

Texture signals in whisker vibrations.

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ABSTRACT

Rodents excel in making texture judgments by sweeping their whiskers across a surface. Here, we aimed to identify the signals present in whisker vibrations that give rise to such fine sensory discriminations. First, we used sensors to capture vibration signals in metal whiskers during active whisking of an artificial system and in natural whiskers during whisking of rats *in vivo*. Then, we developed a classification algorithm that successfully matched the vibration frequency spectra of single trials to the texture which induced it. For artificial whiskers, the algorithm correctly identified 1 texture out of 8 alternatives on 40% of trials; for *in vivo* natural whiskers, the algorithm correctly identified 1 texture out of 5 alternatives on 80% of trials. Finally, we asked which were the key discriminative features of the vibration spectra. Under both artificial and natural conditions, the combination of two features accounted for most of the information: The *modulation power* – the power of the part of the whisker movement representing the modulation due to the texture surface – increased with the coarseness of the texture; the *modulation centroid* – a measure related to the center of gravity within the power spectrum – decreased with the coarseness of the texture. Indeed, restricting the signal to these two parameters led to performance three-fourths as high as the full spectra. Because earlier work showed that *modulation power* and *centroid* are directly related to neuronal responses in the whisker pathway, we conclude that the biological system optimally extracts vibration features to permit texture classification.

INTRODUCTION

The whiskers are one of the principal sources of sensory information for rodents; a conspicuous and specialized sensory pathway has evolved to process vibrissal signals. Since the discovery of rodent barrel cortex (Woolsey and Van der Loos 1970), great strides have been made in understanding the relationship between the circuitry and the physiological properties of neurons (Armstrong-James and Fox 1987; Brecht et al. 2003; Staiger et al. 2004). In the last few years, research has begun to turn to another aspect of sensory processing: how does neuronal activity represent the real physical objects with which the animal interacts? Through active movement of their whiskers rats are able to discriminate the shape of small objects, the aperture size of openings, and the distance and location of objects (Hutson and Masterton 1986; Brecht et al. 1997; Krupa et al. 2001). An additional sensory capacity, the focus of the present work, is the discrimination of the surface features of objects; rats can judge the depth and distance between ridges as well as the coarseness of textures (Guic-Robles et al. 1989; Carvell and Simons 1990, 1995). Indeed, when making a texture discrimination by sweeping their whiskers across a surface, rats demonstrate discriminative capacities that rival or exceed those of humans using their fingertips. Here, we aim to identify the signals present in whisker movement that give rise to such fine sensory discriminations.

The nature of the signals present in the whiskers is of interest for several reasons. First, whiskers carry out a signal transformation, acting as the interface between external objects and sensory receptor neurons. Whereas in visual system it is readily apparent that sensory receptors transduce the energy of photons, such a

straightforward statement cannot be made for the whisker sensory system. To probe a texture, rodents actively move their whiskers at a frequency of about 5-12 Hz (Harvey et al. 2001; Carvell and Simons 1990, 1995). Signals arising from contact with the object surface are conducted towards the follicle, where the primary sensory neurons are situated. In this process, the mechanical properties of whiskers modify the signals in ways that are only recently beginning to be understood (Fend et al. 2003; Hartmann et al. 2003; Neimark et al. 2003). Second, the features of the signals that reach the whisker follicle can give us indications of what to expect in neuronal processing. If sensory processing mechanisms have evolved to take advantage of the most informative features of the physical signal, then identifying those informative features will lead us to more precise hypotheses about neuronal processing mechanisms.

In this study we investigate which features of the whisker movements are best suited for the discrimination of textures. We use a hardware model of a whisker system as well as *in vivo* measurements of rat whiskers. Applying a classification algorithm to the power spectra of whisker movements, we identify vibration features which could be extracted to support optimal performance. This leads to a model of texture discrimination that is, we argue, corroborated by recent electrophysiological experiments (Arabzadeh et al. 2005).

