Responses of Rat Trigeminal Ganglion Neurons to Movements of Vibrissae in Different Directions

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Abstract The response properties of 123 trigeminal ganglion neurons were studied, using controlled whisker deflections in different directions. When the distal end of the whisker was initially displaced 5.7° (1 mm) from its neutral position, 81% of the cells responded with statistically more spikes/stimulus to movements in one to three of eight cardinal (45° increment) directions than to the others. The more directionally selective the cell, the more vigorous was its response. On the basis of statistical criteria, 75% of the cells were classified as slowly adapting, 25% as rapidly adapting. A number of quantitative analyses indicated that slowly adapting units respond more selectively than rapidly adapting cells to the direction of whisker movement. Differences in directional sensitivities of rapidly and slowly adapting cells appear to parallel differences between their putative mechanoreceptive endings and the relationships between those endings and the vibrissa follicle's structure. Comparisons between the response properties of peripheral and central neurons in the vibrissa–lemniscal system indicate that the afferent neural signal is progressively and substantially transformed by mechanisms that function to integrate information from different peripheral receptors and from different, individual vibrissae.

Key words whiskers, somatosensory, trigeminal, peripheral neurons

In rodents, the mystacial vibrissae comprise an array of 25–30 discrete tactile organs that are swept back and forth against objects in the animal's sensory environment during exploratory and discriminative behaviors (Vincent, 1912; Welker, 1964; Wineski, 1983; Huston and Masterton, 1986). Sinus hair follicles, of which the vibrissae are a subset, are larger and more complex than other hair follicles (see Andres and von Düring, 1973). They are distinguished by two large blood sinuses (a deep cavernous sinus and a more superficial ring sinus), and by a variety of specialized mechanoreceptors. Different types of mechanoreceptors are associated with different structural components of the hair sinus–follicle complex, and it has been proposed that these anatomical relationships have a functional counterpart in the responses of the mechanoreceptive afferents to whisker movements in different directions (Rice et al., 1986). Each follicle is separately innervated by 150–200 myelinated axons within the deep

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vibrissal nerve (Vincent, 1913; Lee and Woolsey, 1975; Dörfl, 1985; Rice et al., 1986). The parent cell bodies are located in the trigeminal ganglion.

Physiological studies have shown that first-order afferent fibers innervating the vibrissae encode a variety of hair deflection parameters, including amplitude, velocity, duration, frequency, and angular direction (Fitzgerald, 1940; Zucker and Welker, 1969; Hahn, 1971; Gottschaldt et al., 1973; Pubols et al., 1973; Dykes, 1975; Gibson and Welker, 1983a,b). The remarkable sensitivity of the sensory periphery is attested by findings that some first-order neurons respond to whisker deflections as small as 5–10 μm delivered 4 mm from the skin surface (Gibson and Welker, 1983a), and by the ability of some cells to discharge in phased-lock fashion with a 1500-Hz vibration (Gottschaldt and Vahle-Hinz, 1981). Moreover, each peripheral fiber innervating low-threshold mechanoreceptors responds to one and only one vibrissa. The discriminative capacity of the system is demonstrated by recent findings that blindfolded rats can use their whiskers to distinguish between a smooth surface and a rough one consisting of shallow grooves spaced less than 100 μm apart (Carvell and Simons, 1988).

Centrally, the representations of the vibrissae are characterized by whisker-related aggregations of axon terminals and/or cell bodies (for a review, see Woolsey et al., 1981). In layer IV of the first somatosensory cortex, where they were first described, these cell groups are called "barrels" (Woolsey and Van der Loos, 1970; Welker, 1971). The close correspondence between the peripheral and central anatomy is paralleled by physiological findings that the response properties of central vibrissa neurons are qualitatively similar in some respects to those of primary afferent fibers. Thus, many cells in the trigeminal–lemniscal system have single-whisker receptive fields and encode deflection amplitude, velocity, and direction; in some cases, amplitude and velocity thresholds are comparable to those of the first-order neurons (Waite, 1973; Shipley, 1974; Simons, 1978; Ito, 1981).

The aforementioned findings might imply an elementary relay of vibrissal information from periphery to cortex. However, even when simple (e.g., single-whisker) stimuli are used, differences between the response properties of cells at different levels are apparent. For example, compared to neurons in the cortical barrels, those in the ventrobasal thalamic "barreloids" respond more vigorously to whisker stimuli, are more selective for the angular direction of whisker movement, and are more likely to respond in a slowly adapting fashion (Simons and Carvell, 1989). A parallel finding is that surround or cross-whisker inhibition is observed less frequently in the thalamus. Differences between thalamic and cortical response properties can be explained in part by convergence of inputs from more than one neuron in a thalamic barreloid onto individual cells in the corresponding cortical barrel and by local connectivities involving inhibitory neurons.

