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A Comparison of Neuronal and Behavioral Detection and Discrimination Performances in Rat Whisker System

Mehdi Adibi and Ehsan Arabzadeh
School of Psychology, University of New South Wales, Sydney, New South Wales, Australia

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Adibi M, Arabzadeh E. A comparison of neuronal and behavioral detection and discrimination performances in rat whisker system. J Neurophysiol 105: 356–365, 2011. First published November 10, 2010; doi:10.1152/jn.00794.2010. We used the rat whisker touch as a model system to investigate the correlation between the response function of cortical neurons and the behavior of rats in a sensory detection versus discrimination task. The rat whisker-barrel system is structurally well characterized and represents one of the main channels through which rodents collect information about the environment. In experiment 1, we recorded neuronal activity (n = 235) in the whisker area of the rat somatosensory cortex in anesthetized rats while applying vibrotactile stimuli of varying amplitudes to the whiskers. Neurons showed a characteristic sigmoidal input-output function, with an accelerating nonlinearity at low stimulus amplitudes and a compressive nonlinearity at high stimulus amplitudes. We further quantified the performance of individual neurons for stimulus detection and for discrimination across different stimulus pairs with identical amplitude differences. For near-threshold stimuli, the neuronal discrimination performance surpassed the detection performance despite the fact that detection and discrimination represented identical amplitude differences. This is consistent with the accelerating nonlinearity observed at low stimulus intensities. In the second stage of the experiment, four rats were trained to select the higher-amplitude stimulus between two vibrations applied to their whiskers. Similar to neuronal results, the rats’ performance was better for the discrimination task compared with the detection task. The behavioral performance followed the same trend as that of the population of individual neurons. Both behavioral and neuronal data are consistent with the “pedestal effect” previously reported in human psychophysics.

INTRODUCTION

To quantify how brain activity underlies sensory experience, researchers have asked two key questions: How are sensory stimuli represented in neuronal activity? How does neuronal activity contribute to behavior? A body of research has focused on the correlation between neuronal activity and perception (Parker and Newsome 1998) regarding stimulus detection (Cook and Maunsell 2002; de Lafuente and Romo 2005; Hawken and Parker 1990; Johansson and Vallbo 1979; Mountcastle et al. 1972; Palmer et al. 2007) and stimulus discrimination (Britten et al. 1992; Celebrini and Newsome 1994; Cohen and Newsome 2009; Hernández et al. 2000; LaMotte and Mountcastle 1975; Luna et al. 2005; Mountcastle et al. 1990). Here, we provide a fresh approach by comparing the detection and discrimination performances at two separate levels: 1) at the level of cortical neurons recorded in anesthetized rats and 2) at the behavioral performance of rats engaged in an active detection/discrimination task.

As nocturnal animals, instead of using vision, rats rely on their whiskers to collect information from their surrounding environment (Brecht 2007; Brecht et al. 1997; Carvell and Simons 1990; Knutsen and Ahissar 2009; Vincent 1912; von Heimendahl et al. 2007). Due to its functional efficiency and well-described anatomical characteristics (Chmielowska et al. 1989; Durham and Woolsey 1977; Herron and Schweitzer 2000; Petersen 2007; Woolsey 1996), the rodent whisker touch provides a suitable model system for studies in systems neuroscience (Diamond et al. 2008). The whisker region of the primary somatosensory cortex of rodents contains a group of anatomically distinguishable clusters of neurons called “barrels” (Woolsey and van der Loos 1970). In rats, each barrel is about 0.3–0.5 mm in maximal diameter (Hodge Jr et al. 1997) and contains an average of 2,500 neurons (Jones and Diamond 1995; Woolsey and van der Loos 1970) that respond primarily to their corresponding whisker (Welker 1971).

To provide a comparison of detection and discrimination performances, at the neuronal and behavioral levels, the present experiments used sinusoidal stimuli. This is an ideal stimulus for two reasons: first, because it simulates and is highly informative about naturally occurring stimuli (Arabzadeh et al. 2003, 2005); second, because its simple parameters—amplitude (A) and frequency (f)—can be precisely controlled in experimental settings. Previous research has demonstrated that single neurons and cortical ensembles reliably encode the product Af of a vibration (Arabzadeh et al. 2003, 2004).

