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Coding of deflection velocity and amplitude by whisker primary afferent neurons: implications for higher level processing

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Abstract

Within the rat whisker-to-barrel pathway, local circuits in cortical layer IV are more sensitive to the initial timing of deflection-evoked thalamic responses than to the total number of spikes comprising them. Because thalamic response timing better reflects whisker deflection velocity than amplitude, cortical neurons are more responsive to the former than the latter. The aim of this study is to determine how deflection velocity and amplitude may be encoded by the primary afferent neurons innervating the vibrissae. Responses of 81 extracellularly recorded trigeminal ganglion neurons (60 slowly and 21 rapidly adapting) were studied using controlled whisker stimuli identical to those used previously to investigate the velocity and amplitude sensitivities of thalamic and cortical neurons. For either slowly (SA) or rapidly adapting (RA) neurons, velocity is reflected by both response magnitude, measured as the total number of evoked spikes/stimulus, and initial firing rate, measured as the number of spikes discharged during the first 2 ms of the response. Deflection amplitude, on the other hand, is represented only by the SA population in their response magnitudes. Thus, in both populations initial firing rates unambiguously reflect deflection velocity. Together with previous findings, results demonstrate that information about deflection velocity is preserved throughout the whisker-to-barrel pathway by central circuits sensitive to initial response timing.

Key words: *trigeminal ganglion, barrels, vibrissa, thalamus, cortex*

Introduction

Understanding neural coding strategies and the circuitry that implements them requires analyses of both the sensory neurons that transduce and transmit stimulus-evoked signals and the central neurons that receive and decode them. Because of its unique anatomical organization, the rodent whisker-to-barrel pathway provides a useful model for examining information processing in a hierarchically organized sensory system. Responses of anatomically identifiable, whisker-related groups of neurons at one level can be directly compared with those evoked in similarly grouped neurons at another level (Simons, 1995).

Whisker deflection parameters are first encoded by axons of trigeminal ganglion cells innervating solely that whisker's follicle (Dörfl, 1985; Lee and Woolsey, 1975; Rice *et al.*, 1986). Information is processed centrally at three levels—the brainstem trigeminal complex, ventral posterior medial thalamic nucleus (VPm) and somatosensory cortex—by identifiable groups of neurons related in a one-to-one fashion to the deflected whisker. These groups comprise "barrelettes" in the brainstem, "barreloids" in the thalamus, and "barrels" in layer IV of the somatosensory region (SI) of cortex (Woolsey and Van der Loos, 1970; Van der Loos, 1976; Ma and Woolsey, 1984).

Previous physiological (Simons and Carvell, 1989; Kyriazi *et al.*, 1994) and modeling (Kyriazi and Simons, 1993; Pinto *et al.*, 1996) studies suggested that barrel circuitry in layer IV is more sensitive to the initial timing of thalamic responses than to the total number of spikes comprising them. This prediction was recently confirmed physiologically by using whisker deflections of different amplitudes and velocities to produce different response profiles in thalamic and cortical neurons (Pinto *et al.*, 2000). Among thalamic neurons, more rapid whisker deflections evoke greater initial firing synchrony. Deflection amplitude, on the other hand, is not strongly reflected in either the temporal distribution of the thalamic response or in the total number of spikes comprising it. Consistent with the computational model of Pinto *et al.* (1996), the cortical response is more sensitive to deflection velocity (and thalamic initial firing rates) than deflection amplitude. Thus, in the whisker/barrel system, layer IV circuitry extracts information about deflection velocity from the initial synchrony of thalamic (VPm) responses.

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The origin of the thalamic temporal code for velocity is not clear. Here, we examine the possibility that a temporal representation of deflection velocity is generated from the outset by the primary afferent neurons innervating the whisker follicle. Trigeminal ganglion cells are known to be sensitive to a variety of whisker deflection parameters such as amplitude, velocity, angular direction, frequency, and duration (Gottschaldt *et al.*, 1973; Dykes, 1975; Gibson and Welker, 1983; Lichtenstein *et al.*, 1990). Deflection velocity has been found to be correlated in some neurons with the frequency of their discharges during whisker movement (Gibson and Welker, 1983). The latter findings suggest that primary afferent fibers themselves may provide the basis for encoding of velocity in the temporal domain.

In the present study, we examined the responses of trigeminal ganglion neurons to whisker deflections differing in amplitude and velocity. Stimuli are identical to those used previously by Pinto *et al.* (2000) to investigate neural coding strategies used in thalamocortical circuits. Results indicate that first-order neurons in the whisker system can unambiguously encode deflection velocity by firing synchronously during the earliest component of the primary afferent response.