An important idea that emerged from early single-unit studies of the somatosensory system is that common strategies of information transfer are used by different synaptic stations in the ascending lemniscal system (see Mountcastle and Powell, 1959). One hypothesis, therefore, is that changes in unit properties between the ventrobasal thalamus and the somatosensory cortex are *qualitatively* similar to those between the periphery and brainstem and/or between the brainstem and thalamus. Accordingly, we studied the response properties of trigeminal ganglion cells, using controlled single-whisker stimuli and data analyses identical to those used in our previous studies of thalamic and cortical neurons. Results support the hypothesis stated above, since first-order vibrissa neurons are more responsive to whisker deflections and more selective for the angular direction of single-whisker movements than

cells in either the thalamus or cortex; also, unlike units in the latter areas, most ganglion cells are slowly adapting. Finally, the directional properties of peripheral neurons are consistent with the hypotheses of Rice et al. (1986) concerning the relation between the morphology of the tactile organs and the stimulus-evoked responses of the axons that innervate them.

MATERIALS AND METHODS

PREPARATION

Seven adult female albino rats weighing 215–365 g (Sprague–Dawley strain; Zivic–Miller Laboratories, Allison Park, PA) were used in the experiments. Each animal was anesthetized initially with methoxyflurane vapors (Metofane; Pitman–Moore), followed by pentobarbital sodium (Nembutal, 50 mg/kg, i.p.) and atropine (0.3 mg/kg). A silastic catheter was inserted into the external jugular vein and led out from the nape of the neck (Harms and Ojeda, 1974). This catheter was used for intravenous injection of Nembutal as needed to maintain areflexia to foot pinch for the remainder of the experiment. A short length of polyethylene tubing was inserted into the trachea as a cannula; the skull was exposed; and a steel post was fixed to it using dental acrylic. This post was used to hold the rat's head in a fashion that permitted unimpeded access to the whiskers on the animal's left face. A stainless steel grounding screw was placed in the right frontal region of the rat's skull. A craniotomy exposed the left hemisphere of the brain, which was gently aspirated so that we could directly visualize the trigeminal ganglion at the base of the skull. The exposed ganglion was bathed in 37°C saline. The core temperature of the animal was maintained also at 37°C through the use of a servo-controlled heating blanket.

ELECTROPHYSIOLOGICAL RECORDINGS AND WHISKER STIMULATION

Extracellular unit recordings were obtained with varnished tungsten microelectrodes (Frederick Haer, Brunswick, ME). The electrode was advanced manually through the ganglion by means of a micromanipulator. During electrode advancement, the whiskers were stroked with hand-held probes, so that even units that displayed no spontaneous activity could be isolated. Recordings were obtained from single units as determined from spike amplitude and waveform criteria. The neural signals were amplified, filtered at 300–3000 Hz, and monitored audiovisually. Action potentials had amplitudes of 50–300 μV and were always initially positive. An analog delay line was used for visualizing the entire spike waveform, and an amplitude discriminator was used to digitize the impulse events. The digitized signals were stored in a laboratory computer (LSI 11/73, Digital Equipment Corp.). Unit recordings were quite stable, and single units could be studied for prolonged periods of time.

When a unit was isolated, its receptive field was determined by using a glass probe to deflect individual vibrissae while observing them with a dissecting microscope. The receptive field was localized using the smallest-amplitude stimulus required to evoke a response. Most cells responded to extremely small whisker movements (e.g., a tremor of the experimenter's hand), and in these cases, responses could be readily attributed to stimulation of one vibrissa. For cells with high-velocity and/or high-amplitude thresholds, the most sensitive whisker could be identified in a similar manner. We cannot rule out the possibility, however, that

some of the cells having the highest thresholds could not be driven by two or more whiskers. We did not investigate the possible contributions of pelage hairs to the receptive fields.