METHODS

Hardware Model

Recording set-up

To probe textures, rodents actively move their whiskers across them. We simulated this process using metal whiskers (steel wire, Fig. 1A; Small Parts Inc, Miami Lakes, FL, USA) fixed at one end to a sensor head (Fig. 1B,C), which was mounted perpendicularly to the rotation axis (Fig. 1B,C). Using a servo motor (Digital Servo S9251, Futaba, Huntsville, AL, USA) the whisker could be swept back and forth (Fig. 1B). The motor was controlled by a microprocessor (Atmega163, Atmel, San Jose, CA, USA) interfaced via a serial port to a PC. The whisking frequency was set to 1 Hz, where 1 sinusoidal cycle was a complete back and forth movement.

The texture of interest was placed in front of and orthogonal to the whisker (Fig. 1B). A miniature magnetic field sensor (KMZ51 Philips, Philips-Semiconductors, Eindhoven Netherlands), attached near the base of the whisker, recorded the distortions of the magnetic field induced by the movements of the whisker (Fig. 1B,C). The motor position was measured via a potentiometer (variable resistor). Motor position and the deflection of the whisker were digitized (National Instruments DAQCard-6036E, Austin, TX, USA) at a sampling rate of 4,000 Hz.

Artificial whiskers

The set of artificial whiskers consisted of 4 metal whiskers with the same diameter (0.305 mm) but different length (W94: 94 mm; W88: 88 mm; W77: 77 mm; W73: 73 mm). To determine the fundamental resonance frequencies and the damping coefficients as two characteristic features for each whisker, we fixed one end and then deflected and released the free tip, fitting a damped oscillation to the resulting motion. The resonance frequencies of the whiskers under these conditions ranged from 20-40 Hz (W94: 23.9 Hz; W88: 27.2 Hz; W77: 35.3 Hz; W73: 40.1 Hz) and the damping coefficient was 1.1 ± 0.15 s for all whiskers. However, these values do not apply to the more complex boundary condition that occurred while sweeping a whisker across a texture; in that case, the whisker was partly fixed at the “free” end.

Textures

We recorded whisker movements across 8 sandpapers of different coarseness. Coarseness is routinely defined by the P-value, a standard measure of grain size and density (<http://www.fepa-abrasives.org/>). The 8 sandpapers (and average grain diameter) were P40 (425 μm), P60 (269 μm), P80 (201 μm), P100 (162 μm), P120 (125 μm), P150 (100 μm), P180 (82 μm) and P240 (58.5 μm).

Processing of metal whisker signals

Whisker movement resulted in a superposition of the deflection signal and the earth magnetic field. To correct for the earth magnetic field, we measured its contribution at

each motor position and subtracted it from the total recorded signal. In one whisking cycle a whisker moved across the surface 2 times, analogous to the protraction/retraction cycle in natural whisking. Around the inflection points, where the movement direction reversed, the metal whiskers did not contact the texture but oscillated at their resonance frequency (Fig. 1D). Using motor position as a reference, we discarded these segments and selected those when the whisker touched the texture (gray shading, Fig. 1D). We refer to these as sweeps. The two directions were treated separately and gave equivalent results; analyses are based on sweeps in one direction only. After low pass filtering (150 Hz; chebyshev type II filter of 5th order) and subtracting a polynomial of 3rd order, we applied a Hanning window (raised cosine window) and zero padding (adding zeros in the temporal domain to increase the frequency resolution), and then calculated the power spectra.

In Vivo recording

Recording set-up

The data were originally collected as described in Arabzadeh et al. (2005). Experiments were conducted in accordance with NIH and institutional standards for the care and use of animals in research. Subjects were ten adult male 250–350-g Wistar rats anesthetized with urethane (1.5 g/kg) and data are presented from 1 case with the most complete stimulus set; the whisker in this dataset was C3. “Electrical whisking” (Brown and Waite 1974; Szwed et al. 2003) was generated by stimulating the right facial nerve (Fig. 1E) with 1–2-V pulses of 100 μ sec at 200 Hz for 60 ms to produce whisker protraction, followed by a passive 65-ms whisker retraction (also see

Fig. 1 in Arabzadeh et al. (2005)). The angle traversed at the whisker base, averaged across all trials and all textures, was 25 degrees (SD 6.1 degrees). Horizontal and vertical movements at the base were registered by a two-channel optical sensor, each channel consisting of an LED light source and phototransistor. The two voltage signals were digitized (7,634 samples per second). Whisker movement was recorded in contact with five surfaces of different coarseness for 10 minutes each (compact disk and 4 Sandpapers: P1200 (15.3 μm), P400 (35.0 μm), P280 (52.2 μm), P100 (162 μm); Fig. 1F illustrates P280 and P400).