Here, in experiment 1 we recorded neuronal activity from the barrel cortex of anesthetized rats and characterized the response of individual neurons to a range of vibration amplitudes. The neuronal response function made quantifiable predictions for the detection versus discrimination performance that was tested in experiment 2 in which rats engaged in a detection/discrimination task. Finally, we demonstrate that the behavioral performance followed the same trend as that of the population of individual neurons.

METHODS

Experiment 1: electrophysiology

SUBJECTS, SURGERY, AND RECORDING. Sixteen adult male Wistar rats, weighing 390–540 g, were used for acute recording. All components of the experiment were conducted in accordance with the APA guidelines for the treatment of animals and approved by the Animal Care and Ethics Committee at the University of New South Wales. Anesthesia was induced by intraperitoneal administration of urethane (30% wvp, 5 ml/kg body weight) to the right side. During the recording sessions, the level of anesthesia was monitored by the...
hindpaw and the corneal reflexes and maintained at a stable level by administering 10% of the original dose, if necessary. The rat’s head was fixed in a stereotaxic apparatus, an incision was made from bregma to lambda, and the fascia was removed. Craniotomy was performed directly over the barrel cortex on the right hemisphere on an area of 3 × 4 mm, centered at 2.6 mm posterior to bregma and 5 mm lateral. The dura mater was left intact.

Neuronal activity was acquired using tungsten electrodes, with an impedance of 2–4 MΩ at 1 kHz. During each penetration the electrode was lowered by means of a micromanipulator until a single neuron or a neuronal cluster was identified. The principal whisker was determined by manual flicks imposed to individual whiskers. Data acquisition and on-line amplification were performed using Cheetah data acquisition hardware and software (Neuralynx, Tucson, AZ). During the recording sessions, data were acquired at a sampling rate of 30.3 kHz and filtered on-line by applying a band-pass filter between 600 and 6,000 Hz. From the filtered data, spikes were detected using an amplitude threshold that was set manually. A liberal threshold was used for on-line spike detection to avoid missing neuronal activity. A more rigorous spike sorting was performed off-line using template matching implemented in MATLAB (The MathWorks, Natick, MA). Recordings were limited to barrel cortex (layer IV). This was achieved by monitoring the penetration depth of the recording tungsten electrode and was further confirmed by the fast neuronal response onset latencies (<8 ms) to the stimulus with highest amplitude. Across 16 rats we recorded a total of 93 single neurons and 142 multiunit neuronal clusters.

WHISKER STIMULATION. A series of nine sinusoidal whisker vibrations (frequency of 80 Hz; amplitudes of 3 to 28 μm with equal increment steps) were delivered to the principal contralateral whisker while recording the neuronal activity. Stimuli were generated in MATLAB and were presented through the analog output of a data acquisition card (National Instruments [NI], Austin, TX) at a sampling rate of 44.1 kHz. The output of the NI-Card was amplified (25.4 dB gain) before arriving at a piezoelectric ceramic (Morgan Matroc, Bedford, OH). Using a custom-built infrared optic sensor, the vibrotactile stimulators were calibrated and their vibration trajectory was measured at 10 kHz sampling frequency and verified to follow and precisely match the desired sinusoidal stimuli. For the vibration stimuli, the frequency of 80 Hz was selected because it allowed a wide range of amplitudes (0–30 μm) to be reliably produced.

To ensure precise whisker stimulation, a lightweight thin piece of plastic micropipette was glued to the piezoelectric ceramic. The principal whisker was placed into the micropipette such that the distance of the micropipette tip to the base of the whisker was 5 mm, with a precision of ±1 mm. To engage the whisker with the inside border of the micropipette opening, the stimulator was slightly tilted by about 10° with respect to the relaxed position of the whisker shaft. Each trial consisted of a 500-ms stimulation followed by an inter-stimulus interval of 500 ms. Each stimulus was presented 100 times in a pseudorandom order to provide a measure of trial-by-trial variability in the neuronal response.

