest that sensory systems have evolved to take advantage of spatio-temporal correlations in the structure of incoming data via computations of the total derivative. In the context of the rat vibrissal system, we find it plausible that whisker-related neural responses in the trigeminal nuclei of the brainstem could be calculating gradients of radial object distance. Generalizing across modalities, it may be that the role of brainstem and brainstem-like structures is to organize the spatial structure of incoming sensory data so that it can be interpreted by the thalamus and cortex. Brainstem nuclei may thus convert the spatial aspects of incoming sensory data into a format that can be interchanged across cortical areas. In other words, we conjecture that the *brainstem selects and computes spatial gradients so that the animal can predict movements in the environment relative to its own movements.*

4.3. Applications and comparison with non-bio-inspired technology

Metrology, the measurement of lengths, is mostly concerned with accuracy. High precision length measurement techniques such as interferometry or surface profilometry are typically performed in controlled and static environments in which the measuring device does not move. However, there are a very large number of engineering applications, especially in the robotic exploration of unknown environments, where accuracy is not as important as speed and robustness. For example, a wall following robot exploring a space, such as a mine-shaft or a rover on a planetary surface, need to make quick and accurate (on the scale of the robot) measurements of distances to aid in navigation. A robot with (say) an overall length of a foot and a turning radius of about 2 feet, has no use for a length measuring technique that provides sub-micron accuracy, such as those provided by an optical interferometer or a profilometer. In fact, this accuracy provides no additional information given the rough textures that such exploring robots encounter. What is required is a robust and rugged measurement technique that is cheap to implement, and whose readout can be translated into hardware very simply.

The whisker sensobot provides one such bio-inspired strategy. It is very cheap to assemble, and the code needed to convert the moment measurements into distances can easily be programmed onto a microcontroller that can be mounted onboard the robot. Further, compared to any metrological technique that converts phase differences into distance measurements (such as optical interferometry), there is no phase rollover error involved. Phase measurements have an ambiguity when the phase difference exceeds 2π, and there exists a considerable literature on unwrapping such phase errors. The whisker sensobot, in contrast, provides a direct readout of length.

Acknowledgments

References

[1] Webb B 1995 Using robots to model animals: a cricket test *Robot. Auton. Syst.* **16** 117–34

[2] Lewis M A, Hartmann M J, Etienne-Cummings R and Cohen A H 2001 Control of a robot leg with an adaptive aVLSI CPG chip *Neurocomputing* **38** 1409–21

[3] Webb B 2001 Robots can be (good) models—response *Behav. Brain Sci.* **24** 1081–94

[4] Fend M, Yokoi H and Pfeifer R 2003 Optimal morphology of a biologically-inspired whisker array on an obstacle-avoiding robot *Advances in Artificial Life, Proceedings* pp 771–80

[5] Hafner V V, Fend M, Lungarella M, Pfeifer R, Konig P and Kording K P 2003 Optimal coding for naturally occurring whisker deflections *Artificial Neural Networks and Neural Information Processing: ICAN/ICONIP 2003* pp 805–12

[6] Mitchinson B, Gurney K N, Redgrave P, Melhuish C, Pipe A G, Pearson M, Gilhespy I and Prescott T J 2004 Empirically inspired simulated electro-mechanical model of the rat mystacial follicle-sinus complex *Proc. R. Soc.* B **271** 2509–16

[7] Collins S, Ruina A, Tedrake R and Wisse M 2005 Efficient bipedal robots based on passive-dynamic walkers *Science* **307** 1082–5

[8] Fend M 2005 Whisker-based texture discrimination on a mobile robot *Advances in Artificial Life, Proceedings* pp 302–11

[9] Fend M, Bovet S and Pfeifer R 2006 On the influence of morphology of tactile sensors for behavior and control *Robot. Auton. Syst.* **54** 686–95

[10] Webb B 2006 Validating biorobotic models *J. Neural Eng.* **3** R25–35

[11] Mitchinson B, Martin C J, Grant R A and Prescott T J 2007 Feedback control in active sensing: rat exploratory whisking is modulated by environmental contact *Proc. R. Soc.* B **274** 1035–41

