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Whisker primary afferents encode temporal frequency of moving gratings

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Abstract

To investigate the encoding of behaviorally relevant stimuli in the rodent whisker–somatosensory system, we recorded responses to moving gratings from trigeminal ganglion neurons. This allowed us to quantify how spike patterns in these neurons encode behaviorally distinguishable tactile stimuli presented with the variability inherent in a freely moving whisker paradigm. Our stimulus set consisted of three grating plates with raised bars of the same thickness (275 μ m) having different spatial periods (1.0, 1.1, and 1.5 mm) swept rostro-caudally past the whiskers at velocities ranging from 50 to 330 mm/s. This resulted in 20 presentations each of nine different temporal frequencies (ranging from 50 to 220 Hz) for every grating plate. We found that despite the additional degrees of freedom introduced in this freely moving whisker paradigm, firing patterns from the majority (83%) of trigeminal ganglion neurons were statistically distinguishable, and corresponded to the temporal frequency of stimulation. The range of velocities (100–160 mm/s) that resulted in the most accurate and least variable representation of stimulus temporal frequency by trigeminal firing patterns closely corresponds to the whisking velocities employed by trained rats performing similar discrimination tasks. This suggests that, during naturally occurring whisking, individual primary afferents faithfully encode temporal frequency evoked by whisker contacts.

Keywords

Trigeminal; vibrissae; coding; spike timing; discrimination; rat

Introduction

Rats rapidly and accurately perform tactile discriminations using their whiskers and are capable of making certain discriminations using only a single whisker and following a single contact. When investigating potential coding mechanisms underlying this remarkable ability, it is important to fully characterize the initial neuronal representations of whisker inputs in response to behaviorally relevant stimuli. Perception can only arise through a transformation of the spike patterns already present at the whisker primary afferent level, as they provide the only input from the whiskers to the brain. Understanding the coding capacity of the primary afferents provides the initial limits on sensory information perception and processing.

In the whisker–barrel system, tactile stimuli are first represented in trigeminal ganglion primary afferent neurons. We have previously demonstrated that single spike trains from these neurons

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can accurately reconstruct complex whisker movements (Jones et al. 2004a). However, these results were obtained in a paradigm where individual whiskers were directly attached to the stimulating device and movements were precisely controlled. A whisker-attached paradigm does not allow for any of the variability reported in whisker movements that occur during tactile discrimination tasks. For example, rats have been shown to whisk at different velocities when discriminating different textures and whiskers have been shown to bend, cross over each other, stick to and slip on the stimulus, as well as resonate (Carvell and Simons 1990; Bermejo et al. 1998; Hartmann 2001; Harvey et al. 2001; Hartmann et al. 2003; Andermann et al. 2004; Moore 2004).

The majority of tactile processing studies in the whisker system have employed ramp-and-hold stimulation of single whiskers and measured neuronal responses to repeated presentations of these controlled deflections. This paradigm reveals many of the basic coding capabilities in this system, but does not reveal how natural whisker–stimulus interactions produce the neural representations that might underlie behavioral discrimination, where whisker movements are much more variable. Recent studies have begun to address this important issue: Szwed et al. (2003) used electrical stimulation of the muscles innervating the whisker pad to approximate whisking in an anesthetized animal, and studied how trigeminal neurons represented the location of a contact. Arabzadeh et al. (2005) used a piezoelectric stimulator to play back whisker–texture interactions recorded during a similar artificial whisking paradigm against sandpaper of different mean grain diameters, and studied how trigeminal neurons responded to these more realistic whisker movements.

The neural representations of tactile stimuli in primates have been studied by using psychophysical discrimination results to guide stimulus presentation in neurophysiological experiments (for example, see Mountcastle et al. 1967). In this approach, stimuli are chosen to test the spatial limits of behavioral discrimination, and are presented dynamically by sweeping the stimulus across the finger tip at the same velocities that the monkey uses when actively discriminating (Darian-Smith et al. 1980; Darian-Smith and Oke 1980; Morley et al. 1983; Yoshioka et al. 2001). This allows for the complex, natural interactions of sensory receptors with textured stimuli that occur in the behaving animal to be accounted for in the electrophysiological recording preparation.