NEURONAL ANALYSES: ROC. The sequences of spikes corresponding to trials of the same stimulus were separated and aligned with respect to the stimulus onset to generate raster plots (see Fig. 2A). The probability of spiking over time was evaluated by counting the overlap between the poststimulus time window of 50 ms was compared with the histogram of spike counts within a corresponding window of 50 ms before the stimulus onset. The overlap between the two histograms was quantified by applying all possible values of the decision criterion, ranging from the minimum to the maximum observed. To count the number of spikes within the poststimulus time window of 50 ms was compared across 100 trials of each stimulus amplitude. The ROC area falls within the range of 0 to 1. An ROC area of 0.5 indicates a liberal threshold was selected for estimating the discrimination performance. This allowed two discrimination performances to be measured separately for the ½Th versus 1½Th pair and for the Th versus 2Th pair (Figs. 5 and 9).

Experiment 2: behavior

SUBJECTS, BEHAVIORAL APPARATUS, AND PROCEDURES. Four adult male Wistar rats, weighing 350–420 g, were used in the behavioral experiment. Rats were maintained on a 12:12-h light:dark cycle (with lights on at 7 am) in a climate-controlled colony room. Rats were water deprived and were rewarded with a 5% sucrose solution during the experiment. After each daily experiment session, the rats had unrestricted access to water for 1 h and were fed 15–18 g of rat chow. The experiment was performed in a Plexiglas chamber with the following dimensions: 30 × 20 × 50 cm (length × width × height). The rat was placed on a platform composed of metal bars spaced at 1 cm as flooring that was raised 20 cm from the ground. An aperture (40 × 40 cm) was located in the front wall of the chamber. A nose-poke into the aperture were detected by infrared optical sensors. Two mesh plates (35 × 30 mm) were positioned 2 mm from the edges of the aperture slanted toward each other at a 55° angle (Fig. 1). These two mesh plates were attached to piezoelectric ceramic bars that delivered vertical sine-wave vibration stimuli to the whiskers. The position of the nose-poke sensor was adjusted in a way that the rats were required to maintain a consistent head posture to receive the stimulus. This minimized the trial-by-trial variability of head position with respect to the meshes and of head movements during the stimulus presentation. The reward was delivered through two drinking spouts located at either side of the aperture in the front wall (Fig. 1).
behavior of the rat (nose-poke or the response at either reward spout) was continuously registered into a data acquisition card (National Instruments) using a custom-built circuit that measured contact at the spouts or nose-poke through optical sensors. A MATLAB script controlled the presentation of the stimuli, registered the behavior of the rats along with the corresponding time stamp of each behavioral action, and controlled the delivery of rewards through two separate water pumps. The behavior of the rats was monitored during the experiment using an infrared camera positioned in front of the aperture.

The stimulus set consisted of sine-wave vibrations with a frequency of 80 Hz and a maximum duration of 3 s. The stimuli were generated in MATLAB and sent to a low-latency sound card (Creative Sound Blaster X-Fi series; Creative Labs) at a 44.1 kHz sampling rate and sent to the piezoelectric stimulators through an amplifier (25.4 dB gain). To quantify each rat’s sensitivity, stimuli were presented at multiple amplitudes ranging from 0 to 30 gain. To do so, we used a variable-delay procedure, after which the rat received a vibration stimulus on one of the 2 plates (3). Having identified the vibrating plate, the rat made a behavioral choice (4) by turning toward the corresponding drinking spouts (circles). Correct choices were rewarded by sucrose water (5).

Figure 1: Schematic representation of the detection task. (1) The rat initiated a trial by nose-poking into the stimulus aperture while touching the 2 mesh plates with its whiskers. After a random delay period (2) during which nose-poke was continually maintained, the rat received a vibration stimulus on one of the 2 plates (3). Having identified the vibrating plate, the rat made a behavioral choice (4) by turning toward the corresponding drinking spouts (circles). Correct choices were rewarded by sucrose water (5).

