

Angular Tuning and Velocity Sensitivity in Different Neuron Classes Within Layer 4 of Rat Barrel Cortex

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Lee, Soo-Hyun and Daniel J. Simons. Angular tuning and velocity sensitivity in different neuron classes within layer 4 of rat barrel cortex. *J Neurophysiol* 91: 223–229, 2004. First published September 24, 2003; 10.1152/jn.00541.2003. Local circuitry within layer IV whisker-related barrels is preferentially sensitive to thalamic population firing synchrony, and neurons respond most vigorously to stimuli, such as high-velocity whisker deflections, that evoke it. Field potential recordings suggest that thalamic barreloid neurons having similar angular preferences fire synchronously. To examine whether angular tuning of cortical neurons might also be affected by thalamic firing synchrony, we characterized responses of layer IV units to whisker deflections that varied in angular direction and velocity. Barrel regular-spoke units (RSUs) became more tuned for deflection angle with slower whisker movements. Deflection amplitude had no effect. Barrel fast-spoke units (FSUs) were poorly tuned for deflection angle, and their responses remained constant with different deflection velocity. The dependence of angular tuning on deflection velocity among barrel RSUs appears to reflect the same underlying response dynamics that determine their velocity sensitivity and receptive field focus. Unexpectedly, septal RSUs and FSUs are largely similar to their barrel counterparts despite available evidence suggesting that they receive different afferent inputs and are embedded within different local circuits.

INTRODUCTION

A striking feature of neurons in the whisker-to-barrel pathway is that they respond differently depending on the angular direction in which the whisker is displaced. At each subcortical station along the afferent pathway, neurons respond to a whisker movement with transient responses composed of different numbers of spikes depending on the angular direction of the whisker's displacement and how it corresponds to the cell's preferred deflection angle (Bruno and Simons 2002; Minnerly and Simons 2003; Shoykhet et al. 2000; Simons and Carvell 1989). In layer IV barrels of the somatosensory cortex, circuitry within individual whisker-related barrels renders the firing of regular spike units (RSUs), presumed excitatory cells, insensitive to the number of spikes in the incoming thalamic response but highly responsive to the initial firing synchrony of neuron populations in the corresponding thalamic barreloid (Pinto et al. 2003). For example, barreloid neurons, on average, fire more spikes with either faster or larger whisker movements. Deflection velocity, but not amplitude, is robustly encoded by the initial firing synchrony within the barreloid (Pinto et al. 2000; Temereanca and Simons 2003). Because barrel circuitry is sensitive to this code, the strength of RSU responses depends on deflection velocity not amplitude (Pinto et

al. 2000; see also Ito and Kato 2002). For similar reasons, barrel RSUs respond more robustly to principal (PW) versus adjacent (AW) whisker deflections, the former evoking more synchronous thalamic firing (see Pinto et al. 2003). These findings raise the issue of whether angular tuning is similarly encoded and decoded with the barreloid-to-barrel circuit.

A recent study showed that, in thalamic barreloids, the magnitude of local field potentials (LFPs), a measure of local population activity, varies with the direction of whisker deflection (Temereanca and Simons 2003). This finding suggests that thalamic barreloid neurons are clustered with respect to their angular tuning preferences and that they may encode the direction of whisker movement by synchronous activity during their initial responses. Specifically, small subpopulations of nearby thalamocortical neurons may fire more synchronously with each other when the whisker is deflected in their common, preferred angle.

Here we exploit the velocity sensitivity of the thalamocortical circuit to investigate the possible dependence of barrel angular tuning on thalamic initial firing synchrony. We use simple ramp-and-hold deflections varying in onset velocity and angular direction to examine how angular tuning of barrel and trigeminal ganglion cells is affected by deflection velocity. Neither velocity nor angular sensitivity has been investigated in behavioral studies, and thus the behavioral relevance of these stimulus features is unclear. Nevertheless, whisker deflections varying along these stimulus dimensions have been shown to be useful for probing functional circuitry in this system. We report that the angular tuning of barrel RSUs is affected by deflection velocity but not amplitude, with slower movements evoking responses that, although less vigorous, are more selective for the angular direction of the movement. The angular response properties of RSUs thus may reflect the same local circuit dynamics that underlie their more robust responses to the onset of high (vs. low) velocity PW (vs. AW) deflections. Together with data from trigeminal ganglion cells, results indicate that angular sensitivity, like deflection velocity, is encoded throughout the whisker-to-barrel pathway by processes acting at short latency and millisecond time scales.