[12] Gallant J L, Connor C E and Van Essen D C 1998 Neural activity in areas v1, v2 and v4 during free viewing of natural scenes compared to controlled viewing *Neuroreport* **9** 2153–8

[13] Vinje W E and Gallant J L 2000 Sparse coding and decorrelation in primary visual cortex during natural vision *Science* **287** 1273–6

[14] Vinje W E and Gallant J L 2002 Natural stimulation of the nonclassical receptive field increases information transmission efficiency in v1 *J. Neurosci.* **22** 2904–15

[15] Mennie N, Hayhoe M and Sullivan B 2007 Look-ahead fixations: anticipatory eye movements in natural tasks *Exp. Brain Res.* **179** 427–42

[16] Mergenthaler K and Engbert R 2007 Modeling the control of fixational eye movements with neurophysiological delays *Phys. Rev. Lett.* **98** 138104

[17] Tong J L, Aydin M and Bedell H E 2007 Direction and extent of perceived motion smear during pursuit eye movement *Vis. Res.* **47** 1011–9

[18] von Wartburg R, Wurtz P, Pflugshaupt T, Nyffeler T, Luthi M and Muri R M 2007 Size matters: saccades during scene perception *Perception* **36** 355–65

[19] Welker W I 1964 Analysis of sniffing of the albino rat *Behaviour* **22** 223–44

[20] Kay L M 2005 Theta oscillations and sensorimotor performance *Proc. Natl Acad. Sci. USA* **102** 3863–8

[21] Kepecs A, Uchida N and Mainen Z F 2006 The sniff as a unit of olfactory processing *Chem. Senses* **31** 167–79

[22] Rajan R, Clement J P and Bhalla U S 2006 Rats smell in stereo *Science* **311** 666–70

[23] Uchida N, Kepecs A and Mainen Z F 2006 Seeing at a glance, smelling in a whiff: rapid forms of perceptual decision making *Nat. Rev. Neurosci.* **7** 485–91

[24] Semba K and Komisaruk B R 1984 Neural substrates of two different rhythmical vibrissal movements in the rat *Neuroscience* **12** 761–74

[25] Hartmann M J and Bower J M 1998 Oscillatory activity in the cerebellar hemispheres of unrestrained rats *J. Neurophys.* **80** 1598–604

[26] Guic-Robles E, Valdivieso C and Guajardo G 1989 Rats can learn a roughness discrimination using only their vibrissal system *Behav. Brain Res.* **31** 285–9

[27] Carvell G E and Simons D J 1995 Task- and subject-related differences in sensorimotor behavior during active touch *Somatosens. Mot. Res.* **12** 1–9

[28] Neimark M A, Andermann M L, Hopfield J J and Moore C I 2003 Vibrissa resonance as a transduction mechanism for tactile encoding *J. Neurosci.* **23** 6499–509

[29] Szwed M, Bagdasarian K and Ahissar E 2003 Encoding of vibrissal active touch *Neuron* **40** 621–30

[30] Polley D B, Rickert J L and Frostig R D 2005 Whisker-based discrimination of object orientation determined with a rapid training paradigm *Neurobiol. Learning Memory* **83** 134–42

[31] Brecht M, Preilowski B and Merzenich M M 1997 Functional architecture of the mystacial vibrissae *Behav. Brain Res.* **84** 81–97

[32] Berg R W and Kleinfeld D 2003 Rhythmic whisking by the rat: retraction as well as protraction of the vibrissae is under active muscular control *J. Neurophys.* **89** 104–17

[33] Gao P H, Bermejo R and Zeigler H P 2001 Whisker deafferentation and rodent whisking patterns: behavioral evidence for a central pattern generator *J. Neurosci.* **21** 5374–80

[34] Harvey M A, Bermejo R and Zeigler H P 2001 Discriminative whisking in the head-fixed rat: optoelectronic monitoring during tactile detection and discrimination tasks *Somatosens. Motor Res.* **18** 211–22

[35] Harvey M A, Sachdev R N S and Zeigler H P 2001 Cortical barrel field ablation and unconditioned whisking kinematics *Somatosens. Motor Res.* **18** 223–7