The stimulus set consisted of sine-wave vibrations with a frequency of 80 Hz and a maximum duration of 3 s. The stimuli were generated in MATLAB and sent to a low-latency sound card (Creative Sound Blaster X-Fi series; Creative Labs) at a 44.1 kHz sampling rate and sent to the piezoelectric stimulators through an amplifier (25.4 dB gain). To quantify each rat’s sensitivity, stimuli were presented at multiple amplitudes ranging from 0 to 30 μm based on the method of constant stimuli. Figure 1 illustrates the basic experimental design and sequence of events in the task. The rat initiated a trial by a nose-poke (snout entry in between the two meshes) through the aperture. Nose-poke resulted in the presentation of the stimulus, which was the vibration of the meshes at different amplitudes. The stimulus started with a variable delay after the nose-poke initiation, provided that the rat maintained the nose-poke throughout this delay. The onset delay was selected from a uniform distribution from 100 ms to 1 s. Observation of behavior indicated that in a great majority of the trials the rats kept their head fixed until they started to retract to choose one of the drinking spouts. Furthermore, monitoring of whisking motion showed that on the majority of trials the rats did not whisk against the meshes during stimulus presentation. The rat then responded by choosing one of the two reward spouts during a window from 50 ms after the stimulus onset lasting for 5 s. The first lick at either drinking spout was considered as the behavioral choice and its time instance was recorded as the response time. A correct response was to turn toward the spout located on the side of the mesh with the higher-amplitude vibration. Correct trials were rewarded with 0.08 ml of sucrose solution. For incorrect responses no reward was given and an extra time-out penalty of 4 s was imposed. The proportion of the stimulus presentation at each side was adaptively chosen based on the inverse proportion of the history of responses the rat made toward either side. This adaptive strategy prevented the rat from forming a response bias by ensuring that roughly equal numbers of choices were made toward either spout. Retrospective analysis of the stimulus side revealed that the bias correction strategy did not have a significant effect on the proportion of stimulus assignments at each side [i.e., for none of the rats, the sequence of left/right assignments was significantly different (P < 0.05) from a binomial distribution with a probability of 50%].

The first behavioral experiment used a detection task based on the method of constant stimuli. A sinusoidal vibration was delivered on only one of the meshes. The amplitude of the stimulus was adjusted for each rat (Fig. 6). After the familiarization to the setup and the initial shaping of the behavior, the detection task was conducted over 5 days. Rats performed an average of 50–65 blocks of trials in which each block contained a pseudorandom order of stimuli of varying amplitudes. The detection performance was characterized by fitting a cumulative Gaussian function to the empirical data (Fig. 6). Once the psychometric curves were obtained for each rat, the detection threshold corresponding to the 60% correct performance was calculated from the fitted curve and was used for the second phase of the behavioral experiment.

In the second phase, the rats performed a discrimination task. The detection threshold (Th) obtained from phase 1 was used to generate multiple base amplitudes to be added to both sides. This procedure constructed new stimuli with the base amplitudes of zero, ½Th, and Th. The stimulus pairs thus consisted of 0 verses Th (i.e., detection), ½Th versus ½Th, and Th versus 2Th. All pairwise discriminations thus represent an amplitude difference equal to the absolute detection threshold obtained in phase 1. A high-amplitude stimulus that was easily detectable was presented in one fourth of trials to increase the overall performance and keep the rats motivated in the task. The three pairs of stimuli in addition to the easily detectable stimulus were presented in a pseudorandom order in blocks of four trials. This procedure ensured that all stimulus pairs were presented for similar number of trials that varied from 150 to 330 per stimulus for different rats.

Results

The aim of these experiments was twofold: first, to characterize how barrel cortex neurons respond to a selected set of vibration stimuli and, second, to investigate the performance of rats in a detection and discrimination task involving the same stimulus set. Experiment 1 measured the responses of rat barrel cortex neurons to sinusoidal vibrations of varying amplitude.
Figure 2 illustrates a step-by-step quantification of the response of a typical barrel cortex neuron. Figure 2A shows the response of the neuron to an 80 Hz/22 μm vibration, with the corresponding peristimulus time histogram (PSTH) aligned to the instant of stimulus onset. The neuronal response increased after stimulus onset, with a peak at 16 ms poststimulus onset. Figure 2B shows the response of the same neuron to the entire set of vibration stimuli (black data points) measured as the average number of spikes during the 0- to 50-ms window poststimulus onset (black rectangle in Fig. 2A), as well as its spontaneous activity (gray data point) defined as the average number of spikes in a 50-ms window preceding stimulus onset (−10 to −60 ms, as indicated by the gray rectangle in Fig. 2A). As vibration amplitude increased, average spike count increased in the form of a sigmoid function ($r^2$ of the fit was >0.99).