Controlled stimulation of individual whiskers was accomplished by means of multiangular electromechanical stimulators (Simons, 1983). The stimulators are constructed from two sets of piezoelectric bimorph benders that are cemented together so that their planes of movement are orthogonal to each other. Separate driving voltages are applied to each stage, and the resulting movement at the end of the stimulator can be varied over 360° of angular displacement. A stimulator was attached to a vibrissa 10 mm from the base of the hair. Care was taken to align the axis of the stimulator with that of the hair shaft. The stimulators were mounted on a steel frame that was mechanically isolated from a self-leveling recording table, and the frame was decoupled from floor vibrations by means of inflatable inner tubes. Stimulus waveforms were ramp-and-hold trapezoids that produced 1-mm displacements of 200 msec duration; onset and offset velocities were 135 mm/sec. The stimuli were thus identical to those used in a recent study of vibrissa-activated units in the thalamus and the cortex (Simons and Carvell, 1989).

Individual whiskers were deflected in eight different angular directions (i.e., in 45° increments relative to the horizontal alignment of the whisker rows). Stimuli were delivered randomly for each sequence of eight angles, and each battery was repeated 10 times for a total of 80 stimulus presentations. Interstimulus intervals were at least 2 sec. The computer was used to control whisker stimuli and to match each stimulus with its neuronal response. Data collection for each stimulus lasted 500 msec, centered around the whisker displacement. Spike interevent times were measured with a resolution of 100 μsec and retained in a format that allowed complete reconstruction of the spike discharge pattern for each stimulus presentation. All data were stored on disk for later analysis. At the conclusion of each experiment, the animal was killed with a lethal overdose of Nembutal.

DATA ANALYSIS

The initial step in the analysis was to convert the raw data, which consisted of individual spike trains, into peristimulus time histograms (PSTHs) with 1-msec bins. The mean and variance of spike discharges for selected time periods following the stimulus were computed from the individual spike trains. These times corresponded to the onset and offset of stimulation, and the stimulus plateau; spontaneous activity measures were derived from prestimulus activity. The data were analyzed further with the LSI 11/73 or with an IBM PC/XT running a statistics package (SPSS, Inc.). Data analyses were identical to those used previously (see Simons and Carvell, 1989).

Quantitative criteria were used to classify cells as either slowly adapting or rapidly adapting. For each unit, polar plots were examined to identify the deflection angle that elicited the maximal response during the middle 100 msec of the stimulus plateau. Two-tailed t tests and a 95% confidence limit were used to compare this plateau response to equivalent periods of prestimulus activity, and a cell was classified as "slowly adapting" if the evoked response was significantly greater than spontaneous activity (i.e., $p < 0.025$). By default, the remaining cells were classified as "rapidly adapting."

Two methods were used to quantify the directional properties of the cells. In one, units were classified into eight "angular tuning" categories on the basis of how many angles

elicited responses that were statistically smaller than that evoked by movement of the whisker in its maximally excitatory angle (t tests, p's < 0.05, one-tailed). This procedure was used separately to analyze ON, OFF, and plateau responses. The other method quantified the consistency of a cell's responsiveness to whisker movements in a particular direction regardless of the hair's initial position. A "directional consistency index" was computed as follows:

$$\text{Directional consistency index} = \text{MAX}_{\text{OFF}}/\text{MAX}_{\text{ON}} \times r \times (-1)$$

where MAX_{OFF} is the largest of the eight OFF responses in mean spikes/stimulus, MAX_{ON} is the largest of the eight ON responses in mean spikes/stimulus, and r is the correlation coefficient between ON and OFF responses computed for the eight different deflection angles. For cells that respond equivalently to stimulus onset following initial movement in one direction and stimulus offset following the return movement from initial displacements in the opposite direction, the correlation (r) between ON and OFF responses for the eight different angles will approach -1.0. Such cells will display relatively large positive indices (see Fig. 1B and text below).

RESULTS

GENERAL OBSERVATIONS

We recorded from 123 ganglion cells during seven experiments. All but 10 of these units had receptive fields on the largest mystacial vibrissae—that is, whiskers in the four caudalmost arcs on the mystacial pad (straddlers and arcs 1–3, in the nomenclature of Woolsey and Van der Loos, 1970). The receptive fields for the remaining cells were located in the next three arcs. The general topographic organization of the trigeminal ganglion corresponded to that described by Zucker and Welker (1969). Dorsal vibrissae tended to project medially and ventral vibrissae laterally, whereas caudal whiskers usually projected dorsally and rostral whiskers ventrally. All cells displayed single-whisker receptive fields. Although responses could sometimes be evoked from neighboring whiskers, the thresholds for these responses were much higher; this probably can be attributed to mechanical spread of the stimulus through the skin (see also "Discussion"). The ganglion was relatively silent in the absence of stimulation. Some cells, however, did fire spontaneously at low rates, even though they displayed no signs of injury by the microelectrode.