METHODS

Preparation

Thirteen adult female rats weighing 250–350 g (Sprague-Dawley strain, Hilltop Labs, Scottsdale, PA) were used in this study. Details of the surgical procedure have been presented elsewhere (Bruno and

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Simons 2002; Simons and Carvell 1989). Briefly, animals were anesthetized with 1.5–2.0% halothane during surgical preparation. A small area (~0.5 mm²) of skull and dura overlying the barrel cortex was removed to allow for single-unit recordings. Core body temperature was maintained at 37°C by a servo-controlled heating blanket (Harvard Apparatus, Cambridge, MA). For neuronal recordings, halothane was discontinued, and the rat was subsequently maintained in a lightly narcotized and sedated state by intravenous infusion of fentanyl (~10 µg · kg⁻¹ · h⁻¹). Rats were immobilized with pancuronium bromide (1.6 mg · kg⁻¹ · h⁻¹) and artificially respired (~90 breaths/min) using a positive pressure respirator. The condition of the rat was monitored throughout the experiment by a computer program that continually assessed electroencephalogram, mean arterial pressure, arterial pulse rate, and the tracheal airway pressure waveform. Experiments were terminated if any of the preceding indicators could not be maintained within normal physiological ranges. At the termination of the recording session, rats were deeply anesthetized with pentobarbital sodium (Nembutal, 100 mg/kg iv) and perfused transcardially for cytochrome oxidase histochemistry.

Electrophysiology

For cortical recordings, extracellular single-unit recordings were obtained using double-barrel glass micropipettes (Simons and Land 1987). One barrel was filled with 3 M NaCl (~1 µm tip diameter; 5–10 MOhms impedance at 135 Hz) and was used for unit recordings. The other barrel was filled with 10% wt/vol horseradish peroxidase (HRP) in 0.5 M Tris-HCl to mark recording sites and/or the end of recording tracks. In later experiments, we used 90% quartz-insulated platinum and 10% tungsten core fibers (Uwe Thomas Recording, Giessen, Germany) pulled and ground to an impedance of 5–9 MS at 1,000 Hz. When ground to a pencil-like point, the metal-in-quartz electrodes yield equivalent, good isolation of both regular-spike and fast-spike units (see following text). Electrodes were slowly advanced perpendicular to the pial surface using a hydraulic microdrive (David Kopf Instruments, Tujunga, CA). Signals were amplified by conventional means and band-pass-filtered 300–10,000 Hz. Analog signals were digitized at 32 kHz using a 1-GHz PC equipped with a PCI-MIO-16E-1 board (National Instruments, Austin, TX). Data-acquisition software was written in LabView (National Instruments). Spike waveforms exceeding amplitude thresholds were parsed from the continuous signals, displayed, and stored to disk along with the time stamp and trial information. Waveforms were inspected off-line, as necessary, to assure good spike isolation. Spike occurrences were saved separately at a resolution of 100 µs. Units were classified as regular-spike units (RSUs) or fast-spike units (FSUs) on the basis of their waveform (see Bruno and Simons 2002; Simons 1978).

The right hemisphere was sectioned tangential to the pial surface overlying the barrel field. Alternate sections were processed for either HRP or cytochrome oxidase (CO) histochemistry (Simons and Land 1987). During the recording session, electrode tracks were noted on sketches of the surface vasculature and subsequently identified in serial tangential sections beginning at the pial surface and followed through to layer IV. HRP spots, made through the glass micropipettes, or lesions, made through the metal-in-quartz electrodes, were used to verify the depth of layer IV, which in our hands is consistently found at microdrive readings of 750–950 µm. Data are reported only from histologically identified electrode tracks. Barrel centers are defined by the presence of dark CO-staining, whereas the less densely CO-reactive areas surrounding each barrel consists of both intervening “septa” and barrel sides (Land and Simons 1985). Recordings were considered to be in the inter-barrel septum if the electrode track passed through the CO-sparse region between barrels. Septal recordings could, therefore, include some neurons in the barrel side. In most cases, the electrode tracks were displaced from the edge of the CO-rich barrel center by at least several tens of micrometers. A few

tracks passed close to the barrel/septum border, and in these cases, recorded units were discarded from the analyses.

Three animals were used for trigeminal ganglion (NVg) recordings (see Shoykhet et al. 2000). Surgical and maintenance procedures were identical to those employed for cortical recordings. Recordings were obtained with insulated stainless steel microelectrode with impedances of 4–6 MOhms at 1 kHz (Frederick Haer, Brunswick, ME). A craniotomy was made in the skull over the left trigeminal ganglion, and electrodes were lowered into it from the dorsal surface of the brain. Brains were not processed for histologic assessment.