Although the spike counts summated across 100 trials clearly represent the stimulus amplitude, sensory judgments usually are made from small numbers of trials or single contacts with external stimuli (von Heimendahl et al. 2007) rather than averages across many trials. In fact, the recorded neuron exhibited a high degree of trial-to-trial variation, which questions the extent to which the stimulus could be identified on the basis of a single trial observation. Figure 2C illustrates this variability in spike counts observed in the post- and prestimulus windows across 100 trials. We further quantified the trial-to-trial response variability using an ROC analysis (Fig. 2D). The area under the ROC curve for the detection performance of this neuron was 0.83, indicating a significant increase in the hit rate compared with the false alarm rate across the full range of response criteria.

Figure 3A shows the area under ROC to quantify the neuronal detection performance for the full range of stimulus amplitudes as well as pairwise discrimination performances across all pairs of stimuli. For the illustrated neuron, the absolute detection performance (i.e., when base amplitude equals zero) increased with stimulus amplitude. This neuron could not detect vibrations <6 μm amplitude, but its detection performance for all other amplitudes was significantly better than chance. Although 6 μm was not detectable against no stimulation (base amplitude of 0), the same increment was highly detectable when added to a base amplitude of 9 μm (the discrimination between 9 and 15 as indicated by the arrow in Fig. 3A). Further increases in the base amplitude resulted in a decline in the discrimination performance, pointing to the compressive nonlinearity in the response of the neuron at high stimulus amplitudes. This compressive nonlinearity is equivalent to Weber’s law. Figure 3B and C show the generality of the principal results obtained in a single neuron to the full set of recorded neurons. Across all neurons, at low base amplitudes, the discrimination performance improved with increasing the base amplitude.

The neuronal analysis up to here focused on firing rates in a 50-ms window poststimulus onset. This window was chosen based on the adaptation profiles observed in the neuronal...
PSTHs recorded here (see Fig. 2A for a typical response) and was consistent with previous observations of the spike count information in rat somatosensory cortex during decoding of vibrotactile stimuli (Arabzadeh et al. 2004, 2006). To further quantify the effect of the integration time window on the detection/discrimination performances, we repeated the preceding analysis on multiple integration time windows. The selection of the window lengths was based on the behavioral results obtained in experiment 2 (see Fig. 8 in the following text). From the analyses of behavioral reaction times the sensory integration time was estimated to be between 50 and 400 ms. Figure 4 illustrates the ROC values for integration time windows across this range (specifically 50, 100, 200, and 400 ms) presented separately for single neurons (Fig. 4A) and multiunit clusters (Fig. 4B). The neuronal detectability and discriminability indices followed the same trend.

**FIG. 3.** Neuronal detection/discrimination performance defined as the area under ROC. *A:* the ROC values for all pairwise stimulus comparisons supported by the example neuron illustrated in Fig. 2. Each line connects the stimulus pairs with similar amplitude difference. As indicates the peak-to-peak amplitude difference in each pair. Neuronal responses are defined as spike counts over the 50-ms time window poststimulus onset. ROC values averaged across 93 single units (*B*) and 142 multiunits (*C*) recorded in experiment 1. Error bars are the SE ROC values across recordings.

**FIG. 4.** Neuronal integration time window. To investigate the effect of neuronal integration time, we repeated the same analysis as in Fig. 3, with multiple windows of lengths 50, 100, 200, and 400 ms. Average ROC values for all pairwise stimulus comparisons across 93 single neurons (*A*) and 142 multiunit clusters (*B*) recorded in experiment 1. Error bars are the SE ROC values across integration time. Filled circles indicate pairwise comparisons that showed no significant effect of integration window (ANOVA, $P > 0.05$), whereas open circles indicate pairwise comparisons that showed a significant effect of integration time window (ANOVA, $P < 0.05$). The inset shows the average ROC values for each integration window for all pairwise comparisons at 9 μm peak-to-peak amplitude difference. Error bars in the inset correspond to the SE ROC values for the 100-ms integration time window. For clarity, error bars are shown for only one integration time window.
across multiple integration windows. Although at high base amplitudes longer integration times significantly improved discrimination performances (open circles in Fig. 4, A and B), the integration time window had no effect at lower base amplitudes (filled circles).