We did not attempt to determine threshold levels systematically, since this information has been obtained previously (Gibson and Welker, 1983a). Approximately 10% of the cells had thresholds too high for activation by the mechanical stimulator, but could be driven manually by high-velocity "flicks" of the whisker. Conversely, many of the cells clearly responded to the smallest deflections that could be produced manually. This sensitivity required that considerable care be taken in positioning the stimulator so that the hair was in a neutral position. Particularly for slowly adapting cells (see below), eccentric positioning of the stimulator or slight alterations in the bending of the hair could produce unintended "spontaneous" activity. Even with careful positioning, some cells displayed hysteresis effects, in that they would continue to discharge after the termination of the controlled stimulus. Though this could be due in part to failure of the stimulator to return precisely to its original position, these cells frequently displayed a similar hysteresis with manual stimulation; in

these circumstances, the discharge could be reset to the cell's normally low level of spontaneous activity by briefly flicking the whisker in the opposite direction.

RESPONSES TO CONTROLLED WHISKER STIMULI

Figure 1 shows response profiles from two representative ganglion cells. The unit in Figure 1A responded transiently to stimulus onsets and to stimulus offsets at all deflection angles. The maximal response (4.60 ± 0.52 spikes/stimulus onset) was obtained with initial whisker movements in an up and forward direction (135°; see figurine). The magnitudes of ON responses at the eight deflection angles are plotted in polar coordinates at the bottom of the figure. This cell was not active spontaneously or during the plateau phase of the stimulus.