[36] Gao P H, Hattox A M, Jones L M, Keller A and Zeigler H P 2003 Whisker motor cortex ablation and whisker movement patterns *Somatosens. Motor Res.* **20** 191–8

[37] Hattox A, Li Y and Keller A 2003 Serotonin regulates rhythmic whisking *Neuron* **39** 343–52

[38] Mosconi T M, Rice F L and Song M J 1992 Sensory innervation in the inner conical body of the vibrissal rollicle-sinus complex of the rat *J. Comp. Neurol.* **328** 232–51

[39] Rice F L, Fundin B T, Arvidsson J, Aldskogius H and Johansson O 1997 Comprehensive immunofluorescence and lectin binding analysis of vibrissal follicle sinus complex innervation in the mystacial pad of the rat *J. Comp. Neurol.* **385** 149–84

[40] Ebara S, Kumamoto K, Matsuura T, Mazurkiewicz J E and Rice F L 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** 103–19

[41] Kleinfeld D, Ahissar E and Diamond M 2006 Active sensation: insights from the rodent vibrissa sensorimotor system *Curr. Opin. Neurobiol.* **16** 435–44

[42] Ahissar E and Arieli A 2001 Figuring space by time *Neuron* **32** 185–201

[43] Simons D J 1978 Response properties of vibrissa units in rat si somatosensory neocortex *J. Neurophysiol.* **41** 798–820

[44] Simons D J 1983 Multi-whisker stimulation and its effects on vibrissa units in rat sml barrel cortex *Brain Res.* **276** 178–82

[45] Lichtenstein S H, Carvell G E and Simons D J 1990 Responses of rat trigeminal ganglion neurons to movements of vibrissae in different directions *Somatosens. Motor Res.* **7** 47–65

[46] Kyriazi H, Carvell G and DJ S 1994 Off response transformations in the whisker/barrel system *J. Neurophysiol.* **72** 392–401

[47] Brumberg J C, Pinto D J and Simons D J 1999 Cortical columnar processing in the rat whisker-to-barrel system *J. Neurophysiol.* **82** 1808–17

[48] Shoykhet M, Doherty D and Simons D J 2000 Coding of deflection velocity and amplitude by whisker primary afferent neurons: implications for higher level processing *Somatosens. Motor Res.* **17** 171–80

[49] Minnery B S and Simons D J 2003 Response properties of whisker-associated trigeminothalamic neurons in rat nucleus principalis *J. Neurophysiol.* **89** 40–56

[50] Shetty P, Shoykhet M and Simons D J 2003 Whisker plucking alters responses of rat trigeminal ganglion neurons *Somatosens. Motor Res.* **20** 233–8

[51] Shoykhet M, Shetty P, Minnery B S and Simons D J 2003 Protracted development of responses to whisker deflection in rat trigeminal ganglion neurons *J. Neurophysiol.* **90** 1432–7

[52] Jones L, Depireux D, Simons D and Keller A 2004 Robust temporal coding in the trigeminal system *Science* **304** 1986–9

[53] Jones L, Lee S, Trageser J, Simons D and Keller A 2004 Precise temporal responses in whisker trigeminal neurons *J. Neurophysiol.* **92** 665–8

[54] Kwegyir-Afful E E and Keller A 2004 Response properties of whisker-related neurons in rat second somatosensory cortex *J. Neurophysiol.* **92** 2083–92

[55] Kwegyir-Afful E E, Bruno R M, Simons D J and Keller A 2005 The role of thalamic inputs in surround receptive fields of barrel neurons *J. Neurosci.* **25** 5926–34

[56] Hill D, Bermejo R, Zeigler H P and Kleinfeld D 2006 Whisking by rat consists of 3 phases of muscle contraction: EMG, kinematics, and biomechanical analysis *Neuroscience Meeting Planner Program number* 144.2/F3 (Atlanta, GA: Society for Neuroscience) Online

[57] Hill D, Bermejo R, Zeigler H P and Kleinfeld D Rhythmic whisking is driven by a three-phase pattern generator (in preparation)