Processing of in vivo whisker signals

We examined the principal direction of whisker movement, corresponding to the horizontal forwards- backwards axis. Movement in this axis contained all the texture-specific signals (Arabzadeh et al. 2005) and allowed an analysis in 1 dimension, similar to that of the metal whiskers (Fig. 1G). We extracted 300 protraction and retraction segments for each texture (illustrated by gray backgrounds in Figure 1G). After band pass filtering (cut off frequency 30 Hz, 150 Hz; chebyshev type II filter of 5th order), we applied a Hanning window, zero padding, and then calculated the power spectra.

Classification

The whisker movements in each sweep across a texture were characterized by their power spectrum, a good representation of whisker kinetics (see Fig. 1, Arabzadeh et al. 2005). However, the frequency resolution and the wide frequency band

investigated yielded vectors of several hundred dimensions, unsuitable for classification. To estimate the classification performance supported by whisker movements' power spectrum, we reduced the dimensionality of the data using the generalization of Fisher's linear discriminant to multi dimensions (Fisher transform), applied density estimation, maximum likelihood classification and then documented the results as hit-matrices, fraction correct classified and mutual information. The steps are next described in detail.

Generalization of Fisher's linear discriminant (Fisher transform)

The Fisher transform finds a linear projection such that the classes are best separated (Bishop 1995). This is achieved by maximizing the product of the between-class scatter matrix (S_B) and the inverse of the within-class scatter matrix (S_W):

$$(1) \quad S_B = \sum_t n_t (\mu_t - \mu) \cdot (\mu_t - \mu)^T$$

$$(2) \quad S_W = \sum_t \sum_{s \in t} (x_s^t - \mu_t) \cdot (x_s^t - \mu_t)^T$$

where t is the texture class index (8 classes for metal whiskers and 5 for the rat whisker); n_t is the number of samples in class t ; x_s^t is the s^{th} sweep from texture class t ; μ_t is the mean of class t and μ is the mean over all sweeps. In this notation we use column vectors and T indicates the transpose. We refer to this transform as *Fisher transform*.

Parametric density estimation

We approximated the probability distribution of feature vectors pertaining to each texture class by a multi-dimensional Gaussian (n dimensions). Given a set of feature vectors x_t^s , e.g. the vector components after the Fisher transform, relating to texture t and sweep s , we computed the class specific means μ_t and covariance matrices Σ_t . This yields an estimation of the probability distribution of the feature vectors for each class:

$$(3) \quad p_t(x) = \frac{1}{\sqrt{(2\pi)^n \cdot \det(\Sigma_t)}} \cdot e^{-\frac{1}{2}(x-\mu_t)\Sigma_t^{-1}(x-\mu_t)^T}$$

Class assignment

For classification, we randomly select two disjoint subsets: 100 sweeps for the metal whisker data, 150 sweeps for *in vivo* data. One subset was used to compute the Fisher transform and to estimate the class probability densities (training). The second subset was used to measure performance. Each sample feature vector of the validation set was then assigned to the texture class with the maximum likelihood.

$$(4) \quad c(\phi_i^s) = \arg \max_t (p_t(\phi_i^s))$$

Classification results were visualized as a *hit-matrix* (H), which contained for each sweep from texture class $t=i$ the probability of being assigned to a class $c=j$.

$$(5) \quad H_{i,j} = w(c = j | t = i)$$

To quantify the *classification performance* as a single value we computed the fraction of correctly classified sweeps:

$$(6) \quad C(H) = \frac{\sum_i H_{i,i}}{\sum_i \sum_j H_{i,j}}$$

To compare classification performance of samples from m different textures (chance level: $1/m$) under two different conditions C_1 , C_2 we evaluated the *relative performance* (R) and the *relative performance gain* ($G=R-1$):

$$(7) \quad R = \frac{C_2 - 1/m}{C_1 - 1/m}$$

Additionally, we measured the *mutual information*:

$$(8) \quad I(H) = \sum_{i=1}^m \sum_{j=1}^m w(t = j) \cdot H_{i,j} \cdot \log_2 \left(\frac{H_{i,j}}{w(c = j)} \right)$$

The value of $I(H)$ is in bits.