Whisker stimulation and data analysis

A hand-held probe was used to identify the whisker most effective at evoking activity in an isolated cell, i.e., the principal whisker (PW). This whisker was deflected using a multi-angle piezoelectric stimulator (Simons 1983) controlled by the acquisition computer. The stimulator was attached to the whisker ~10 mm from the base of the hair, which was deflected using ramp-and-hold movements as described previously (Simons and Carvell 1989). Whiskers were deflected randomly in each of eight cardinal directions in 45° increments relative to the horizontal alignment of the whisker rows. Ten blocks of such stimuli were delivered for a total of 80 trials. For the first set of experiments, three deflections were used: 1-mm displacements with ramp velocity of 40 and 200 mm/s and 0.5-mm displacements at 120 mm/s. Stimulus waveforms were filtered to minimize mechanical ringing, and the piezoelectric bimorphs are also nonlinear (see Simons 1983). Onset velocity was therefore measured as the slope of the linear part of the deflection ramp that corresponds to peak velocity. Stimulator movement was calibrated off-line using a photodiode circuit. The second set of experiments employed two additional stimuli, 1-mm displacements having onset velocities of 10 and 20 mm/s. Peak velocities of the five deflections were 204, 127, 45, 22, and 13 mm/s, respectively, and average velocities were 108, 73, 40, 20, and 12 mm/s. Peak velocity is the highest velocity during the onset movement; average velocity is calculated across the entire movement phase of the stimulus.

Spike data were accumulated into peristimulus time histograms (PSTHs) having 1-ms bins. Unit responses were quantified by measuring the average number of spikes per stimulus occurring during the period immediately after the onset of whisker deflection that includes the transient response. Response windows varied from 30 to 80 ms, depending on the velocity of the movement; slower velocities are associated with more prolonged responses. Population PSTHs were used at the outset of data analysis to identify the time window that contained the entire transient response. For a given velocity, the same time window was used for all cells. For velocities of 40–200 mm/s, the analysis window was 30 ms. For 10- and 20-mm/s deflections, response windows were 50 and 80 ms, respectively, reflecting the more prolonged responses with slower whisker deflections. Angular tuning was quantified as the ratio of the response to the maximally effective deflection angle to the average response over all eight angles. We also computed mean vector angles and magnitudes based on the responses to the eight different deflections. Only responses to stimulus onset were analyzed because responses to stimulus offset are weak in RSUs and depend on stimulus parameters other than just deflection angle. Also, responses of most layer IV units are distinctly phasic, responding transiently and briefly to stimulus onsets and offsets (see Fig. 1); the small proportion of units that fire during maintained whisker deflection do so with low firing rates (see Simons and Carvell 1989).

Many NVg neurons fire during sustained whisker deflections. We identified slowly adapting cells using a *t*-test to compare prestimulus firing with that evoked during the stimulus plateau at the deflection angle producing the largest plateau response (see Lichtenstein et al. 1990). Cells with statistically significant plateau firing were classified as slowly adapting (SA) and all others, by default, as rapidly adapting

(RA). Using these criteria, most NVg cells (~75%) are found to be SA (e.g., Lichtenstein et al. 1990; Minnery and Simons 2003). The present sample contained 55% RA and 45% SA due to an attempt to sample roughly equal proportions.

RESULTS

Effects of velocity on angular tuning in layer IV neurons of barrel cortex

Figure 1 illustrates the effects of whisker deflection velocity on the angular tuning properties of a barrel RSU. In response to 200-mm/s deflections (A), the unit discharged an average of 1.14 spikes/stimulus onset and fired most robustly to deflections in the caudal/dorsal direction. The tuning ratio, defined as the maximal angle response divided by the average response across all eight directions, was 1.49. With lower velocity

movement (40 mm/s, B), the cell maintained its overall preference for caudal deflections, but firing rates at all angles decreased (0.76 spikes/stimulus), with those in nonpreferred directions decreasing disproportionately more. The tuning ratio increased to 1.97. Responses to stimulus offsets were also disproportionately reduced.

Data were similarly obtained for 44 RSUs and 8 FSUs recorded in CO-rich barrel centers. Although not the focus of the present experiment, data are also reported from 25 RSUs and 9 FSUs found, on histological reconstruction, to be located in septa. Figure 2A summarizes their spontaneous activities and maximum angle responses for 200-mm/s deflections. Consistent with previous studies (see DISCUSSION), barrel FSUs fire at higher rates than barrel RSUs; differences are similar but less pronounced for septal neurons, where FSU firing rates are lower than those of barrel FSUs. Linear regression showed that evoked firing rates of barrel and septal RSUs increase with faster whisker deflections over the range of 40–200 mm/s ($P < 0.05$), but the firing of FSUs in both regions was unaffected by velocity. Even at the lowest deflection velocity, FSUs, both barrel and septal, were less tuned for deflection angle than their corresponding RSUs (ANOVA, $P < 0.05$).