Methods

Surgical preparation

Nine adult, female rats (Sprague–Dawley strain, Zivic Miller, Zelienople, PA) were used in the experiments. Each animal was initially sedated with Metofane (methoxyflurane, Pitman-Moore, Mundelein, IL), and subsequently maintained under halothane anesthesia for the remainder of the surgery. A jugular vein catheter and a tracheal cannula were inserted as described previously (Lichtenstein *et al.*, 1990). The animal's skull was exposed, a ground screw was inserted into the bone over the right frontal cortex, and a steel post was attached to the right side of the skull with dental acrylic. Throughout the experiment, the post was used to support the animal's head with unrestricted access to the whiskers on the left side of the face. The skull overlying the left trigeminal ganglion (6.0 mm anterior to lambda, 2.6 mm lateral to midline) was thinned by drilling, and a small section of remaining bone was removed with a scalpel. Ophthalmic ointment was applied to the eyes to prevent drying of the corneas.

The rat was transferred to a vibration isolation table, halothane anesthesia was discontinued, and for the remainder of the experiment, the animal was anesthetized with pentobarbital sodium administered through the jugular vein catheter. We assume that the results of this study on primary afferent neurons were unaffected by the use of sodium pentobarbital (see Larrabee and Posternak, 1952). The animal's core temperature was maintained at 37°C by a servo-controlled heating blanket (Harvard Apparatus, Cambridge, MA). The rat's head was positioned in the stereotaxic plane of Paxinos and Watson (1982). Experiments were terminated by a lethal dose of sodium pentobarbital.

Electrophysiological recordings

Extracellular unit recordings were obtained with lacquer-coated tungsten microelectrodes having impedances of ~10 MΩ at 1,000 Hz (Frederick Haer, Brunswick, ME). The electrode was advanced manually through the brain until it penetrated the trigeminal ganglion, ~10 mm below the cortical surface. This event was evidenced by the abrupt appearance of neural signals in response to manual stimulation of the left whiskers. The microelectrode was then advanced in 4 μm steps by means of a hydraulic stepping microdrive. Because trigeminal ganglion cells display little or no spontaneous activity, whiskers were stimulated manually with a glass probe during advancement of the electrode. Single units were identified on the basis of spike waveform criteria. Spike occurrences were digitized by an amplitude discriminator and stored in a computer (LSI 11/73, Digital Equipment Co., Maynard, MA, USA).

Whisker stimulation

Because a given afferent fiber innervates one, and only one, whisker follicle (Rice *et al.*, 1986), trigeminal ganglion cells have receptive fields limited to one whisker. Therefore, once a single unit was isolated, its corresponding whisker (the principal whisker, or PW) was readily identifiable. The PW was deflected by means of electromechanical stimulators (Simons, 1983; Pinto *et al.*, 2000). For the present experiments, a stimulator was attached to the whisker 5 mm from the base of the hair in the whisker's neutral position. The spatial constraints of placing a stimulator on the whisker without disturbing it, combined with the minimum required whisker length of 5 mm, allowed data collection primarily from the large vibrissae oriented more or less perpendicularly to the rat face, i.e., the ventrocaudal subset of the whisker array. We, therefore, did not investigate whether the position of the whisker within the mystacial pad array was correlated with its stimulus-evoked responses.

A "standard" multiangle stimulator (Simons, 1983) was used to deflect the whisker in eight different directions in 45° increments (caudal direction defined as 0°). Stimulus parameters were as follows: onset/offset velocity 125 mm/s; amplitude 0.5 mm (~5.6°); plateau duration 200 ms; and interstimulus interval 2–3 s. Note that the amplitude of deflection measured in degrees matches that used in previous studies in this laboratory wherein stimulators were attached to the whisker 10 mm from the

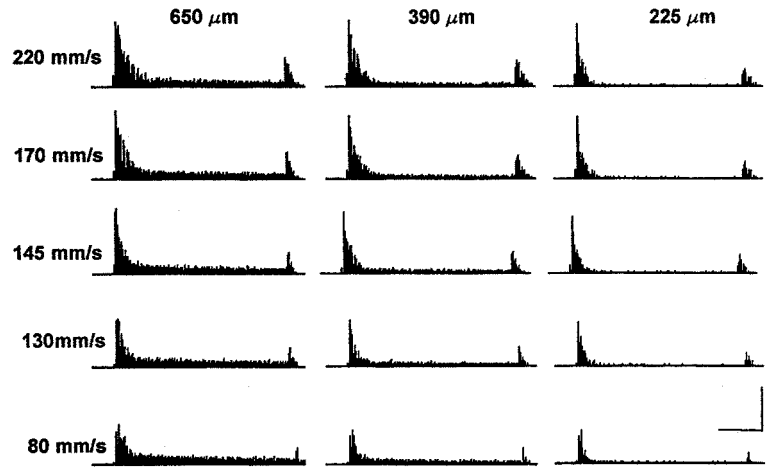

FIGURE 1. Population response profiles. Peristimulus time histograms (PSTHs) show responses of 81 trigeminal ganglion neurons to whisker deflections at three amplitudes (650, 390, and 225 μm) and five velocities (220, 170, 145, 130, and 80 mm/s) delivered in each unit's preferred direction (see Methods). Each stimulus was repeated ten times for a total of 810 deflections per histogram. Vertical scale represents the probability of observing an action potential within a 1 ms bin; calibration bar = 0.30. Horizontal scale is time, and the calibration bar is 50 ms.

surface of the skin. For a given stimulus battery, directions were randomized, and this was repeated ten times for a total of 80 deflections. The unit's maximally effective direction, i.e., its preferred direction, was determined on-line using spike counts evoked by stimulus onset.