Figure 5 further quantifies the effect of base amplitude at the level of individual recordings, by comparing the detection performance of individual neurons (squares) and neuronal clusters (circles), with their corresponding discrimination performance at identical amplitude increments. Overall, 89% of recordings showed an improved discrimination performance compared with the detection performance. Moreover, this was true both for \( \frac{1}{2} \text{Th} \) versus \( \frac{3}{2} \text{Th} \) discrimination (marked in black) and for \( \text{Th} \) versus \( 2 \text{Th} \) discrimination (marked in gray). This figure demonstrates that at low base amplitudes the single neuron and neuronal clusters nearly always improve their performance when tested at discrimination compared with an absolute detection. A Wilcoxon signed-rank test on the difference in performance between detection and discrimination showed that across recordings discrimination was significantly better than detection (\( P < 0.001 \)).

Since in behavioral experiments involving whisker discrimination paradigms, the animal’s judgment of stimulus has been shown to closely correlate with the spike count per trial in barrel cortex (von Heimendahl et al. 2007), we expected that rats engaged in a vibration discrimination task would show a similar improved performance when presented with a low-amplitude discrimination task, compared with an absolute detection. Experiment 2 tested this hypothesis in four rats.

In the first stage of the experiment, rats were trained to perform a simple detection task (Fig. 1). Rats were trained to nose-poke into the stimulus aperture to receive a vibration stimulus on one of the two stimulus plates. Having identified the vibrating plate, the rat made a behavioral choice by turning toward the corresponding drinking spout to receive a sucrose reward. Figure 6 shows the psychometric detection performance of each of the four rats as a function of stimulus peak velocity. Despite the variability in sensitivity across subjects, all showed the characteristic sigmoid profile. Similar to the neurometric functions the empirical data were well fit by the cumulative Gaussian (the \( r^2 \) values of the fits were...
>0.96). The sigmoid curve allowed us to estimate a detection threshold separately for each rat. The detection threshold was defined as the stimulus amplitude corresponding to 60% correct performance (dashed lines in Fig. 6). The estimated thresholds were 10.7, 13.9, 16.2, and 20.9 μm and these values were used for the second stage of experiment 2.

Using a similar paradigm, the second stage of experiment 2 compared the detection and discrimination performances for each individual rat. At this stage of the experiment, on nose-poking into the aperture the rat either received a single vibration equal to the rat’s threshold amplitude obtained from experiment 1 on one side (i.e., detection task) or two vibrations with different amplitudes on either side of the snout (i.e., discrimination task). Figure 7A shows the discrimination and detection performances across all rats. The median discrimination performance at both low (i.e., half threshold) and intermediate (i.e., threshold) base amplitudes was higher than the median detection performance. Figure 7B shows the discrimination performances relative to the detection performance for each individual rat. A Wilcoxon signed-rank test on the reaction times showed that across rats discrimination was significantly better than detection (P < 0.01). This difference was significant for all four rats. Furthermore, across the three experimental trials (threshold detection and the two discrimination tasks), reaction times varied systematically with task difficulty (both in terms of the median and the interquartile range). This trend is better visualized in Fig. 8B, which demonstrates the median reaction times averaged across rats: reaction times decreased as the base amplitude increased.

Finally, Fig. 9A compares behavioral detection thresholds with those of single neurons and multiunit clusters obtained in experiment 1. Average thresholds were significantly lower for multiunit clusters than for single barrel neurons (P < 0.001). Multiunit clusters also outperformed rats by showing detection thresholds that were significantly lower than the behavioral thresholds (P < 0.01). However, single neurons’ detection sensitivity was not significantly different from the behavioral sensitivities obtained in four rats (P = 0.49). Although single neurons had a mean threshold of 14.1 μm (interquartile range: 8.7–18.8 μm), the average behavioral detection threshold was 15.4 μm. The most sensitive single neuron showed a detection threshold of 3.7 μm, which was lower than the detection threshold of the most sensitive rat (10.7 μm).

We further compared the detection and discrimination performances based on average values obtained from single neurons and neuronal clusters recorded in experiment 1, with the performance values obtained from the four rats in experiment 2. The analysis was limited to those recordings that met the following criteria: 1) a near-threshold (55–65%) performance...
at one of the used stimuli and 2) stimuli at ½Th, 1½Th, and 2Th were also present in the stimulus set. Thirty-five single units and 58 multiunit clusters met the inclusion criteria. Figure 9B illustrates the behavioral and neuronal detection/discrimination performances averaged separately across single neurons (light gray bars) as well as multiunit clusters (intermediate gray bars). Both for single neurons and for multiunit clusters, the average performances followed a trend that was remarkably similar to that of the behavioral performances (dark gray bars).