All data processing was in MATLAB (<http://www.mathworks.com>).

RESULTS

We first illustrate texture-induced vibrations in the hardware model of the whisker system and introduce a spectral analysis algorithm that yields good classification performance. We then uncover two features of whisker vibration that, by themselves, can support a high level of discrimination performance. Finally, we apply this same simple signal processing algorithm to the data obtained *in vivo*.

Texture-induced vibrations in the hardware model

We analyzed 2 blocks (B1, B2) of 100 sweeps for each of the 8 textures (#1 - #8) and 4 whiskers (W94, W88, W77, W73) summing to a total of 6,400 sweeps. An example of two sweeps of the shortest whisker (W73) across the coarsest (#8) and the finest sandpaper (#1, P40) is shown in Figure 1D. The gray shading indicates the period of interest, where the whisker contacted the texture. In Figure 2 additional stages of signal analysis are shown for whisks on texture #8. The bending of the metal whisker during the sweep becomes evident (Fig. 2A, slow shift in red signal); it can be approximated well by a 3rd order polynomial (Fig. 2A, black curve). Because the slow bending parameters were characteristic of a given whisker and its position relative to the texture but not the texture surface, this signal was extracted and was not further analyzed. Once the texture-independent bending was subtracted from the raw signal, the residual signal contained higher frequency components (Fig. 2A, green trace). The power spectrum of the raw signal is illustrated in Figure 2B by the red line. The spectrum is also shown broken down into its components: the bending signal (texture-nonspecific) composed of very large power at frequencies up to about 20 Hz (Fig. 2B,

transparent gray plot) and the residual signal (Fig. 2B, green plot). Thus, the separation into (i) bending and (ii) residual components corresponded to (i) low and (ii) high pass filtering, respectively, of the total signal. The peak corresponding to the strongest component in the power spectrum is marked by a blue asterisk. To what extent does the peak of the power spectrum reflect the characteristics of the raw signal? To answer this question, the inset of Figure 2B shows the residual signal (green trace, carried over from part A) overlaid (blue trace) by the 27 Hz predominant frequency component in the signal. This illustrates how the peak value of the power spectrum (asterisk) captured the critical temporal patterns within the raw signal.

Figure 2C shows the average power spectra of the residual signal for 4 different metal whiskers applied to the coarsest texture (#8). The shape of the power spectrum was similar, qualitatively, across all whiskers. More than 98% of total power (90% of the residual power) was within the range of 0 to 150 Hz. To summarize, three components of the total signal were excluded: (i) oscillations occurring when the whisker was not in contact with the texture, (ii) very low frequency movements caused by whisker bending, and (iii) very high frequency vibrations (>150 Hz) containing less than 2% of the total signal power. Subsequent analysis therefore focuses on the possible texture information carried by the modulation power spectrum at frequencies up to 150 Hz.

Quantifying texture discrimination performance

To quantify the performance we randomly chose distinct subsets of 100 sweeps for training and validation. The parameters for classification were established on the

training set. The performance was then evaluated on the validation set (see Methods). This process was repeated 20 times. Classification is documented by hit-matrices, correct classification percentage, and mutual information.

Overall, classification performance among 8 textures using the modulation power spectrum was about 39% correct (chance performance = 12.5%) with a mutual information of 0.83 bits (upper limit = 3 bits). Performance also varied slightly across whiskers (W94: 36%; W88: 40%; W77: 36% and W73: 47%). The standard deviation of the classification across repeated tests was low (maximum: $\pm 3\%$), indicating the robustness of the classification algorithm. The hit-matrices (Fig. 3A) reveal that misclassification mainly resulted from confusing textures of similar coarseness. Averaging of all whiskers (Fig. 3B) shows that 47% of all errors arose from confusing neighboring textures (chance: 25%). The total number of neighbors with a certain distance decreases with the distance (e.g. 14 neighbors of distance 1 but just 2 neighbors of distance 7); to account for this, in Figure 3C we show mean error probability for each distance. Chance corresponds to equally distributed errors (dotted line). This reveals that the classifier extracted coarseness of the surfaces, capturing the inherent order in this feature. In other words, the power spectrum classifier was measuring the P rating of each texture. Discriminating between just the coarsest and finest textures (#8, #1) yielded a performance of 93% and a mutual information of 0.69 bits (upper limit = 1 bit). Thus, the information in the modulation power spectrum of one sweep with one whisker was sufficient to support above-chance discrimination between textures of similar coarseness and to reliably discriminate between a coarse and a fine texture.