With decreasing deflection velocity, barrel RSUs showed a small but significant increase in angular tuning (Fig. 2C), as indicated by a higher tuning ratio ($R^2 = 0.04$, $P = 0.02$). Mean vector magnitudes were also smaller at 40 versus 200 mm/s (paired t -test, $P < 0.05$). The angular tuning of septal RSUs increased at trend level. The angular tuning of FSUs was unaffected by deflection velocity. However, the tuning ratio of barrel FSUs slightly increased with lower deflection velocities, and values at 40 mm/s were larger than those at 200 mm/s (paired t -test, $P = 0.04$). Average polar plots in all cases were circular, indicating that all angles were represented equally and that, within the population, velocity affected all directions equivalently. Similar results were obtained when spontaneous firing rates were subtracted from evoked spike counts, with the exception that septal RSUs now showed a significant decrease in tuning at 200 versus 40 mm/s (paired t -test, $P = 0.028$).

With deflection velocities between 40 and 200 mm/s, changes in the angular tuning of RSUs, though statistically significant, were modest. We therefore performed a second set of experiments incorporating lower velocities (10–200 mm/s). Data were obtained only from barrel RSUs ($n = 28$). As shown in Fig. 3A, evoked responses increased with increasing deflection velocity while angular tuning decreased nonlinearly. For each unit, tuning ratios were linearly regressed with \log_{10} velocity. Although only five cells had statistically significant regression values, all but four units showed an inverse relationship between angular tuning and velocity (Fig. 3B). Consistent with the effects of velocity on both firing rates and angular tuning, mean vector magnitudes were significantly smaller for the 200- than 10-mm/s deflections (0.37 ± 0.02 vs. 0.93 ± 0.04 , paired t -test $P < 0.005$). Furthermore, normalized vector magnitudes, constructed after maximal angle responses were set to 1.0, were greater with the lowest versus the highest velocity, indicating that responses to the former were more angularly tuned (1.14 ± 0.05 vs. 0.77 ± 0.03 , paired t -test, $P < 0.01$).

Firing rates and angular tuning at the highest and lowest velocities are illustrated graphically by the average polar plots in Fig. 3C. Here, each individual polar plot was rotated so that

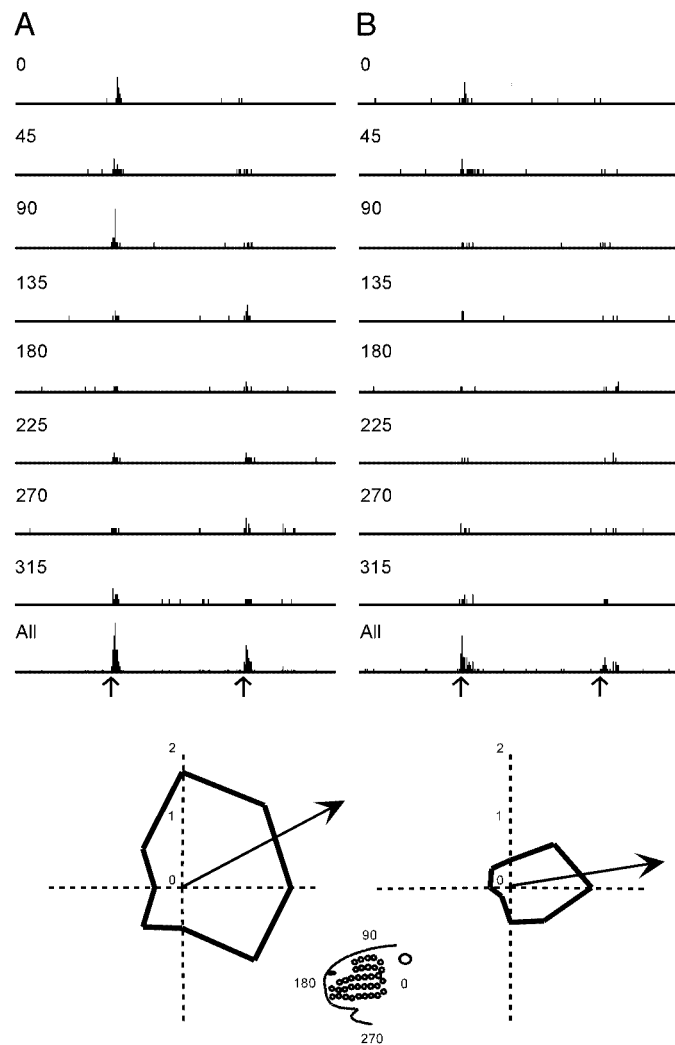


FIG. 1. Responses of a single barrel regular spike unit (RSU) to ramp-and-hold deflections of its principal whisker (PW) using deflection velocities of 200 mm/s (A) and 40 mm/s (B). Top: peristimulus time histograms (PSTHs; 1-ms bins) show responses accumulated over 10 trials to each of the 8 deflection angles and the response combined over all angles. PSTHs are 500 ms, and arrows indicate stimulus onset and offset. Each small tick denotes 1 spike. Bottom: The unit's angular tuning is plotted in polar coordinates; see figurine for orientation. Axes represent spikes per stimulus onset. Arrows denote mean vector angles and magnitudes.