Once the directional preference of the neuron was established, its responses to whisker deflections varying in amplitude and velocity were assessed using a modified stimulator (Pinto *et al.*, 2000). The stimulator was made shorter than the standard one in order to eliminate mechanical ringing at high stimulus velocities. Whisker deflections consisted of sigmoidally shaped ramp-and-hold stimuli which were delivered, in randomly interleaved sequences, at five velocities (80, 130, 145, 170, and 220 mm/s) and three amplitudes (225 μm or 2.6°, 390 μm or 4.5°, and 650 μm or 7.4°). These stimuli were identical to those used previously by Pinto *et al.* (2000). Movement velocity, measured with a photo-diode, was calculated using the highest amplitude ramp for each velocity and was computed as the average rate of rise over the full deflection distance. Each stimulus was presented ten times with an interstimulus interval of 2–3 s. Stimuli were applied in the unit's preferred direction and in the caudal direction (0°). The latter procedure ensured that all neurons were studied with exactly the same stimuli.

Both the standard and the velocity stimulators were controlled by an LSI 11/73 computer. Interspike intervals were measured with a resolution of 100 μs, and data were collected for a 500 ms period bracketing the stimulus. To ensure that the whisker was engaged by the stimulator immediately following movement onset, the stimulator was positioned so that the vibrissal hair rested against the inside wall of the tubing that held the whisker. For this reason, only responses to stimulus onset are examined.

Data analysis

Data obtained with the standard stimulator were used to classify cells as RA or SA, according to the criteria of Lichtenstein *et al.* (1990). Sequential interspike intervals were converted into peristimulus time histograms (PSTHs) having 1 ms bins, and spike counts during the middle 100 ms of the stimulus plateau were used to identify the deflection angle that evoked the largest response; this usually corresponds to the maximally effective angle as determined by responses to stimulus onset. A unit was defined as "slowly adapting" if the mean plateau activity exceeded the mean spontaneous (prestimulus) activity with a 97.5% confidence limit (one-tailed *t*-test). Cells that did not meet this criterion but still responded to the whisker stimulus, albeit transiently, were classified as "rapidly" adapting.

For analyzing the velocity/amplitude data, responses during the 25 ms following stimulus onset were accumulated into PSTHs having 100 μs bins. This epoch includes virtually all of the spikes comprising the transient phase of the responses for all stimulus parameters. From these, mean spikes/stimulus were computed, and this is hereafter referred to as *total response magnitude* or, simply, response magnitude. Other analyses examined spike timing using interspike interval measures at 100 μs resolution.

Results

Data were collected from a total of 81 trigeminal ganglion neurons in nine experiments. Sixty cells (74%) were classified as slowly adapting on the basis of plateau activity, and the remaining 21 (26%) were designated as rapidly adapting. These percentages are nearly identical (75%, 25%) to those reported by Lichtenstein *et al.* (1990) using similar recording

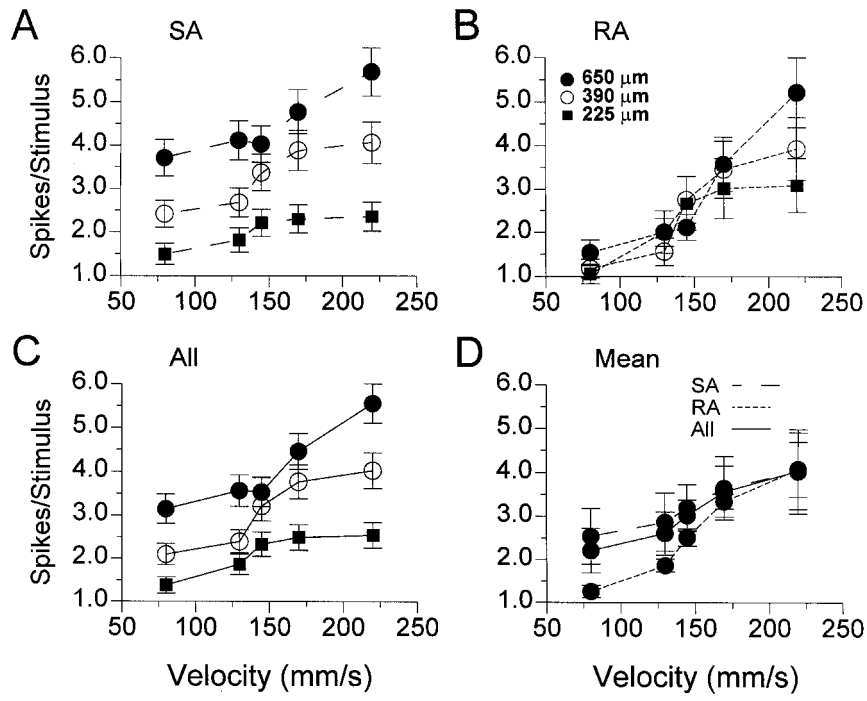

FIGURE 2. Effects of deflection velocity and amplitude on response magnitude. (A), (B) Average number of spikes discharged as a function of deflection velocity by 60 SA and 21 RA neurons, respectively, during the 25 ms time period following stimulus onset. (C) Averaged responses for *all* neurons. In (A)–(C), each curve represents the average response at each of the three amplitudes tested (see legend in B). (D) Responses were averaged across amplitudes, and data for SA, RA, and combined populations are shown. Error bars denote ± 1 SEM.