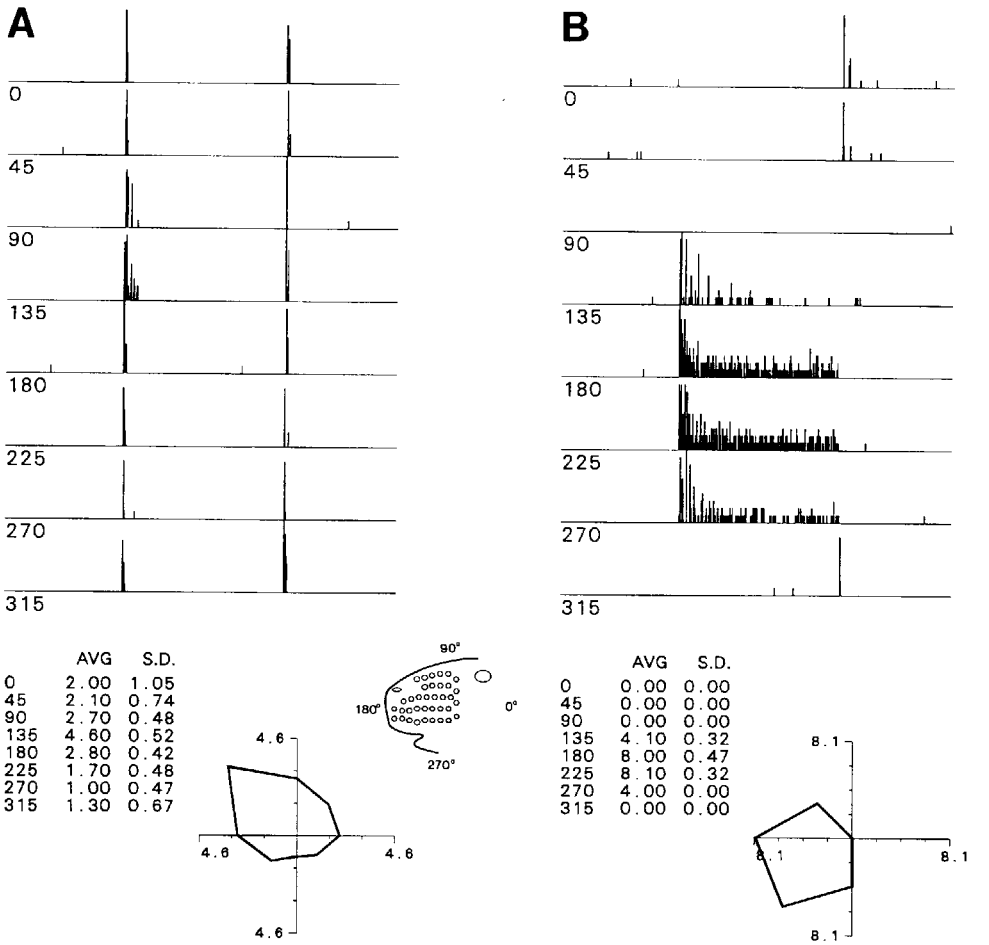

FIGURE 1. Angular properties of two well-tuned units. Panel A shows a rapidly adapting cell; the cell in panel B is slowly adapting. PSTHs in upper panels show accumulated response of each cell to 10 deflections at eight different angles. 0° represents an initially caudal deflection, 90° an initially upward direction (see inset). Duration of the PSTH is 500 msec, and individual ticks represent bins of 1 spike/msec. Below, polar plots show responses to stimulus onset plotted in polar coordinates (caudal, or 0°, at right; see inset). Mean discharge and *SD* in spikes/stimulus onset are indicated for each angle.

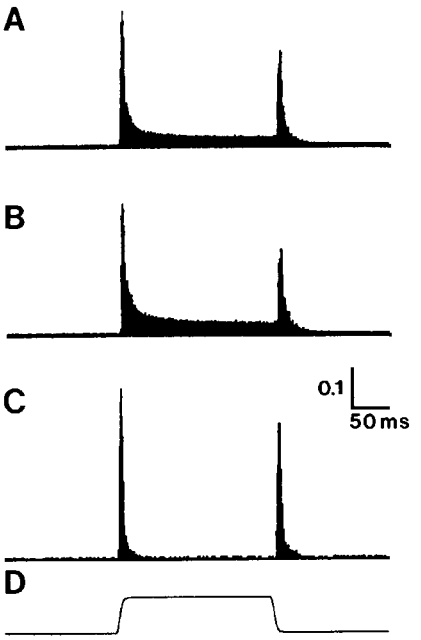

FIGURE 2. Population profiles. PSTH in panel A shows accumulated responses of 123 cells to *all* eight deflection angles. For each unit, 80 spike trains were summed. Vertical scale represents the observed probability that an action potential occurred in a 1-msec bin. Panels B and C show accumulated responses of the 92 slowly adapting and 31 rapidly adapting cells in the population, respectively. Panel D displays the stimulus waveform. Note that the same scale applies for all three PSTHs.

A different type of response is shown in Figure 1B. This unit responded selectively to forward whisker movements, whether these occurred at the onset of whisker displacement or upon the hair's return to its neutral position from an initially caudal deflection (i.e., stimulus onsets at 135–270° and stimulus offsets following initial movements at 0°, 45°, and 315°). This cell thus displayed directional consistency. Also, in contrast to the unit in Figure 1A, this cell discharged during the stimulus plateau. The cell's preference for rostrally directed deflections was similar for both the ON response and the plateau response.

Figure 2A is a summary of all 123 data files formed into a population PSTH. The profile was constructed by a bin-by-bin accumulation of all spike trains evoked by the eight deflection angles. Note the relatively low level of spontaneous activity. The stimulus-evoked response is characterized by an initially rapid increase in spike activity that decays exponentially to a stable level, with no peaks, dips, or other incongruencies during the plateau phase of the stimulus. The smaller OFF response is followed by a similar decay of activity at the conclusion of the deflection.

RAPIDLY VERSUS SLOWLY ADAPTING CELLS

As illustrated in Figure 1, two principal types of responses were observed within the sampled cells. These were distinguished by the presence or absence of discharges during the plateau phase of the stimulus. According to the statistical criterion described above, 92 of the 123 cells (74.7%) were classified as slowly adapting; the rest were rapidly adapting. Figures 2B and 2C show separate population profiles for slowly and rapidly adapting cells. The lack of a notable plateau response in the rapidly adapting profile demonstrates the effectiveness of the classification method.

RESPONSE DYNAMICS

Figure 3 shows data for four measures of unit responsiveness. Means and standard deviations are summarized also in Table 1. Figure 3A plots the distribution of spontaneous activities in the population. For each cell, the frequency of spontaneous discharges in spikes/sec was computed from 80 prestimulus time epochs of 100 msec each. The average spontaneous activity was 1.59 ± 4.08 spikes/sec. Over 70% of the cells discharged ≤ 1 spike/sec. The spontaneous activity of slowly adapting cells was greater than that of rapidly adapting cells (1.92 vs. 0.63 spikes/sec); we attribute at least some of the greater spontaneous activity of slowly adapting cells to hysteresis of the hair and to slight alterations of the resting position or degree of bending of the hair shaft caused by attachment of the stimulator.