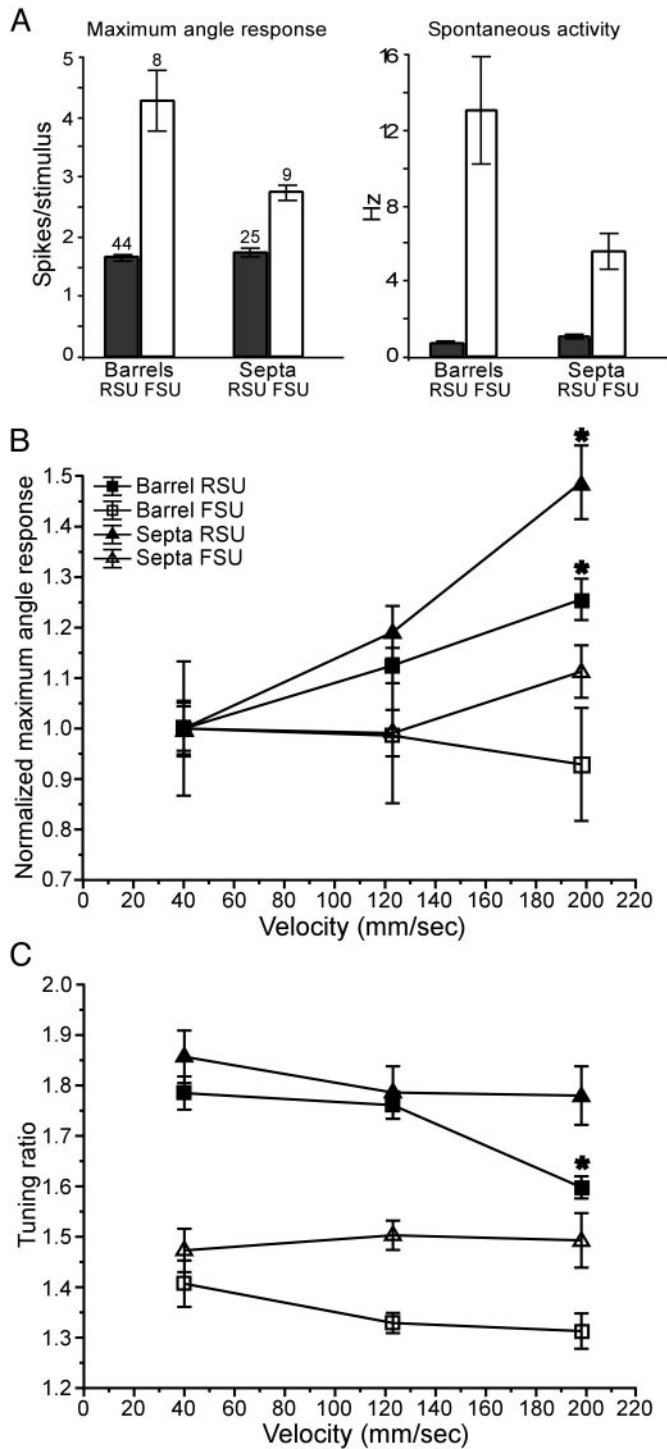


FIG. 2. Effect of deflection velocity on response magnitudes and angular tuning in four populations of layer 4 units. *A*: average response magnitudes evoked at each cell's maximally effective angle using 200 mm/s deflections (*left*) and average spontaneous activities (*right*). Numbers indicate sample size. *B*: relationship between deflection velocity and maximum angle responses normalized to responses evoked with 40 mm/s deflections. *C*: relationship between deflection velocity and angular tuning ratio. Legend as in *B*. For all panels, error bars indicate mean \pm SE. The deflection amplitude at 120 mm/s was 0.5 mm; all others were 1.0 mm. **P* values < 0.05 (linear regression).

all maximal angle responses were aligned (to 180°). In ~40% of cells, two or more deflection angles evoked responses that were maximal and equivalent, especially with low-velocity

deflections that evoked small numbers of spikes. This is reflected in the "lobular" appearance of the low-velocity average polar plot. The greater decrease of evoked responses at the nonpreferred angle in the 10- versus 200-mm/s plots indicates