Spatial and temporal integration of information

Behavioral studies reveal that rats, while probing textures in a discrimination task, contact the surface with many whiskers over several whisking cycles (Carvell and Simons, 1990). Thus, rats might normally reach optimal performance by combining the signals from different whiskers (*spatial integration*), while collecting data over time (*temporal integration*). To learn more about how performance could be improved through spatial and temporal integration, we combined the signals acquired from multiple whiskers and multiple sweeps. With a single whisker, the performance using 2, 3 and 4 sweeps was $48 \pm 6\%$, $55 \pm 6\%$ and $59 \pm 6\%$ respectively. This corresponds to a relative performance increase (see Methods) of 29%, 55% and 69% compared to that of a single sweep. Thus, increasing the number of whisking cycles is a potentially powerful way to increase the performance.

We also measured the classification performance using several sweeps from distinct whisker/direction combinations. For 4 whiskers and 2 directions there exist 28, 56 and 70 possible combinations of 2, 3 and 4 sweeps, respectively. The average performance was $50 \pm 4\%$, $57 \pm 4\%$ and $62 \pm 5\%$ corresponding to a relative performance increase of 36%, 62% and 80% compared to a single sweep. Similarly to temporal integration, each additional whisker added progressively less performance improvement. However, the average performance increase achieved by spatial integration was greater than that achieved by temporal integration.

Features of the power spectrum that support texture discriminability

In the previous section we illustrated classification performance based on the complete modulation power spectrum over the range 20-150 Hz. Next, we investigated whether some subset of spectral features was particularly relevant in the classification process. The approach was to look for the texture-specific differences in the power spectra. We compared the power spectra averaged over all sweeps (shortest whisker: W73, Fig. 4A). The most evident texture-related difference was the total *modulation power* in the signal, i.e. the area below the curves. Vibrations induced by coarse textures had high *modulation power*, while vibrations induced by fine textures had low *modulation power*. To look for other potentially informative features, we then normalized the area under the curve of all the spectra, thereby excluding *modulation power* as a feature (Fig. 4B). After this normalization, the peak of the power spectrum emerged as an informative feature: it was at low frequencies for coarse textures and at higher frequencies for fine textures. This could result from the whiskers performing many small jumps while sweeping across a fine texture and fewer, larger jumps across coarse textures. We quantified this feature as the *modulation centroid*.

$$\text{ModulationCentroid} = \int |X(f)|^2 \cdot f^n df \Big|_{n=2} = \int |f \cdot X(f)|^2 df = \int |V(f)|^2 df ,$$

where $X(f)$ and $V(f)$ are the Fourier transform of the modulation signal and its velocity. For $n=1$ this corresponds to the center of gravity of the power spectrum. However, we used $n=2$ as this corresponds to the power in the velocity signal, a quantity which is easy to extract. In Figure 4C all sweeps of W73 are shown in the space spanned by the *modulation power* and *centroid*; color identifies the sandpaper.

The signals from the coarsest and the finest sandpapers can be clearly discriminated, while signals from neighboring textures are partially overlapping. Thus, a high capacity for texture discrimination appears to be supported by the reduction of the full power spectrum to just two features, *power* and *centroid*. This key finding was general to the other metal whiskers.

Next, we quantified the fraction of the classification performance the two features of interest conveyed, relative to the whole spectrum. Performance was tested for each feature singly and for both features together 20 times. The average classification performance using the *modulation power* alone, *modulated centroid* alone, and both, were $29 \pm 6\%$, $23 \pm 3\%$ and $32 \pm 6\%$, respectively. This should be compared to the performance using the whole power spectrum, 39%. The relative performance (Eq. 7) is 62%, 40% and 74% respectively. Thus, the *modulation power* and *modulation centroid* together can account for about three-fourths of the total information available.