[58] Bermejo R, Houben D and Zeigler H P 1998 Optoelectronic monitoring of individual whisker movements in rats *J. Neurosci. Methods* **83** 89–96

[59] Bermejo R, Szwed M, Friedman W, Ahissar E and Zeigler H P 2004 One whisker whisking: unit recording during conditioned whisking in rats *Somatosen. Motor Res.* **21** 183–7

[60] Nicolelis M A L and Chapin J K 1994 Spatiotemporal structure of somatosensory responses of many-neuron ensembles in the rat ventral posterior medial nucleus of the thalamus *J. Neurosci.* **14** 3511–32

[61] Nicolelis M A L, Lin R C S and Chapin J K 1997 Neonatal whisker removal reduces the discrimination of tactile stimuli by thalamic ensembles in adult rats *J. Neurophysiol.* **78** 1691–706

[62] Fanselow E E and Nicolelis M A L 1999 Behavioral modulation of tactile responses in the rat somatosensory system *J. Neurosci.* **19** 7603–16

[63] Ghazanfar A A, Stambaugh C R and Nicolelis M A L 2000 Encoding of tactile stimulus location by somatosensory thalamocortical ensembles *J. Neurosci.* **20** 3761–75

[64] Fanselow E E, Sameshima K, Baccala L A and Nicolelis M A L 2001 Thalamic bursting in rats during different awake behavioral states *Proc. Natl Acad. Sci. USA* **98** 15330–5

[65] Krupa D, Matell M, Brisben A, Oliveira L and Nicolelis M A L 2001 Behavioral properties of the trigeminal somatosensory system in rats performing whisker-dependent tactile discriminations *J. Neurosci.* **21** 5752–63

[66] Nicolelis M A L and Fanselow E E 2002 Thalamcortical optimization of tactile processing according to behavioral state *Nat. Neurosci.* **5** 517–23

[67] Wiest M C and Nicolelis M A L 2003 Behavioral detection of tactile stimuli during 7–12 Hz cortical oscillations in awake rats *Nat. Neurosci.* **6** 913–4

[68] Krupa D J, Wiest M C, Shuler M G, Laubach M and Nicolelis M A L 2004 Layer-specific somatosensory cortical activation during active tactile discrimination *Science* **304** 1989–92

[69] Leiser S C and Moxon K A 2007 Responses of trigeminal ganglion neurons during natural whisking behaviors in the awake rat *Neuron* **53** 117–33

[70] Wiest M C, Bentley N and Nicolelis M A L 2005 Heterogeneous integration of bilateral whisker signals by neurons in primary somatosensory cortex of awake rats *J. Neurophysiol.* **93** 2966–73

[71] Hartmann M J, Johnson N J, Towal R B and Assad C 2003 Mechanical characteristics of rat vibrissae: resonant frequencies and damping in isolated whiskers and in the awake behaving animal *J. Neurosci.* **23** 6510–9

[72] Birdwell A and Hartmann M 2006 A biomechanical model of rat vibrissae that permits radial distance detection *Society for Neuroscience Annual Meeting (Atlanta, Georgia)*

[73] Solomon J H and Hartmann M J 2006 Sensing features with robotic whiskers *Nature* **443** 525

[74] Hipp J, Einhauser W, Conradt J and Konig P 2005 Learning of somatosensory representations for texture discrimination using a temporal coherence principle *Netw. Comput. Neural Syst.* **16** 223–38

[75] Hipp J, Arabzadeh E, Zorzin E, Conradt J, Kayser C, Diamond M E and Konig P 2006 Texture signals in whisker vibrations *J. Neurophysiol.* **95** 1792–9

[76] Gurney K, Prescott T J, Wickens J R and Redgrave P 2004 Computational models of the basal ganglia: from robots to membranes *Trends Neurosci.* **27** 453–9

[77] Humphries M, Gurney K and Prescott T 2005 Is there an integrative center in the vertebrate brain-stem? A robotic evaluation of a model of the reticular formation viewed as an action selection device *Adaptive Behavior.* **13** 97–113