**DISCUSSION**

We trained rats in a vibrotactile task and compared their detection performance with their discrimination performance at various stimulus intensities, which we define as the product of amplitude (A) and frequency (f), in line with primate studies. Rats nose-poked into an aperture where they received a vibration on only one side (i.e., detection task) or two vibrations with different amplitudes on each side of the snout (i.e., discrimination task). To receive a reward, rats had to turn toward the side with the vibration (in the detection task) or the side with the higher-amplitude vibration (in the discrimination task). We also recorded neuronal activity from the barrel cortex of anesthetized rats while passively applying the same set of stimuli as used in the behavioral task. This allowed the comparison of the behavioral performances of rats engaged in the active detection/discrimination task with the neuronal findings recorded in anesthetized animals.

All neurons showed a characteristic sigmoid input–output function with an accelerating nonlinearity at low stimulus amplitudes (near detection threshold) and a compressive nonlinearity at high stimulus amplitudes. This is compatible with findings across sensory modalities where sensory processing is normally characterized by a transfer function, with a sigmoidal shape converting the physical stimulus into neural response (Laughlin 1989). In the presence of a constant noise level, a minimum perceptual difference is required for a perceiver to reliably discriminate between two stimulus intensities. Given the accelerating nonlinearity, as stimulus intensity increases, progressively smaller increments generate the minimum response difference that is needed to overcome the noise. Quantification of neuronal discrimination performance was consistent with this prediction: for near-threshold stimuli, the neuronal discrimination performance was significantly higher than the absolute detection performance. Similar to the neuronal results, the behavioral performance was better for the discrimination task compared with the detection task. Furthermore, the effect of base amplitude on behavioral sensitivity was remarkably similar to its effect on neuronal discriminability (Fig. 9B).

Previous psychophysical experiments across different modalities in human subjects indicated that adding a base intensity or “pedestal” to two stimuli can improve discriminability of those stimuli, a phenomenon known as the pedestal effect (Nachmias and Sansbury 1974; Solomon 2009). This is because at low stimulus levels progressively smaller stimulus increments are required to produce the smallest stimulus difference detectable by the subject: the just noticeable difference (JND). This gives the subject’s sensitivity a characteristic profile where the JND dips for low pedestals and is thus called the “dipper” function (Graham 1989; Nachmias and Kocher 1970). A recent experiment applied tactile sinusoidal vibrations to fingertips of human participants that performed a detection/discrimination task and measured their JND thresholds for vibrations of different amplitudes. Participants showed a clear dipper function with the lowest JND thresholds observed for pedestal values around threshold (Arabzadeh et al. 2008). This is consistent with our rat psychophysics findings reported in experiment 2 (Fig. 7).

Electrical microstimulation has been used as a powerful technique to establish a causal link between behavior and the activity of neuronal populations (Penfield and Rasmussen 1950). These studies have established the close link between behavior and neuronal activity in the somatosensory cortex (Romo et al. 1998, 2000) as well as multiple higher-order visual areas (Afraz et al. 2006; Britten and Van Wezel 1998; Salzman et al. 1992). These experiments demonstrated that the activation of a population of cortical neurons with similar tuning properties (e.g., face-selective neurons in the inferior temporal cortex or motion-selective neurons in the middle temporal area) by electrical microstimulation can generate a simple perceptual bias toward the response property of the selected population. In a two-interval vibration-discrimination task, Romo and colleagues (1998) trained the monkeys to compare a vibration with a train of current pulses injected into the primary somatosensory cortex. Animals reliably judged the frequency of the mechanical signal with respect to that of the electrical stimulation, even when both frequencies changed across trials. These findings imply that electrical stimulation could sum with the neuronal activity evoked by external sensory stimuli. This means that microstimulation could potentially act as a pedestal to enhance perceptual sensitivity by increasing the baseline activity of the neuronal population. In a recent experiment using transcranial magnetic stimulation (TMS) in human visual cortex, we found that the activation of...
visual cortical neurons by TMS can improve detection performance (Abrahamian et al., unpublished data). Future experiments may test this in animals implanted with microelectrodes, where more controlled activity can be introduced in a selective population of neurons.