Texture signals in rat whisker vibrations

We now turn to the whisker signals recorded during whisking in anesthetized rats (Figs. 1E-G). We used 300 whisks across each of 5 textures of different coarseness (see Figure 1G for example traces). Similar to the artificial whisker, we extracted the modulation signal by high pass filtering the whisker movement signal. We separated the protraction and retraction phases of each whisk (Fig. 1G, gray shadings) and performed the complete analysis for both phases. Results were qualitatively similar for the two phases, although discrimination performance was slightly lower for the

protraction phase. This can be understood by the more structured whisker velocity profile in retraction compared to protraction (see Figure 1G and Figure 1B in Arabzadeh et al. 2005). For these reasons here we concentrate on the whisker retraction results. Figure 4D shows the average power spectrum of the retraction phase for all 5 textures. The plotted part of the spectrum (30-150Hz) covers most of the power (>90%). Just as for the artificial whiskers, the *modulation power* increased with the coarseness of the texture, while the *modulation centroid* in the normalized power spectrum (Fig. 4E) decreased with the coarseness of the texture. Figure 4F shows all sweeps from each texture and the texture means in the space spanned by *modulation power* and *modulation centroid*. Except for neighboring textures on the coarseness scale, the sweeps were well separated.

To quantify the reliability afforded by *power* and *centroid*, we compared the classification performance based on the whole power spectrum to the classification performance based on just these two features. More precisely, we split the 300 sweeps across each texture randomly into training and validation sets of 150 sweeps each. The classification was performed 20 times and the mean and standard deviation of correct performance were derived. Using the whole power spectrum, the performance was $91 \pm 1\%$ while using the *modulation power* and *centroid* yielded $78\% \pm 1\%$ correct classified. The *modulation power* and *centroid* thus captured, by themselves, 83% of the texture discrimination performance available in the whole power spectrum.

Model of signal processing in the somatosensory system

Motivated by the finding that approximately three-fourths of the texture information could be captured by the *modulation power* and *centroid* we propose a model for simple and rapid texture discrimination applicable to both the metal whiskers and the natural whiskers (Fig. 5). First, the signal is band pass filtered to extract the relevant modulation signal (in the case of metal whisker: approximately 20 Hz and 150 Hz cut-off frequencies, real whisker: 30 Hz and 150 Hz cut-off frequencies). Measuring the power in the band pass filtered signal gives the *modulation power*. In parallel, the temporal derivative of the band pass filtered signal is taken, which corresponds to multiplication of the power spectrum by f^2 . Determining the power of the velocity signal and normalizing it by the total power in the high pass filtered signal yields the *modulation centroid*. Thus, the main features contributing to texture discrimination, under these experimental conditions, can be extracted by three simple operations: band pass filtering, temporal differentiation and normalization. In the Discussion, we will explore the possibility that neuronal activity observed in the rat whisker sensory system (Arabzadeh et al. 2005) is a representation of these two whisker vibration features.

DISCUSSION

As a rodent palpates an object, what signals are transmitted from the whisker shaft to the sensory receptor neuron to initiate the process of sensory discrimination? In the present study, the whisker vibration frequency power spectrum obtained from single sweeps permitted our classification algorithm to correctly decode the contacted texture from among textures of varying coarseness on about 80% of trials for real whiskers and 40% for metal whiskers. As shown for the metal whiskers, this performance can be improved by combining the signals from different whiskers (*spatial integration*) and by collecting data over several sweeps (*temporal integration*). Because sensory systems may optimize discriminations by transmitting only the most relevant stimulus features to the brain, we asked whether the spectrogram could be reduced to some fundamental features while still allowing reliable classification. The *modulation power* – the power of the part of the whisker movement representing the modulation due to the texture surface – increased with the coarseness of the texture. The *modulation centroid*, a measure related to the center of gravity within the power spectrum, decreased with the coarseness of the texture. After condensing the spectrogram to *modulation power* and *modulation centroid*, the classification algorithm retained approximately three-fourth of its discriminative performance. Thus, as few as two features of whisker movements carried the bulk of the information necessary to discriminate among candidate textures.