methods and analyses. Also, the overall magnitudes of responses evoked by the standard stimulus are similar to those in the earlier study. Figure 1 shows population peristimulus time histograms (PSTHs) constructed from the responses of all 81 cells to 15 different combinations of deflection amplitude and velocity. Stimuli were delivered in each unit's preferred direction as defined in Methods. Qualitatively, it is apparent that primary afferent neurons discharge more spikes with increases in either deflection amplitude or velocity. As reported by Gibson and Welker (1983), during the maintained phase of the stimulus, responses were also clearly amplitude dependent; this aspect of the response will not be considered further.

Effects of deflection velocity and amplitude on response magnitude

Figure 2 shows the effects of deflection velocity and amplitude on the number of spikes evoked during the first 25 ms following whisker stimulation. This epoch encompasses the entire transient phase of the population response. In panels A–C, data are presented separately for SA, RA, and combined populations. Slowly adapting units, on average, display monotonic increases in response magnitude with increases in either deflection velocity or amplitude (two-way ANOVA, $p < 0.001$). There was no significant interaction between velocity and amplitude ($p = 0.38$). Furthermore, a three-fold change in either deflection velocity or amplitude is associated in both cases with an approximate two-fold increase in response magnitude. The average response magnitude of RA cells, on the other hand, is a function of deflection velocity but not amplitude (two-way ANOVA, $p < 0.001$ for velocity, $p = 0.208$ for amplitude). A three-fold increase in deflection velocity leads to an approximate four-fold increase in RA response magnitude. Figure 2C presents data for the entire population of recorded neurons. Stimulus–response relations are clearly dominated by the majority, SA population. This is evident also in panel D where means are computed across amplitudes.

Effects of deflection velocity and amplitude on initial firing rates

To assess whether deflection parameters may be represented by response parameters other than total response magnitude, we examined the average first interspike interval (ISI) as a function of velocity and amplitude. Data from any given trial were included only if the neuron fired at least two spikes, and means were computed for each cell. Figure 3A, B shows that the average ISI is unrelated to deflection parameters for either RA or SA populations (two-way ANOVA, $p > 0.15$). For each cell, we also regressed its average ISI with deflection amplitude or velocity. In panels C and D, the correlation coefficient (R^2) is plotted as a function of the slope of the stimulus–response curve. At best, only a small subset of neurons displayed a