The present results confirmed previous observations on sensory coding in barrel cortex. Neuronal firing rate increases with whisker velocity (Arabzadeh et al. 2003; Gibson and Welker 1983; Pinto et al. 2000). It is important to note that unlike a ramp-and-hold stimulus where amplitude and velocity can be varied independently of each other (i.e., velocity can be held constant and greater amplitude achieved by applying the ramp for a longer period), in a sinusoidal vibration greater amplitude directly leads to greater velocity. In the current experiment stimulus frequency was kept constant and only the amplitude varied across trials. Therefore both at the level of single neurons and behavior, velocity can be considered the critical stimulus feature. Velocity coding also underlies the representation of ecologically important sensory stimuli such as surface textures (Arabzadeh et al. 2005; Lottem and Azouz 2008). Rats move their whiskers back and forth in a controlled manner (Mitchinson et al. 2007) to collect information from their surrounding environment. As the whiskers contact different surfaces, rapid changes are observed in their movement trajectory; these high-velocity deflections are represented throughout the whisker sensory pathway with remarkable precision (Arabzadeh et al. 2005; Lottem and Azouz 2009; Petersen et al. 2008).

Our recordings revealed that, at least in the anesthetized condition, the average detection threshold of single neurons is comparable to the range of thresholds obtained in four rats (Fig. 9A). We know from anatomical studies that each barrel column contains nearly 8,500 neurons (De Kock et al. 2007). Given the high level of information carried by single cortical neurons in our recordings, and given the fact that the activity of a single cortical neuron can potentially affect the behavior (Houweling and Brecht 2008), one may question the contribution of the high number of cortical neurons to tactile perception. Our results showed a high degree of variability across neurons in their absolute detection threshold, their response saturation, and their response range. In general, individual neurons had a response range narrower than the range of amplitudes across which the rats were able to discriminate. It is therefore possible that barrel cortex uses a high number of neurons to broaden the range of stimuli that the rats could behaviorally process.

To verify this possibility, we calculated the discrimination/detection performance of the pooled population of neurons recorded across multiple sessions in experiment 1. The analysis demonstrated an errorless discrimination performance across all stimulus pairs (data not shown). This suggests that a population of the order of 100 neurons would be adequate for a perfect detection/discrimination across the range of stimuli used in the current study and thus support a higher level of sensitivity than what was achieved by the rats. Previous research has shown that the variability in neuronal response can be correlated across neurons recorded at the same time (Darian-Smith et al. 1973; Petersen et al. 2001; Snippe 1996). Such “noise correlation” might prevent the pooled response of neurons that are simultaneously recorded to reach the high levels of performance observed here. In this study, however, noise correlation could not be quantified because the neuronal activity was pooled across different sessions.

It is also important to note that, although experiments 1 and 2 used similar stimuli, they entail fundamentally different experimental conditions. In experiment 1, the rat was anesthetized and head-fixed and the vibration stimuli were always presented at a specific distance from the base of the whiskers while no whisking action was present. In contrast, in experiment 2, rats were free to whisk against the vibrating plates while keeping their head under the optical sensor in the middle of the nose-poke aperture. Although monitoring whiskers showed little whisking action during stimulus presentation and despite the fact that the behavioral setup minimized the trial-by-trial variability in the head position, there was still some residual variability present in the distance from snout to the vibrating plates and the angle of contact. These differences could potentially cause higher response variability in neurons and impair performance in the behaving rats. Despite the different experimental conditions under which behavioral and neuronal data were collected, detection and discriminations followed similar trends (Fig. 9B): the coexistence of the pedestal effect thus reflects the ubiquity of sigmoid response functions and rate coding at the level of single neurons, neuronal populations, and behavior.

Due to the difference in the conditions of experiments 1 and 2, one cannot draw a causal link between the rats’ choice behavior and the precise neuronal firing rates measured here. To link neural activity and perception, a further step in our approach is to record from barrel cortex neurons during the psychophysical detection and discrimination tasks. This can eliminate intersubject variability, the differences in the stimulus presentation, and the level of arousal between the two experimental conditions used here and thus allow a direct investigation of the contribution of single cortical neurons and neuronal ensembles to behavior.

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D I S C L O S U R E S

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R E F E R E N C E S