In the current study, we adopted this powerful approach of stimulus presentation with independently varied spatial and temporal parameters to investigate potential neural substrates of roughness in the whisker system. Here we allowed the whiskers to create their own natural scene by interacting with different gratings moved across the whiskers at different velocities, chosen to correlate with those used in behavioral studies. Behavioral results from Carvell and Simons (1995) have demonstrated that rats can distinguish gratings with spatial periods of 1.0, 1.06, 1.125, 1.25, and 1.5 mm. We used this to guide the selection of stimulus spatial periods in this study. Harvey et al. (2001) reported that velocities at which rats whisk to determine the presence of an object are on the order of 50–300 mm/s; and Carvell and Simons (1990) report that the average protraction velocity rats use to sweep across discriminanda are approximately 120–180 mm/s. We used these ranges to determine the velocities at which the stimuli were presented. This approach allowed us to quantify the effects of both stimulus presentation velocity and the added degrees of whisker freedom on potential encoding mechanisms of psychophysically distinguishable stimuli.

Materials and methods

Data were obtained from eight female rats (Sprague–Dawley, Charles River, Wilmington, MA), weighing 250–350 g. Trigeminal ganglion recordings were made under urethane anesthesia (Jones et al. 2004a). Extracellular recordings of well-isolated single units were

obtained using platinum-in-quartz electrodes (2–4 M Ω). Spikes were discriminated off-line using amplitude threshold and principal component analysis (Offline Sorter, Plexon, Dallas, TX). The stimuli consisted of three different plates (1.7 mm hard durometer Dupont Cyrel plates, North American Graphics, Detroit, MI) consisting of raised bars of 275 μ m thickness, depth 1.0 mm, at 1.0, 1.1, and 1.5 mm spatial periods. The plate dimensions were 7.0 cm $\times$ 2.2 cm and consequently consisted of 70, 60, and 45 bars, respectively. These plates were positioned parallel to the rostro-caudal axis with bars running vertically, and swept rostro-caudally across the whisker pad using a servo-motor (Smart motor servo system, Animatics, Santa Clara, CA) on a linear actuator (single-axis Unislide system, Velmex, Bloomfield, NY). Due to constraints imposed by the stimulus apparatus we recorded only from neurons responding to the large caudal whiskers (whiskers 1–4 in rows A–E, as well as the straddlers α – δ). Stimulus plates were positioned normal to the principal whisker's resting position (approximately parallel to the rostro-caudal axis of the animal) at a distance that allowed contact at approximately 5 mm from the tip of the whisker (see supplemental material). The contact angle remained constant across all stimulus presentations and any vibrissa of the same length or longer simultaneously contacted the plate. Temporal frequencies of 50, 52.5, 55, 100, 105, 110, 200, 210, and 220 Hz were presented 20 times for each of the three plates. The linear velocities necessary to present these temporal frequencies (stimulus temporal frequency = velocity of stimulus/spatial period) were 50, 52.5, 55, 100, 105, 110, 200, 210, and 220 mm/s for the 1.0 mm plate; 55, 57.8, 60.5, 110, 115.5, 121, 220, 231, and 242 mm/s for the 1.1 mm plate; and 75, 78.7, 82.5, 150, 157.5, 165, 300, 315, and 330 mm/s for the 1.5 mm plate (Figure 1). Multitaper power spectra of individual spike trains elicited in response to a single rostro-caudal presentation of the stimulus plate were computed in Matlab [Thompson's multitaper algorithm, sampling rate: 10 kHz, Slepian sequence length: 50,000, time-bandwidth parameter: 3.5 (Thomson 1982)] for each spike train obtained in response to a single stimulus sweep in the rostro-caudal direction, and plotted as the mean $\pm$ standard deviation (SD). Inter-spike-interval (ISI) distributions were also created from data for rostro-caudal responses to all 20 trials in 0.1 ms bins. Box plots and the two-sample Kolmogorov–Smirnov test from the Matlab statistics package were used to compare responses to different temporal frequencies with a Bonferroni corrected significance level of 0.0056 ($p = 0.05$ corrected for nine group comparisons: 50/100, 50/200, 100/200, 50/52.5, 50/55, 100/105, 100/110, 200/210, 200/220 Hz temporal frequencies). Group comparisons were chosen to examine both gross differences in frequency ($\geq 100\%$, e.g., 50/100) and fine differences ($\leq 10\%$, e.g., 50/55) at each of the three base ranges (50, 100, and 200 Hz).