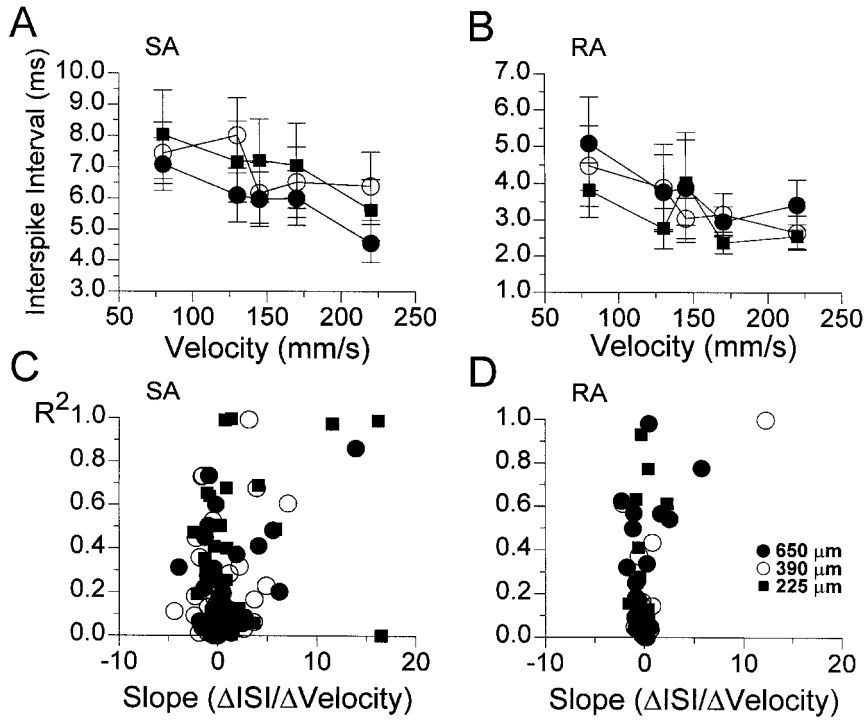

FIGURE 3. Effect of deflection parameters on the average first interspike interval (ISI). (A), (B) Effects of deflection amplitude and velocity on the average first ISI in the SA and RA populations, respectively. The average ISIs were computed as follows: each cell's average ISI was determined from those trials in which that cell fired at least two spikes; the individual values were then averaged over the entire population. Because the number of spikes discharged by a given cell varies as a function of stimulus parameters (see Fig. 2), the number of cells for which the first ISI could be computed using this procedure varied between stimuli (SA: $N = 56$ at the highest velocity, highest amplitude deflection, $N = 36$ at the lowest amplitude, lowest amplitude deflection; RA: $N = 21$ and 10, respectively. The ANOVA does not require equal sample sizes). As in Figure 2, each curve represents a deflection of different amplitude (see legend in D). Error bars are ± 1 SEM. (C), (D) Slope and linear regression correlation coefficient of each cell's stimulus/response function with deflection velocity as the stimulus parameter and ISI as the response. As indicated by the clustering of slope values around zero for both SA and RA neurons, in the majority of cells, the ISI is not a function of either deflection amplitude or velocity. A few outlying data points are omitted from the graphs but not the analyses. The legend in (D) applies to (A)–(D).

robust dependence between ISI and velocity or amplitude.

In order to incorporate into the analyses data from trials in which a neuron fired only a single spike, we measured response latency, computing means across all trials for all cells. Figure 4A, B shows that for both SA and RA cells, response latency decreases with increases in deflection velocity (two-way ANOVA, $p < 0.001$), but asymptotes at ~ 135 mm/s. Amplitude has an effect in the SA population at the smallest deflections ($p < 0.05$). Response latency, in and of itself, could be a potentially relevant code only if the distribution of latencies within the population changed systematically as a function of stimulus parameters. For example, faster movements could be represented by many neurons firing their first spike within a narrower time window. Figure 4C, D shows latency variance of SA and RA responses as a function of deflection parameters. For both populations, variance tends to decrease with faster movement, with no systematic effect of deflection amplitude.

We also examined whether velocity could be encoded by overall firing rates computed during various time epochs following response onset. This measure takes into account the variability among neurons with respect to latency, the presence of two or more spikes, and the interval between them. Figure 5A shows that for SA neurons, the average initial firing rate over the first 1.2 ms of the response is directly proportional to deflection velocity but is independent of deflection amplitude (two-way ANOVA, $p < 0.001$ and $p = 0.834$, respectively). Firing rates increase five-fold with a three-fold increase in deflection velocity; similar results are observed for the RA neurons (not shown). By 2.0 ms into the SA response, amplitude begins to exert an effect at the highest velocity (two-way ANOVA, $p = 0.05$), and by 8.0 ms it does so at all velocities but the lowest. As described above, amplitude has no effect on RAs even with the 25 ms response window.

Responses in preferred vs caudal directions

Results presented so far have concerned the responses of trigeminal ganglion neurons to whisker deflections in each cell's preferred direction, defined as the one that evoked the greatest number of spikes during the 25 ms following the standard stimulus. We also

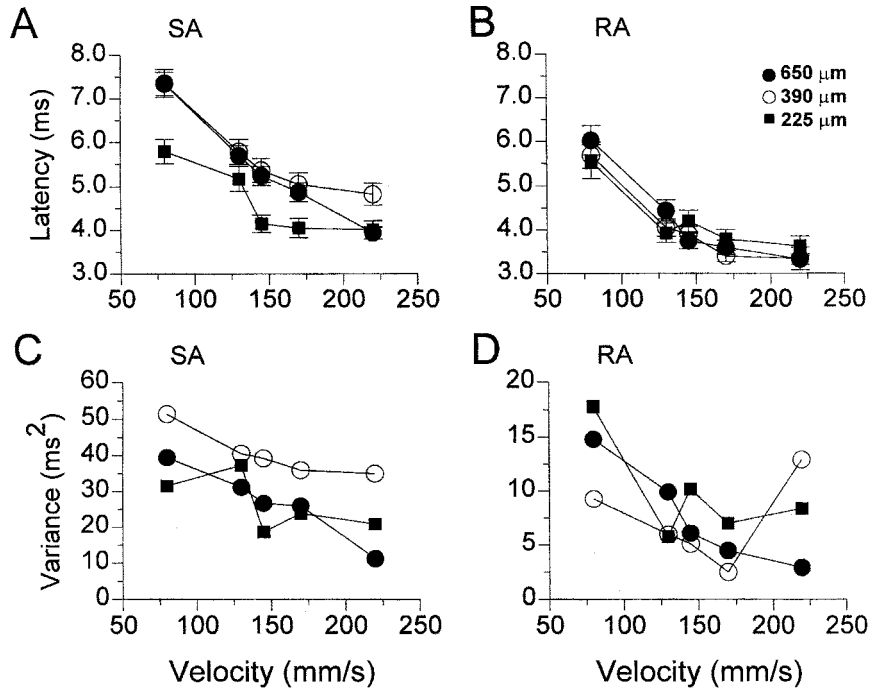

FIGURE 4. Effects of deflection velocity and amplitude on response latency. Average response latencies of the slowly (SA) and rapidly adapting (RA) neurons are shown in (A) and (B), respectively, as functions of deflection velocity. Latency was defined as the time to first action potential discharged within 40 ms following whisker movement onset. Error bars are ± 1 SEM. (C), (D) The variability in response latencies is affected by deflection parameters by plotting variance (s^2) of latencies for SA and RA cells as a function of deflection velocity. In all panels, each curve represents one of the amplitudes tested, and the legend in (B) applies to all panels in this figure.