We analyzed two different types of whiskers, metal whiskers and rat whiskers *in vivo*. Metal whiskers provided a controlled setup to allow highly reproducible recording of whisker movements. In contrast to real whiskers, metal whiskers do not change their

properties due to abrasion or ageing and are unaffected by changes in humidity or temperature. Therefore, they are more applicable to artificial sensing systems. On the other hand, the *in vivo* setup aimed at providing realistic natural signals, simulating the whisker movements in the living animal. However, it should be noted that the whisker movements induced by electrical whisking differ from those in awake behaving animals. For instance, in awake animals, the whisker kinetics might be affected by the muscle force applied to the follicle; moreover, the sensory signals picked up by the whiskers appear to lead to rapid modulation of the motor output (Ahissar and Kleinfeld 2003). For the metal whisker setup we used 8 relatively similar sandpapers, therefore creating a difficult classification problem. In contrast, for the real whisker setup we used 5 different textures with more pronounced differences. A direct quantitative comparison of the performance is therefore not possible. Moreover, in both conditions we measured the percent of correct discriminations among a large number of textures; in behavioral situations, discriminations are commonly made between just two possible stimuli (e.g. forced choice paradigm). Percent correct would be much higher if discriminations were considered between stimulus pairs (also see discussion below). Regardless of the exact parameters of the stimulus set, the fact that the general findings are true for both a natural whisker *in vivo* and a metal whisker suggests that a whisker need not possess special mechanical properties in order to generate texture-specific vibrations. Indeed, for whiskers of widely differing properties, the sensory system could discriminate textures by performing band-pass filtering (including temporal derivatives) and division operations.

An emerging picture of texture discrimination

To discriminate textures, rodents use active whisking. Previous studies that analyzed the properties of whisker vibrations used passive stimulation of whiskers (Arabzadeh et al. 2003, 2004, Hartmann et al. 2003; Neimark et al. 2003). Passive stimulation by a piezoelectric wafer or by a rotating drum has the great advantage of characterizing the system in a steady state. However, potentially important properties of active whisking are neglected, such as the continuous change in geometry of the whisker relative to the texture. Furthermore, under more natural whisking conditions, the contact point of the whisker with the surface and the forces at the contact point are likely to change continuously, producing a dynamic modulation of the mechanical properties of the system. Here, the whiskers were moved forth and back across textures in an attempt to mimic the dynamics of natural whisking.

The general picture that emerges from the present experiments is that large quantities of information can be introduced into the sensory system through a single whisker. Consistent with this proposal, behavioral experiments demonstrate that the performance of rats in a difficult texture discrimination task remains intact even when the whiskers are clipped from the normal complement of more than 30 down to 2 (Carvell and Simons 1995). Our results do not rule out the possibility that rats exploit the gradient of mechanical properties across the whisker array, as proposed in the “resonance frequency hypothesis” (Neimark et al. 2003; Hartmann et al. 2003; Moore 2004; Andermann et al. 2004; Metha et al. 2004). However, we did not observe prominent resonance frequencies within the analyzed range that carried most power

(up to 150 Hz). This might be due to the difference between active and passive whisking discussed above.

Relation to behavioral evidence

How does the observed classification performance compare to other available behavioral evidence? In many texture discrimination tasks rats decided where to continue at a Y-junction based on texture cues (Guic-Robles et al. 1989; Carvell and Simons 1990). In these experiments the decision was based on a stimulus set of two textures appearing with equal probability, which corresponds to a maximum available information of 1 bit. The difference of the texture cues ranged from smooth surface vs. surface with $30\mu\text{m}$ grooves spaced $90\mu\text{m}$ (Carvell and Simons 1990) to 2 sandpapers with grain diameters of $400\mu\text{m}$ vs. $2000\mu\text{m}$ (Guic-Robles et al. 1989). The behavioral performance discriminating such stimuli was 85% in both studies. The artificial whisker set up in the present study used 8 sandpapers with grain diameters ranging from $59\mu\text{m}$ - $425\mu\text{m}$ while the 4 sandpapers and the compact disc in the *in vivo* recording ranged from smooth (no structure) to $162\mu\text{m}$ grains. For a direct comparison we consider the discrimination performance for the most extreme stimuli. Using the model based on *modulation power* and *centroid* on the movements of one whisker in a single trial to classify the coarsest from the finest sandpaper we observe an average performance of 89% with the artificial whisker and a performance of 95% with the rat whisker. Thus, the behavioral performance of the rats is compatible with the results of the simple model proposed here.