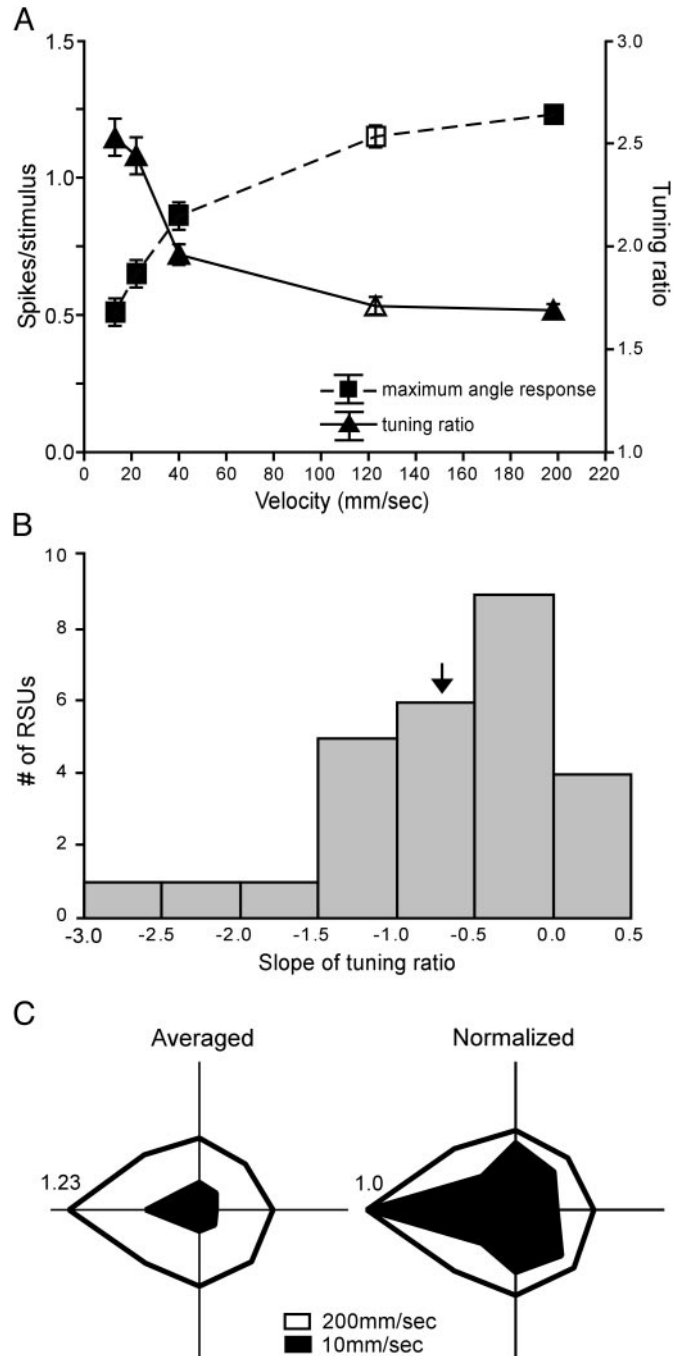


FIG. 3. Barrel RSUs respond less vigorously but more selectively with low-velocity deflections. *A*: relationship between deflection velocity and response magnitude (---) and angular tuning (—) for 29 RSUs studied using a wide range of deflection velocities. Conventions as in Fig. 2. *B*: distribution of slopes describing the relationship between deflection velocity and angular tuning. Arrow indicates the average of the slopes (-0.72). *C*, *left*: average polar plot obtained by aligning all maximum angles responses to 180°; polar plot is scaled to the average response in spikes/stimulus. *Right*: each polar plot was scaled to its maximal angle response and rotated to 180°. Normalized polar plots illustrate the greater angular tuning of barrel RSU cells with lower velocity deflection.

that the responses at nonpreferred deflection angles were disproportionately affected by deflection velocity. Maximal angle responses, on average, were approximately fourfold larger (3.98 ± 1.3) at 200 than at 10 mm/s, whereas responses averaged over all angles were approximately sevenfold larger (6.74 ± 3.36 ; paired *t*-test, $P < 0.0005$); the large variance in the latter case reflects several units having exceptionally small mean responses with the lowest velocity. Analysis of mean vector angles showed that overall angular preference was preserved across deflection velocities. Compared with values obtained at 200 mm/s, average vector angles differed by ± 26.3 , 33.8 , 38.7 , and 34.5° for 120, 40, 20, and 10 mm/s, respectively (ANOVA, $P = 0.34$).

All deflections were 1 mm in amplitude except for those at 120 mm/s, which were 0.5 mm in amplitude. Despite the twofold difference in amplitude, firing rates increased and tuning ratios decreased relative to the slower velocity (and larger amplitude) deflections and were comparable to those at the 200-mm/s velocities. Thus for barrel RSUs deflection velocity, but not amplitude, affects angular tuning.