examined data obtained from all neurons studied with the same, i.e., caudal, deflections. As expected, for corresponding deflection amplitude and velocity combinations, mean total response magnitudes of SA neurons were significantly smaller for caudal deflections than for deflections in each unit's preferred direction (cf. Fig. 2A with Fig. 6A; paired one-tailed *t*-tests, $p < 0.01$ for all 15 stimuli). Interestingly, the average SA firing rates during the first 1.2 ms of the response were unaffected by

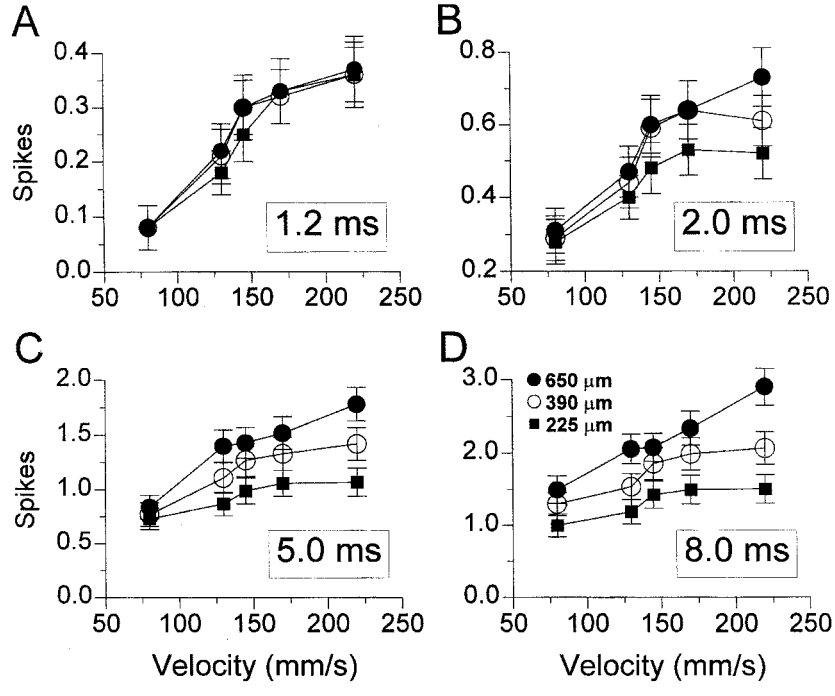

FIGURE 5. Effect of deflection parameters on the initial firing rate. The average number of spikes discharged by the slowly adapting neurons during various time epochs following population response onset. Conventions are identical to those in Figure 2, and the key in (D) applies to (A)–(D). Error bars are ± 1 SEM.

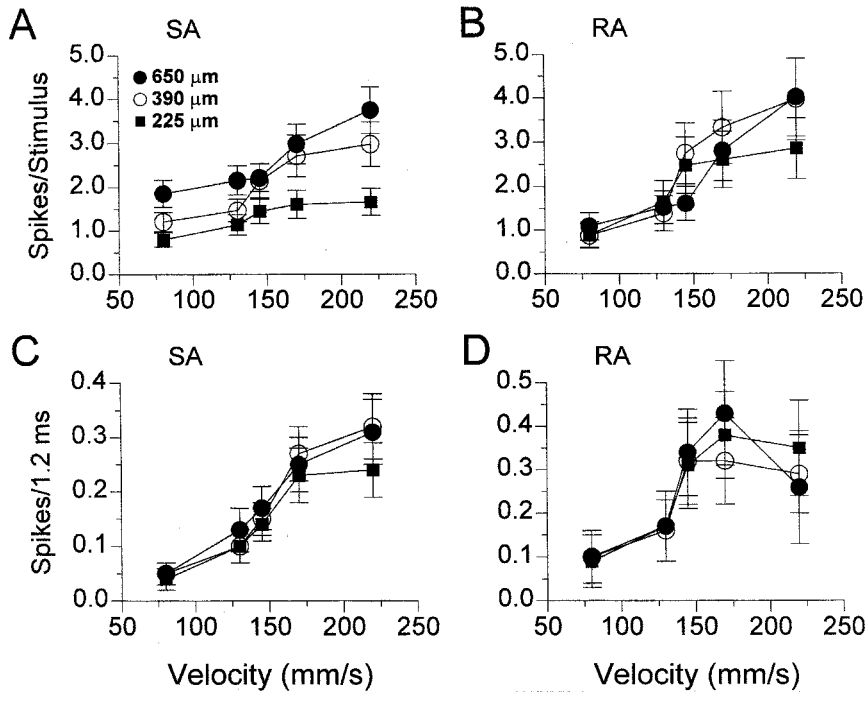

FIGURE 6. Responses in caudal directions. (A), (B) The effects of deflection velocity and amplitude on the total magnitude of the transient response of slowly (SA) and rapidly adapting (RA) neurons to whisker movements in the caudal ±45° direction. (C), (D) The average initial firing rates of the SA and RA populations during the first 1.2 ms of the response in these directions. In all panels, each curve represents one of the amplitudes tested as represented by the legend in (A). Error bars are ± 1 SEM.