Results

We recorded responses from 22 well-isolated trigeminal ganglion neurons in response to the complete set of temporal frequencies (50, 52.5, 55, 100, 105, 110, 200, 210, and 220 Hz), created by moving a grating of raised bars of the same thickness rostro-caudally across the whisker pad at different velocities, and chosen to approximate gratings that rats can behaviorally discriminate (Carvell and Simons 1990; Harvey et al. 2001) (see Methods for further details). The stimulus plates were positioned such that the whiskers would contact the ridges at an approximately normal angle on the whisker's distal 5 mm. Visual inspection revealed that whisker movement was elicited both in response to initial contact with the plate and contact with each of the individual ridges in the grating. The whiskers contacted the stimulus plate, causing a large initial deflection, then swept over the ridges, causing fine whisker displacements, and finally detached from the plate. Whiskers freely bent, crossed, adhered to, or slipped on the stimulus plate, approximating the additional degrees of freedom observed in whisker–stimulus interactions seen in freely behaving rats.

Neurons predominantly responded to the grating ridges in a one-to-one manner, eliciting one spike per bar, regardless of temporal frequency or presentation velocity. We did not explicitly

categorize neurons as rapidly (RA) or slowly adapting (SA), but likely recorded from both classes of neuron as in previous studies. All neurons responded similarly to the high frequency contacts elicited by these series of gratings. Figure 2A depicts these spike trains for an individual neuron, showing rasters elicited in response to each of the temporal frequencies for sweeps in the rostral-caudal direction. We found that 18/22 (81%) neurons responded in a similar fashion, spiking faithfully to ridges at all temporal frequencies. The four neurons that did not fire reliably to stimulus ridges are addressed in the Discussion, and the 18 responders are further considered in the analyses presented below.

We asked whether individual neurons could, in response to a single sweep across the stimulus plate, reliably distinguish this range of behaviorally relevant stimuli. To test the fidelity of these responses for each neuron, we computed multitaper power spectra of individual spike trains for each of 20 rostral-caudal sweeps across the grating. Figure 2B illustrates that the peaks in these spectra (mean $\pm$ SD) are visibly distinguishable and correspond to the approximate temporal frequency. Small deviations from the expected frequency were seen in the power spectra from most neurons, with no correlation to stimulus parameters. These small shifts are most likely due to windowing effects of the spectral estimation procedures rather than properties of the neuronal response.

Temporal frequency is linearly encoded and distinguishable

To statistically quantify how distinguishable the elicited spike trains were for each frequency, we computed ISI (0.1 ms bins) distributions from each neuron's responses to all of the temporal frequencies. Figure 3A (bottom) depicts three such distributions corresponding to the 100, 105, and 110 Hz stimuli for an individual neuron. We then tested whether these ISI distributions were significantly different from each other in a series of comparisons (Bonferroni corrected Kolmogorov-Smirnov tests). For this example, the distributions were statistically different ($p = 0.005$) for the 100 vs. 105 Hz and for the 100 vs. 110 Hz comparisons. The majority of neurons produced statistically different responses for all temporal frequency comparisons. Table I reports the number of neurons that had statistically different ISI distributions for each of the comparisons listed (p 's ≤ 0.0056). For example, ISI distributions from all neurons were significantly distinguishable for the large difference between the 50 and 200 Hz temporal frequencies, as well as the much smaller (5%) difference between the 100 and 105 Hz gratings.