Effects of velocity on angular tuning in trigeminal ganglion neurons

Velocity is encoded in populations of trigeminal ganglion cells during the first few msec of the response to whisker deflection (Shoykhet et al. 2000). We therefore examined whether angular tuning of primary afferent neurons depends on deflection velocity and whether such effects are similarly most robust during the early phase of the response. We recorded 21 rapidly and 17 slowly adapting NVg neurons. Effects on firing rates were similar to those reported by Shoykhet et al. (2000); notably, RAs increased their overall response magnitude with faster deflections, whereas SAs were sensitive to velocity only during the first few milliseconds of the response (data not shown). Figure 4 shows mean tuning ratios computed for different time epochs after response onset. For both populations, angular tuning was greater with lower velocity stimuli at most epochs. Interestingly, RA tuning ratios remained relatively constant with time epochs >5 ms, whereas SA tuning ratios for lower velocity deflections declined as the response window became longer. As analyzed in detail by Shoykhet et al. (2000), amplitude effects dominate SA response magnitudes as the response evolves in time (and as the whisker is further displaced). Note, for example, that tuning ratios are consistently smaller with the lower amplitude deflection at the longer time epochs.

DISCUSSION

Consistent with previous findings, we observed that the transient responses of barrel RSUs to stimulus onset are velocity sensitive with faster deflections evoking more spikes (Ito and Kato 2002; Pinto et al. 2000). Also consistent with previous results, deflection amplitude has little or no effect on response magnitude, as larger responses were evoked by higher velocity movements despite a deflection amplitude of half the size. Barrel RSUs maintain the same preferred angular direction with different deflection velocities (see also Schultz et al. 1976) but respond more selectively to deflection angle when whiskers are moved slowly. Velocity-dependent angular tuning

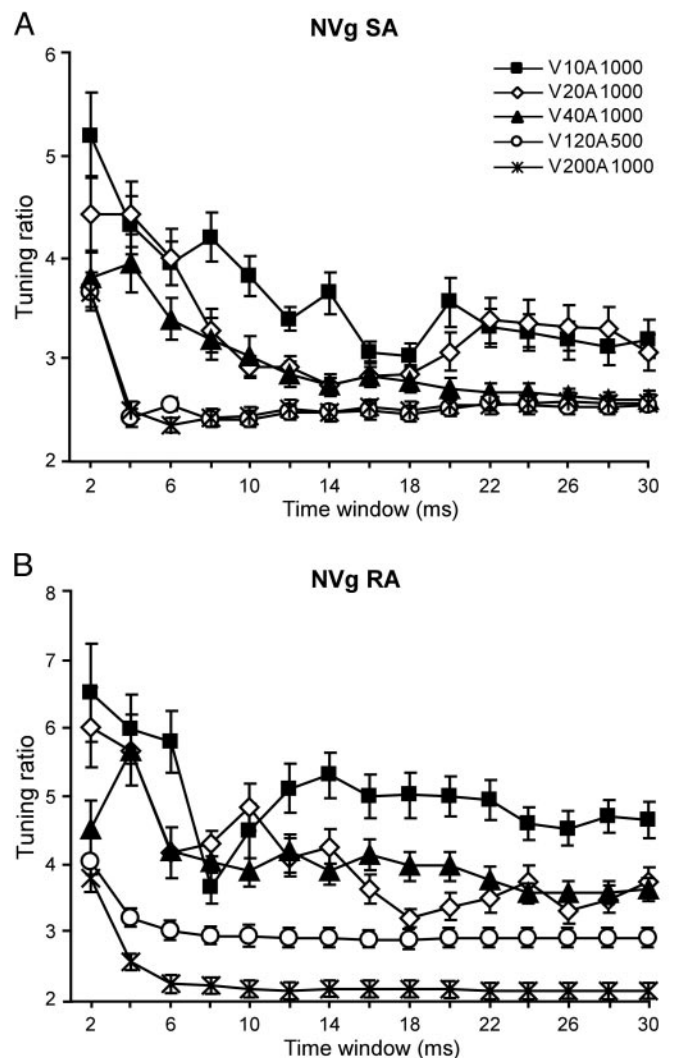


FIG. 4. Effect of deflection velocity on angular tuning in trigeminal ganglion (NVg) neurons. Relationship between tuning ratio and time window after response onset in NVg slowly adapting cells (SA; A) and rapidly adapting (RA; B; legend as in A). For all panels, error bars indicate means \pm SE. The deflection amplitude at 120 mm/s was 0.5 mm; all others were 1.0 mm.