direction in eight of the 15 amplitude and velocity combinations (cf. Fig. 5A with Fig. 6C; paired one-tailed *t*-tests, $p < 0.05$ for the following seven stimuli: 130 and 145 mm/s deflections at all three amplitudes, and 220 mm/s deflection at the lowest amplitude of 225 μm). Consistent with the previous finding that RA neurons are less directionally selective than SA cells (Lichtenstein *et al.*, 1990), responses of RA cells in this study, whether measured by total magnitude or initial firing rate, varied little or not at all between deflections in the best and caudal directions (Fig. 6B, D).

Another possible explanation for the above findings is that caudal angles (caudal ±45°) are over-represented in the sample, such that a disproportionately large number of units responded best to caudal deflections. This is not the case, however. Twenty-five of the 81 sampled neurons were observed to respond best to caudal deflections; this is close to what would be expected ($0.375 \times 81 \sim 30$) if the "best" angles were randomly distributed within the sample.

Discussion

We investigated the responses of trigeminal ganglion neurons to 15 whisker deflections differing in movement amplitude and velocity. Given the sensitivity of thalamocortical circuitry to the latter, data were examined to determine which, if any, characteristic of the peripheral response reflects deflection velocity to a much greater extent than deflection amplitude. Figure 7 summarizes the major findings by showing normalized slopes of the stimulus–response curves derived from data such as those presented in Figure 2A, B. For each curve, both axes were scaled so that all values were expressed as a fraction of the highest value, which was set to 1.0. This procedure allows for a direct comparison of different stimulus/response function slopes that otherwise have different units of measurement. A steeper normalized slope indicates a stronger dependence of a given response measure on the specific deflection parameter. Rapidly adapting neurons are clearly more sensitive to velocity than amplitude (Fig. 7B, D). This is true regardless of whether their responses are measured as the total number of spikes evoked by the whisker movement or as the number of spikes discharged during the first 1.2 ms. The RA population could thus provide the velocity-specific input to the thalamocortical circuit. Rapidly adapting neurons, however, comprise only 25% of low-threshold neurons innervating the whisker follicle. Our analyses indicate that the majority population, SA neurons, can indeed encode velocity distinct from amplitude, but only during the earliest phase of their response. By 2 ms into the response of the SA population, velocity can no longer be clearly dissociated from amplitude. Total response magnitude, encompassing the phasic component of the response to whisker movement (25 ms), is entirely ambiguous in that a high amplitude, low velocity stimulus produces a similar number of spikes as a lower amplitude but higher velocity one.

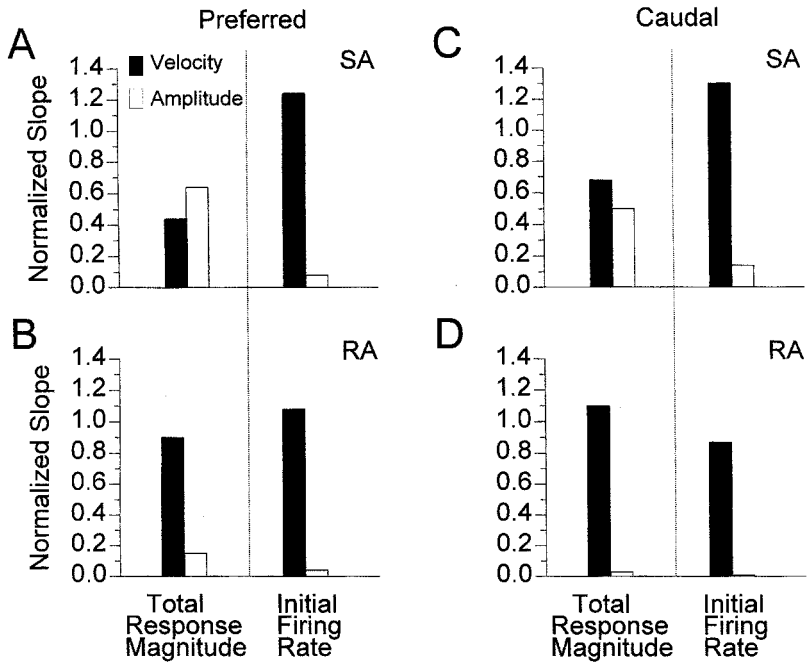

FIGURE 7. Normalized slopes of stimulus–response functions for trigeminal ganglion neurons. Normalized values were computed by converting the abscissae and ordinates to unit scales where the maximal mean response (spikes/stimulus and firing rate during the first 1.2 ms of the response) and the maximal value of the stimulus parameter (amplitude, velocity) were assigned values of 1.0. Data points representing mean values were then expressed as fractions of the highest value, and slopes were computed using the least squares approximation. Amplitude, open bar; velocity, closed bar.