Stimuli in the 100 Hz range produced the most accurate neural response discrimination, having ISI distributions that were the least variable (Figure 4) as evidenced by their low coefficient of variation [CV = $24.1 \pm 3.1\%$ (50 Hz range), $4.9 \pm 0.1\%$ (100 Hz range), $52.4 \pm 3.2\%$ (200 Hz range)] and small standard deviation [SD = 4.6 ± 0.5 ms (50 Hz range), 0.5 ± 0.0 ms (100 Hz range), 3.5 ± 0.3 ms (200 Hz range)]. The majority (>83%) of neurons produced significantly different ISI distributions in response to all stimuli tested (Table I). In a small number of neurons, the ISI distributions were indistinguishable for a subset of the comparisons, particularly at the 50 Hz range (50/52.5 Hz comparison was not significantly different for 3/18 neurons) and the 200 Hz range (200/210 Hz comparison was not significantly different for 2/18 neurons). The majority of comparisons in the 100 Hz range were statistically distinguishable: for the 100/105 Hz comparison—18/18 neurons, 100% of ISI distributions were distinguishable; for the 100/110 Hz comparison—17/18, 94% of ISI distributions were distinguishable (see Table I).

Temporal frequency vs. absolute velocity

This stimulus protocol did not explicitly account for the possibility that neurons were representing the absolute velocities of the moving stimulus plates rather than the temporal frequency of the raised ridges. To dissociate this confound, we used plates with different spatial periods (1.0, 1.1, or 1.5 mm) and moved them at different velocities to stimulate the whiskers

with the same temporal frequencies (see Figure 1). This allowed us to determine if spike trains were responding to temporal frequencies in a velocity dependent manner. Figure 3B, C depicts power spectra and ISI distributions for the same neuron shown in A, but in response to temporal frequencies created using different gratings and motor velocities. The peaks corresponded to the appropriate temporal frequency regardless of spatial period or motor velocity (Figure 2B—blue trace: 105 Hz peak in response to 1.1 mm plate presented at 115 mm/s; green trace: 110 Hz peak in response to 1.5 mm plate presented at 165 mm/s). Further, the ISI distributions were not statistically different when the same temporal frequency was presented in different combinations. Figure 3C illustrates this for the 100 Hz temporal frequency (red trace: created with 1.0 mm plate presented at 100 mm/s; blue trace: 1.1 mm plate presented at 110 mm/s; green trace: 1.5 mm plate presented at 150 mm/s). Note that each plate was of the same total length, and therefore contained a different number of ridges (1.0 mm plate—70 ridges; 1.1 mm plate—60 ridges; 1.5 mm plate—45 ridges). This resulted in fewer spikes per plate (number of spikes is proportional to number of ridges). As a result, there was reduced power in the peaks of the spectra for the stimulus plates with larger spatial periods, and a smaller number of counts in the respective ISI distributions. Analyzing responses from all neurons to these different combinations, we found that it is the temporal frequency, and not the absolute stimulus velocity, that is linearly represented in the spike trains. This is evidenced in both the power spectra and ISI distributions, each corresponding to the temporal frequency regardless of stimulus spatial period and presentation velocity (Figure 3B, C).

Band-pass response properties

Whereas trigeminal neurons were typically entrained by stimuli throughout the 50–220 Hz range, we found one neuron that responded selectively to the 110 Hz stimulus presentation. This unit fired in response to the initial contact of the plate, but did not fire reliably to individual ridges for all other frequencies of stimulation (Figure 5A, B). This unique response is most likely due to band-pass properties of the whisker and/or the neuron rather than an artifact of the stimulation paradigm, because a second neuron recorded simultaneously responded with reliably timed spikes to all frequencies (Figure 5C). If the electrode moved or whisker contact with the stimulus plate was changed at this frequency alone, we would expect to see some change in the firing pattern of this second unit as well.