[78] Pearson M, Gilhespy I, Gurney K, Melhuish C, Mitchinson B, Nibouche M and Pipe A 2005 A real-time, FPGA based, biologically plausible neural network processor *Artificial Neural Networks: Formal Models and Their Applications: ICANN 2005, pt 2, Proceedings* pp 1021–6

[79] Prescott T J, Gonzalez F M M, Gurney K, Humphries M D and Redgrave P 2006 A robot model of the basal ganglia: behavior and intrinsic processing *Neural Netw.* **19** 31–61

[80] Wilson J F and Chen Z H 1995 A whisker probe system for shape perception of solids *J. Dyn. Syst. Meas. Control Trans. ASME* **117** 104–8

[81] Kaneko M, Kanayama N and Tsuji T 1998 Active antenna for contact sensing *IEEE Trans. Robot. Autom.* **14** 278–91

[82] Kaneko M, Kanayama N and Tsuji T 2001 Vision-based active sensor using a flexible beam *IEEE-ASME Trans. Mechatron.* **6** 7–16

[83] Scholz G R and Rahn C D 2004 Profile sensing with an actuated whisker *IEEE Trans. Robot. Autom.* **20** 124–7

[84] Seth A K, McKinstry J L, Edelman G M and Krichmar J L 2004 Active sensing of visual and tactile stimuli by brain-based devices *Int. J. Robot. Autom.* **19** 222–38

[85] Russell R A and Wijaya J A 2005 Recognising and manipulating objects using data from a whisker sensor array *Robotica* **23** 653–64

[86] Andermann M, Ritt J, Neimark M and Moore C 2004 Neural correlates of vibrissa resonance: band-pass and somatotopic representation of high-frequency stimuli *Neuron* **42** 451–63

[87] Szwed M, Bagdasarian K, Blumenfeld B, Barak O, Derdikman D and Ahissar E 2006 Responses of trigeminal ganglion neurons to the radial distance of contact during active vibrissal touch *J. Neurophysiol.* **95** 791–802

[88] Paulin M G 1993 A method for constructing data-based models of spiking neurons using a dynamic linear-static nonlinear cascade *Biol. Cybern.* **69** 67–76

[89] Paulin M G 1997 Neural representations of moving systems *Cerebellum and Cognition* pp 515–33

[90] Paulin M G and Hoffman L F 1999 Modelling the firing pattern of bullfrog vestibular neurons responding to naturalistic stimuli *Neurocomputing* **26–7** 223–8

[91] Paulin M G and Hoffman L F 2001 State-space receptive fields of semicircular canal afferent neurons in the bullfrog *Neurocomputing* **38** 293–8

[92] Paulin M G and Hoffman L F 2001 Optimal firing rate estimation *Neural Netw.* **14** 877–81

[93] Paulin M G, Hoffman L F and Assad C 2001 A model of cerebellar computations for dynamical state estimation *Auton. Robots.* **11** 279–84

[94] Paulin M G, Hoffman L F and Assad C 2004 Distributed coding by single spikes in the bullfrog vestibular nerve: a basis for dynamical computation in neural systems *Neurocomputing* **58–60** 73–7

[95] Paulin M G, Hoffman L F and Assad C 2004 Dynamics and the single spike *IEEE Trans. Neural Netw.* **15** 987–94

[96] Lishman J R 1981 Vision and the optic flow field *Nature* **293** 263–4

[97] Buxton B F and Buxton H 1983 Monocular depth-perception from optical-flow by space-time signal-processing *Proc. R. Soc.* B **218** 27–47

[98] Jain R 1983 Direct computation of the focus of expansion *IEEE Trans. Pattern Anal. Mach. Intell.* **5** 58–64

[99] Simpson W A 1988 Depth discrimination from optic flow *Perception* **17** 497–512

[100] Lappe M, Bremmer F and van den Berg A V 1999 Perception of self-motion from visual flow *Trends Cogn. Sci.* **3** 329–36

[101] Krose B J A, Dev A and Groen F C A 2000 Heading direction of a mobile robot from the optical flow *Image Vis. Comput.* **18** 415–24

[102] Merchant H, Battaglia-Mayer A and Georgopoulos A P 2001 Effects of optic flow in motor cortex and area 7a *J. Neurophysiol.* **86** 1937–54