Analyses indicated that the steepest stimulus–response function was obtained for deflection velocity vs average firing rate during the first 1.2 ms of the evoked response. The strength of this measure derives, in part, from its incorporation of several response measures each of which, taken alone, provides a moderate reflection of whisker velocity. With faster movements, the primary afferent neurons, as a population, display shorter and more consistent latencies to the first evoked spike, and they are more likely to fire two or more spikes in rapid succession. Importantly, this is true for both RA *and* SA neurons, which otherwise have distinctly different response properties mediated by different receptor endings (see Lichtenstein *et al.*, 1990). Most interestingly, the relationship tends to be preserved regardless of whether the whisker is moved in each neuron's "best" direction or in any arbitrarily chosen direction, i.e., caudal. Here, the relationship is at the population level not at the level of individual neurons, which may in some cases fail to respond to a particular stimulus direction. Thus, whisker deflection velocity can be encoded robustly and unambiguously within 2 ms of the onset of the primary afferent response.

We did not find a response measure that was solely a function of movement amplitude during the dynamic phase of the stimulus. Slowly adapting neurons can signal static displacement in their rates of sustained discharge. How and when static whisker displacements may occur during natural whisking behavior is unclear. Kinematic analyses of discriminative whisking reveal the vibrissal hairs to be continually changing in terms of their degree of bending and their position with respect to the palpated surface (Carvell and Simons, 1990). In this regard, it should be emphasized that the present experiments utilized passive whisker deflections that originated from the hair's neutral (undeflected) position. Perhaps, superimposing a stimulus on an already displaced whisker, as occurs during natural behavior, would affect the velocity sensitivities of the peripheral neurons, thus providing a contribution of deflection amplitude in the primary afferent signal.

Coding of deflection velocity in the trigeminal ganglion

A previous quantitative study of the rat trigeminal ganglion (Gibson and Welker, 1983) reported that whisker deflection velocity is represented by the number of spikes discharged during the *movement* phase of the stimulus. Present results confirm these and other findings from cutaneous receptors (Burgess *et al.*, 1983; Poulos *et al.*, 1984) by showing that higher velocity stimuli elicit a greater number of spikes during a brief time period following response onset. Similarly, in the glabrous skin of the racoon forepaw, the frequency of spike discharge during the *dynamic* phase of skin indentation is a function of velocity for both RA and SA units (Pubols *et al.*, 1971). Gibson and Welker (1983) noted a wide range of velocity sensitivities in the sample, much as we have found. Given the variability from one neuron to the next and our finding that during the relevant time

scale of the response (< 2 ms) a single neuron can fire at most two spikes, coding of velocity in the sensory periphery would have to exist at the *population* level.

Response transformations in the whisker-to-barrel pathway

A recent study demonstrated that the responses of cortical barrel neurons are determined by whisker deflection velocity, amplitude having much less of an effect (Pinto *et al.*, 2000). This reflects the sensitivity of barrel circuitry to the initial synchrony of responses among thalamic neurons, which in turn is more strongly influenced by deflection velocity than deflection amplitude (Pinto *et al.*, 1996). On what basis, then, do thalamic neurons distinguish among whisker deflections varying in velocity? The present findings suggest that the velocity dependence of the thalamic, and hence the cortical, response can be explained if brainstem and/or thalamic circuits, like those in the barrel, derive their information about whisker deflection from the earliest component of the peripheral response. This conclusion is strengthened by two findings from the Pinto *et al.*, 2000 study. One, firing rates during the first 2–7 ms of the thalamic response depend on deflection velocity to the same degree as firing rates during the first 2 ms of the primary afferent response. Two, these relationships tend to be maintained whether the whisker is deflected in its preferred direction or in a caudal direction.

A striking similarity also exists between the stimulus–response functions of primary afferent and thalamic neurons measured in terms of total response magnitude. As in the case of SA trigeminal ganglion cells, thalamic neurons, on average, discharge more total spikes with increases in either deflection velocity or amplitude; the only apparent difference is that thalamic cells discharge fewer spikes than the primary afferent neurons. Thus, despite the phasic nature of the responses of most thalamic neurons, these and other findings (see Kyriazi *et al.*, 1994) indicate that SA afferent neurons, the majority population in the periphery, provide the dominant input to the thalamic barreloids. This conclusion is strengthened by findings from an on-going study in our laboratory (Hartings, unpublished observations) that a tonic component of the thalamic response can be unmasked by microiontophoresis of the GABA antagonist bicuculline (see also Lee *et al.*, 1994).

Available evidence suggests that the primary afferent signal arrives in VPm relatively unaltered. The major effects in the thalamus appear to be the suppression of evoked tonic firing and, perhaps relatedly, a reduction in the total number of spikes discharged during the transient phase of the response. Thalamic circuits may therefore function to scale the primary afferent response without altering its most salient features. A substantial and qualitatively different response transformation occurs, however, within the thalamocortical circuit, because barrel neurons no longer display significant sensitivity to deflection amplitude by any of the measures so far examined.

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