Discussion

Previous studies have demonstrated that firing patterns of trigeminal ganglion neurons can phase-lock to high frequency stimuli (Gottschaldt and Vahle-Hinz 1981; Gibson and Welker 1983a, 1983b; Lichtenstein et al. 1990; Shoykhet et al. 2000; Deschênes et al. 2003; Deschênes 2004; Jones et al. 2004a, 2004b; Timofeeva et al. 2004). In these studies, individual whiskers were attached to a stimulating device and stimulated in isolation with precisely reproducible movements. To more closely mimic active sensing in this system, Szwed et al. (2003) used the free-whisker “artificial whisking” paradigm introduced by Zucker and Welker (1969), in which whisker protractions are elicited by electrically stimulating the facial nerve. Szwed et al. (2003) reported that when whiskers are artificially protracted at 5–8 Hz, trigeminal neurons respond with temporal precision to both whisking in air and to whisker contacts. Arabzadeh et al. (2005) recorded similar artificially induced whisker movements across different textures and then “played back” these natural vibrations using a piezoelectric device attached to the whisker. Trigeminal recordings in this paradigm again revealed precise temporal patterns of spikes. In the present study, we emulated the natural whisker movements that occur during whisker contacts with textured surfaces by moving gratings rostro-caudally across the whisker pad, allowing the whiskers to freely interact with the stimuli and create their own complex natural scene. We found that despite the additional degrees of freedom introduced in this free-whisker paradigm, trigeminal ganglion neurons accurately represented a range of behaviorally

relevant stimuli. Spike trains from single neurons recorded in response to a single rostro-caudal presentation corresponded to the temporal frequency of whisker contact with individual ridges, evidenced by both their power spectra and their ISI distributions. The majority of neurons accurately represented all temporal frequencies tested in their firing patterns (Table I). However, spike trains elicited in response to the 100 Hz temporal frequency range were the most distinguishable at the individual neuron level (Table I) and the least variable at the population level (Figure 4), with CVs of only 5% and a standard deviation of 0.5 ms as reported above. This suggests that rats may be able to perform tactile discrimination tasks best when whisking at velocities in this range. Interestingly, contact velocities in this temporal frequency range (100–165 mm/s, Figure 1) closely correspond to those used by successfully trained rats when performing similar discrimination tasks (122–182 mm/s, Carvell and Simons 1990; Harvey et al. 2001), and to finger tip velocities that human subjects use when making similar grating discriminations (160 mm/s, Morley et al. 1983).

More variable responses at low frequencies

The subset of neurons (3/18, 17%) that did not elicit firing patterns that were statistically distinguishable in response to stimuli in the 50 Hz range exhibited greater response variability in the timing of each spike. This resulted in broader ISI distributions that were not statistically distinguishable, but nevertheless had medians that correspond to the stimulus temporal frequency. We previously found similar variability in spike timing elicited in response to low frequency (<25 Hz) white-noise stimuli (Jones et al. 2004a, 2004b). Shoykhet et al. (2000) also demonstrated that response latencies are more variable for low velocity whisker deflections. In all these studies, the same neurons responded with low spike timing variability when stimulated at higher frequencies [this study: 100–200 Hz range, previous white-noise study: <125–625 Hz stimuli (Jones et al. 2004a)]. It appears that trigeminal precision is correlated with the frequency content of the presented stimulus. Spike timing precision increases to less than 1/10 of a millisecond as stimulus frequency increases up to 300 Hz. This effect may be the result of increased variability in whisker movements at slower velocities rather than a property of the transduction or spike generating mechanism. This low range of frequencies (50–55 Hz) corresponds to contact velocities (50–82.5 mm/s) that are slower than the whisking velocities rats are reported to use during tactile discrimination tasks (~122–182 mm/s) (Carvell and Simons 1990; Harvey et al. 2001). Rats may optimize their performance on discrimination tasks by whisking at higher velocities to produce less variable spike trains, and hence more easily distinguishable spike timing.