[103] Sun H J, Lee A J, Campos J L, Chan G S W and Zhang D H 2003 Multisensory integration in speed estimation during self-motion *Cyberpsychol. Behavior* **6** 509–18

[104] Boucher L, Lee A, Cohen Y E and Hughes H C 2004 Ocular tracking as a measure of auditory motion perception *J. Physiol. (Paris)* **98** 235–48

[105] Sun H J, Campos J L and Chan G S W 2004 Multisensory integration in the estimation of relative path length *Exp. Brain Res.* **154** 246–54

[106] Angelaki D E and Hess B J M 2005 Self-motion-induced eye movements: Effects on visual acuity and navigation *Nat. Rev. Neurosci.* **6** 966–76

[107] Bertin R J V and Israel I 2005 Optic-flow-based perception of two-dimensional trajectories and the effects of a single landmark *Perception* **34** 453–75

[108] Galbraith J M, Kenyon G T and Ziolkowski R W 2005 Time-to-collision estimation from motion based on primate visual processing *IEEE Trans. Pattern Anal. Mach. Intell.* **27** 1279–91

[109] Liebermann D G and Hoffman J R 2005 Timing of preparatory landing responses as a function of availability of optic flow information *J. Electromyograph. Kinesiol.* **15** 120–30

[110] Stoffregen T A, Yang C M and Bardy B G 2005 Affordance judgments and nonlocomotor body movement *Ecol. Psychol.* **17** 75–104

[111] Wu J, He Z J J and Ooi T L 2005 Visually perceived eye level and horizontal midline of the body trunk influenced by optic flow *Perception* **34** 1045–60

[112] Hartmann M J 2000 Active sensing capabilities of the rat whisker system *Auton. Robots* **11** 249–54

[113] O'Leary D, Schlaggar B and Tuttle R 1994 Specification of neocortical areas and thalamocortical connections *Ann. Rev. Neurosci.* **17** 419–39

[114] Miller K D, Pinto D J and Simons D J 2001 Processing in layer 4 of the neocortical circuit: new insights from visual and somatosensory cortex *Curr. Opin. Neurobiol.* **11** 488–97

[115] Douglas R and Martin K 2004 Neuronal circuits of the neocortex *Ann. Rev. Neurosci.* **27** 419–51

[116] Buchel C, Price C, Frackowiak R S J and Friston K 1998 Different activation patterns in the visual cortex of late and congenitally blind subjects *Brain* **121** 409–19

[117] Sadato N, Pascual-Leone A, Grafman J, Deiber M P, Ibanez V and Hallett M 1998 Neural networks for braille reading by the blind *Brain* **121** 1213–29

[118] Barlow H 1961 *Possible Principles Underlying the Transformation of Sensory Messages* (Cambridge, MA: MIT Press) (Sensory communication)

[119] Gallant J L, Connor C E, Drury H and Vanessen D C 1995 Neural responses in monkey visual-cortex during free viewing of natural scenes—mechanisms of response suppression *Invest. Ophthalmol. Vis. Sci.* **36** S1052

[120] Olshausen B A and Field D J 1997 Sparse coding with an overcomplete basis set: a strategy employed by v1? *Vis. Res.* **37** 3311–25

[121] Reinagel P 2001 How do visual neurons respond in the real world? *Curr. Opin. Neurobiol.* **11** 437–42

[122] Theunissen F E, David S V, Singh N C, Hsu A, Vinje W E and Gallant J L 2001 Estimating spatio-temporal receptive fields of auditory and visual neurons from their responses to natural stimuli *Netw. Comput. Neural Syst.* **12** 289–316

[123] Lewicki M S 2002 Efficient coding of natural sounds *Nat. Neurosci.* **5** 356–63

[124] David S V and Gallant J L 2005 Predicting neuronal responses during natural vision *Netw. Comput. Neural Syst.* **16** 239–60

[125] Olshausen B A 2005 Sensory coding and the natural environment *Netw. Comput. Neural Syst.* **16** 119–20

[126] Smith E C and Lewicki M S 2006 Efficient auditory coding *Nature* **439** 978–82