of RSUs likely reflects the sensitivity of barrel circuitry to the initial firing synchrony of thalamocortical neurons (Pinto et al. 2003). In thalamic barreloids, preferred angle deflections evoke more local firing synchrony as revealed by the magnitudes of evoked field potentials during the first ~ 1.5 – 8 ms of the response (Temereanca and Simons 2003). Moreover, with low deflection velocities, synchronous firing (within 2 ms) between pairs of single barreloid neurons is maintained primarily among neurons that share common angular preferences (Temereanca 2003). Thus with slow whisker movement, a small number of barreloid neurons will fire sparsely and synchronously to their common preferred deflection angle; the subset of cells that maintain synchronous firing will be even smaller at nonpreferred angles and their firing rates will be lower. Because barrel RSUs receive inputs from subpopulations of barreloid neurons having similar angular tuning (Bruno and Simons 2002), the sensitivity of barrel circuitry to thalamic firing synchrony would lead to greater RSU response differentials to preferred versus nonpreferred deflection angles, as observed here. Thus angular tuning can be preserved over at

least a 20-fold range of deflection velocities in a thalamocortical circuit characterized by extensive divergence and convergence (see Bruno and Simons 2002).

Angular sensitivity originates at the level of primary afferent neurons and is thought to reflect selective circumferential innervation of the sinus hair follicle by their axons (Gottschaldt et al. 1973; Lichtenstein et al. 1990). Present findings demonstrate that both rapidly and slowly adapting NVg cells fire less robustly and are more angularly tuned with lower whisker deflection velocities. Presumably, the spread of mechanical energy through the sinus hair follicle is more spatially limited with low-velocity/acceleration perturbations of the whisker hair. Only mechanoreceptors located at the point of maximal tissue displacement will detect such stimuli. We found that changes in angular tuning ratios are greatest during the first ~7 ms of the response. Interestingly, this time period corresponds to the phase of the thalamic barreloid LFP that robustly reflects both angular tuning and deflection velocity (Temereanca and Simons 2003). Due in part to relatively limited divergence and convergence (see for example, Deschenes et al. 2003), the timing of the primary afferent signal is well preserved at synaptic stations in the principal sensory nucleus (Minnery and Simons 2003) and in thalamic barreloids of the ventral posteromedial nucleus (Minnery et al. 2003). Thus it appears that angular sensitivity, like deflection velocity, is encoded first as synchronous, short-latency firing among both rapidly and slowly adapting trigeminal ganglion cells. This time-dependent code is faithfully preserved in the brain stem and thalamus (see Deschenes et al. 2003). As shown by Pinto et al. (2000), in cortical layer IV this temporally based code is transformed into one based on response magnitude, with excitatory barrel neurons firing more spikes to preferred whisker stimuli, e.g., whisker deflections in a particular angle.

FSUs in the barrels are poorly tuned to deflection angle (Bruno and Simons 2002; Simons and Carvell 1989; Swadlow and Gusev 2002). We found that septal FSUs are similarly nonselective. Moreover, both groups of FSUs are highly active spontaneously and in response to whisker deflection; barrel FSUs are more active, however, than those in the septa. At least in the case of barrel FSUs, high responsiveness and broad angular tuning reflect strong synaptic input and extensive convergence from thalamocortical neurons in the homologous barreloid (Bruno and Simons 2002; Swadlow and Gusev 2002). The observed absence of velocity sensitivity in barrel FSU firing rates, at least over the range of 40–200 mm/s, is consistent with theoretical studies showing that FSU responses are influenced more by overall thalamic response magnitudes, which depend weakly on deflection velocity, than on thalamic population firing synchrony, which depends strongly on deflection velocity (Pinto et al. 2000, 2003). The weak dependence of FSU angular tuning on deflection velocity is consistent with this idea. These conclusions are tempered, however, by the relatively small number of barrel FSUs studied and the limited velocity range over which their responses were examined.

The angular tuning of septal RSUs was equivalent to or slightly greater than that of barrel RSUs. Moreover, septal RSUs, like their barrel counterparts, fired more robustly with increasing deflection velocity with no apparent effect of onset deflection amplitude. Septal RSUs also displayed greater selectivity for deflection angle with lower movement velocities

when spontaneous firing rates were taken into account. Septal neurons are thought to differ from barrel neurons in the number and/or relative proportion of inputs from lemniscal (VPM) and paralemniscal (POm) pathways (see Lu and Lin 1993), whose constituent neurons have characteristic, different response properties (Ahissar et al. 2000; Diamond et al. 1992). The dynamics of septal circuits may also differ from those in the barrel (see Brumberg et al. 1999; Kim and Ebner 1999), where dense interconnections among and between excitatory and inhibitory neurons render the circuitry sensitive to thalamic population firing synchrony. The finding that septal neurons respond robustly, and at short latency (see Brumberg et al. 1999), to whisker stimuli indicates that they receive strong afferent inputs from thalamic nuclei and raises the possibility of more limited convergence than in the barreloid-to-barrel circuit. Perhaps, compared with barrel RSUs, septal RSUs receive inputs from a smaller and more select group of thalamic neurons and these inputs are more uniformly well-tuned for deflection angle, requiring less processing by local circuitry.

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