Non-responders

A sub-population of trigeminal ganglion neurons (4/22, 18%) did not respond to the grating moving rostro-caudally (except for initial contact with the plate), and so were excluded from the detailed analysis above. These neurons responded transiently to the initial contact of the stimulus plate, not to individual ridges on the plate. This transient response was most likely due to the higher amplitude whisker movement produced by initial contact with the plate, much greater than the displacement produced by contact with the individual ridges. This finding is consistent with the broad range of amplitude thresholds previously reported in trigeminal ganglion neurons (Gibson and Welker 1983a). In addition, these neurons may have had an angular preference (Gibson and Welker 1983b; Lichtenstein et al. 1990) opposite to that of our stimulus deflections, such that whisker deflections in this non-preferred direction would not elicit spikes.

Resonance

Included in this “non-responder” group was the neuron that fired exclusively in response to stimulation at 110 Hz, and not to stimuli at lower or higher frequencies (Figure 5A). This band-

pass property may reflect the resonance frequency of the whisker, stimulation at which results in a nonlinear amplification of the whisker's displacement (Hartmann et al. 2003; Neimark et al. 2003; Moore 2004). We cannot definitively conclude that these results are due to resonance, as we did not measure whisker displacements in this study or calculate the effective length of each whisker in contact with the plate. However, such resonance effects have been demonstrated in trigeminal ganglion neuron firing patterns (Andermann et al. 2004) at the 110 Hz frequency. The majority (18/22) of the neurons were entrained by stimuli spanning the entire bandwidth tested, and therefore did not display such band-pass properties, hence we did not find any correlations between firing properties of the neurons and principal whisker. The finding that these neurons did not exhibit resonance-related responses may reflect the fact that their firing thresholds were saturated by the amplitude of the stimuli, the fact that we did not explore the entire parameter space for evoking resonance in their whiskers, or the fact that contact position was not precisely controlled in these experiments. Stimulating along the distal end of the whisker rather than specifically at the tip could result in effectively "shortening" the whisker and hence increasing its resonance frequency beyond the frequencies tested in this study (Ritt et al. 2004).

Sensory-motor integration

The results demonstrate that trigeminal neurons respond to the apparent temporal frequency of the stimulus, which is dependent on both the spatial period of the stimulus and on presentation velocity (Figures 1–3). Similar results were found in the responses of monkey primary afferent fibers to moving gratings (Darian-Smith and Oke 1980). This suggests that for the rat to make accurate comparisons between stimuli, it must either whisk at the same velocity across each stimulus, or encode the velocity of each whisk in addition to encoding the temporal frequency of whisker interactions with the stimuli. There is evidence that when successfully performing tactile discriminations of different textures, rats adjust the velocity of their whisks according to the specific stimuli they are palpating (Carvell and Simons 1995; Brecht et al. 1997). This implies that whisking velocity does not remain constant across sampling of different stimuli, but is itself a dynamic variable. Hence the specific velocity of each whisk may need to be simultaneously encoded along with the temporal frequency information represented in the temporal pattern of individual trigeminal spike trains.

Gibson and Welker (1983a, 1983b) proposed a population-recruitment code to encode the absolute velocity of a stimulus. As stimulus velocity is increased, more neurons are pushed above their specific velocity thresholds, such that the magnitude of the total population response will systematically increase over the range of velocity thresholds displayed by trigeminal ganglion neurons (over three orders of magnitude, Gibson and Welker 1983a). Shoykhet et al. (2000) elaborated on this coding scheme by demonstrating that the velocity of whisker deflections is unambiguously encoded by the initial firing rate of the trigeminal neuronal population. Furthermore, two additional mechanisms for representing whisking velocity have been suggested: (1) a separate population of sensory afferents responding only to whisking in air could reliably encode the whisking velocity (Szwed et al. 2003); and (2) whisking velocity encoded in descending motor commands may be compared with ascending sensory information through sensorimotor loops (Ahissar and Kleinfeld 2003). Specifically where and how this critical task is performed in the whisker system remains to be determined.

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Figure 1.

Parameters used to present stimuli of different temporal frequencies. The three stimulus plates consisted of raised bars of 275 μm width with three different spatial periods of 1.0 mm (black circles), 1.1 mm (grey circles), and 1.5 mm (white circles). These were moved against the whiskers at different velocities (range: 50–330 mm/s, Y-axis) to create the nine temporal frequencies (range: 50–220 Hz, X-axis) that comprise this stimulus set. Inset: spatial period of ridges (shown to scale) for each of the three stimulus plates.