Relation to electrophysiological evidence

Many electrophysiological experiments have been performed to reveal the encoding and transformation of whisker deflections along the whisker pathway from the primary stage, the trigeminal ganglion neurons, to barrel cortex. Trigeminal ganglion neurons reliably encode the kinetics of the whisker movement at a very high temporal resolution (Gibson and Welker 1983a,b; Lichtenstein et al. 1990; Shoykhet et al. 2000; Deschenes et al. 2003; Arabzadeh et al. 2005). More specifically, how does electrophysiological evidence from the whisker system relate to the two features, modulation power and centroid? Neurons in the trigeminal ganglion and the barrel cortex of anesthetized rats, when presented with the stimulus set analyzed here, encoded the “equivalent noise level” (ENL) of the texture-induced vibration in their mean firing rates. The neurons encoded the temporal structure of the vibration – the time difference between the high-velocity events – by a matching response probability profile (Arabzadeh et al. 2005). The ENL is mathematically analogous to the product of modulation power and modulation centroid (Fig. 5, asterisk) and could be extracted by upstream neurons via spike count of barrel cortex populations across the whisker sweep. In summary, the recent electrophysiological experiments support the view that the modulation power and modulation centroid are reflected in neuronal activity and could be extracted explicitly by neurons upstream of barrel cortex.

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FIGURE LEGENDS

Fig. 1 Set-ups

(A) Metal whisker provided with little magnets. (B) Metal whisker recording set-up. (C) Sensor head with magnetic sensor and attached metal whisker. (D) Time course of whisker (W73) signal on the finest (P240, black) and the coarsest (P40, gray) sandpaper and the motor position (dotted line). (E) In Vivo recording set-up. (F) Two textures (Sandpaper P280 and P400). (G) Whisker movement signals on two sandpapers (P280, gray; P400, black). The shaded areas in F and G indicate the intervals when the whiskers are sweeping across the texture.

Fig. 2 Properties of whisker vibrations

(A) A sweep of the shortest whisker (W73) across the coarsest sandpaper (P40). The shaded area indicates the interval when the whisker is sweeping across the texture. The whisker movement (red) is separated into the contribution of bending (black) and modulated part (green). (B) Power spectrum of the trial shown in A, with whisker movement (red), bending (black) and modulation (green). (C) Average power spectra across all sweeps for all whiskers across the coarsest texture (Texture: P40, W94: black; W88: dark gray; W77: gray; W73: light gray).

Fig. 3 Classification: Metal whiskers

(A) Hit matrices and classification performance for all artificial whiskers. The hit matrices illustrate the probability of assigning a certain texture stimulus (y-axis) to a

specific texture class (x-axis). The textures are sorted by their coarseness (#1 smooth to #8 coarse). Correct classifications fall on the diagonal; confusion of neighboring textures on the coarseness scale (e.g. confusion of #1 and #2) falls on the 1st off-diagonals etc. Thus, the hit matrices represent correct discriminations as well as the distribution of the classification error. (B) Average of hit matrices in part A. (C) Distribution of the distance between assigned texture and actual texture on the coarseness scale. The values are corrected for the fact that there are fewer distant than close neighbors. Error bars indicate the standard deviation across whiskers.

Fig. 4 Meaningful features

Power spectra of movements of the shortest metal whisker (W73, A-C) and the real whisker (D-F) across different textures is shown color coded: (A,D) Average power spectrum of modulation part shown for all sandpapers individually. (B,E) Normalized average power spectrum of the modulation part for all sandpapers. (C,F) *Modulation power* and *centroid* of all sweeps. See results for details.

Fig. 5 Model

Evaluation of *modulation power* and *modulation centroid* by a combination of band-pass filters (including temporal derivative) and a division operation. The asterisk marks the link to physiological experiments (see discussion).