Figure 2.

Reliably timed spikes accurately represent a broad range of temporal frequencies. (A) 250 ms segments from sample rasters, aligned to first spike. Three random rasters (out of 20) from a single neuron's responses to each of nine temporal frequencies are depicted from responses to the 1.0 mm plate. (B) Multitaper power spectra [mean (thick lines) $\pm$ SD (thin lines)] computed from the same neuron depicted in A for each of 20 individual trials recorded in response to the nine temporal frequencies. Top panel: 50 Hz cluster; middle: 100 Hz; bottom: 200 Hz. The peaks are distinguishable within each range and correspond to the temporal frequency of each presented stimulus.

Figure 3.

Temporal frequency, not stimulus velocity, is linearly represented and statistically distinguishable over a range of gratings. (A) Top panel depicts multitaper spectra (mean $\pm$ SD) computed from a single neuron's response to 20 presentations each of the temporal frequencies of 100, 105, and 110 Hz created using the 1.0 mm plate. Bottom panel: corresponding inter-spike interval (ISI) histograms computed from responses to all 20 trials in 0.1 ms bins. (B) Data presented as in A, obtained from the same neuron in response to the temporal frequencies of 100, 105, and 110 Hz obtained using three different plates (1.0, 1.1, and 1.5 mm spatial periods). Peaks in both the power spectra and ISI distributions correspond to the temporal frequency as in A. (C) Data presented as in A, obtained from the same neuron in response to the same temporal frequency (100 Hz), obtained using three different plates. Again, peaks are centered on the temporal frequency, and do not correspond to the different motor velocities.

Figure 4.

Population medians approximate stimulus intervals with ms precision, and are both most accurate and least variable in the 100 Hz range. Notched box and whisker plots (McGill et al. 1978) depict the distribution of medians among ISI distributions for each neuron. Lines in each box depict the lower quartile, median, and upper quartile values. The whiskers extending from each end depict data within 1.5 times the inter-quartile range depicted by the box. Notches on each box provide an estimate of 95% confidence intervals about the median. Left panel: comparison of population data for the 50, 52.5, and 55 Hz temporal frequencies for all neurons ($n = 18$). Middle panel: 100, 105, 110 Hz ($n = 18$). Right panel: 200, 210, 220 Hz ($n = 18$). The asterisks depict the temporal frequency of the stimulus, demonstrating that the population medians are a close approximation of the ideal value. Note different scales on the Y-axis. Population variability was lowest for the 100 Hz range as demonstrated by the small spread of the whiskers in the 100 Hz range compared to that of the 50 and 200 Hz ranges.

Figure 5.

Band-pass responses of a trigeminal neuron. (A) Sample rasters for responses to 50, 100, 105, 110, and 200 Hz stimulation. This neuron responded reproducibly only to the 110 Hz stimulation. (B) Corresponding power spectra (mean $\pm$ SD) for the temporal frequencies in A. Note significant peak evident only in response to 110 Hz stimulation. (C, D) Rasters and power spectra from a second unit recorded at the same time as the unit in A, serving as a control for stimulus presentation. Note responses to all frequencies of stimulation.

Table I

Percentage of neurons with distinguishable firing patterns for each temporal frequency comparison.

Comparison (Hz)	Number of neurons	Percentage (%)
50/200	18/18	100
100/105	18/18	100
50/100	17/18	94
100/110	17/18	94
200/220	17/18	94
100/200	16/18	89
200/210	16/18	89
50/52	15/18	83
50/55	15/18	83

Firing patterns from the majority of individual neurons are statistically distinguishable for differences in temporal frequency as low as 5%. Of the 18 neurons that responded to the gratings in the rostral-caudal direction, 83% had distinguishable inter-spike interval (ISI) distributions at all temporal frequencies. Data presented as number and percentage of neurons that had statistically distinguishable ISI distributions for each of the comparisons (Bonferroni corrected Kolmogorov–Smirnov p 's < 0.0056).