Figures 3C and 3D show the magnitudes of ON and OFF responses in terms of spike count averages for a 20-msec epoch following the whisker movements. These data are based on responses evoked by deflecting the whisker at each cell's maximally effective or "best" onset or offset angle. Average ON responses were 4.50 ± 2.29 spikes/stimulus, and average OFF responses were 2.95 ± 1.83 spikes/stimulus. Slowly adapting cells displayed larger ON responses and smaller OFF responses than rapidly adapting cells (see Table 1). In terms of the relative magnitudes of ON and OFF responses, the maximum OFF response was 97%

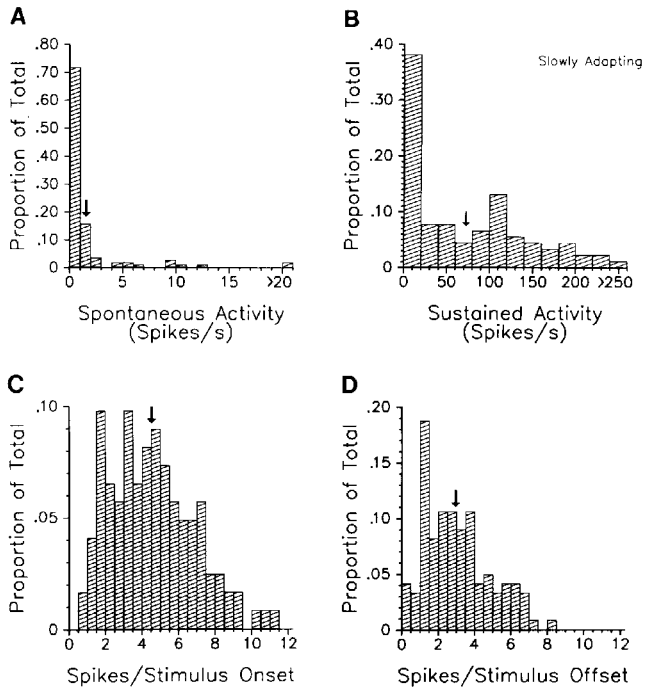

FIGURE 3. Unit responsiveness. Panel A shows the distribution of spontaneous activity in the 123 cells. The distribution of the sustained activity for the 92 slowly adapting cells in the plateau phase of whisker displacement is displayed in panel B. Panels C and D show the distributions of mean discharges in spikes/stimulus evoked by the onset and offset, respectively, of whisker deflections at the stimulus direction that evoked the maximal ON and OFF response from each of the 123 units. In all panels, arrows denote means.

TABLE 1. Response Characteristics of 123 Vibrissal Units in the Trigeminal Ganglion

	All (n = 123)	Rapidly adapting (n = 31)	Slowly adapting (n = 92)
Spontaneous activity[a]	1.59 ± 4.08	0.63 ± 1.18	1.92 ± 4.63
ON[b]			
Maximum	4.50 ± 2.29	3.34 ± 1.60	4.89 ± 2.36
Minimum	0.67 ± 0.92	0.96 ± 0.94	0.57 ± 0.89
OFF[b]			
Maximum	2.95 ± 1.83	3.23 ± 1.77	2.85 ± 1.84
Minimum	0.71 ± 0.89	1.03 ± 0.88	0.60 ± 0.88
Plateau[a]	—	—	71.93 ± 71.50
Well-tuned cells[c]	81.3%	71.0%	84.8%
Poorly tuned cells[d]	3.3%	3.2%	4.4%
Directional consistency[e]	0.051 ± 0.43	−0.16 ± 0.49	0.12 ± 0.38

[a] In mean spikes/sec ± *SD*.

[b] In mean spikes/20-msec epochs ± *SD*.

[c] Angular tuning categories 5–7.

[d] Angular tuning categories 0–2.

[e] Mean ± *SD*.

as large as the maximum ON response for rapidly adapting units, but only 58% as large for slowly adapting ones.

Figure 3B plots the distributions of plateau responses for slowly adapting cells at the deflection angle that yielded the maximal plateau response. Each cell's spontaneous activity was subtracted from its evoked response. On average, these cells discharged 71.93 ± 71.50 spikes/sec during the stimulus plateau. The large standard deviation in part reflects the fact that cells responding even at low discharge levels during the plateau were classified as slowly adapting, because of their even lower levels of spontaneous activity.

DISTRIBUTION OF MAXIMALLY EFFECTIVE ANGLES

Polar plots were examined to identify each cell's maximally effective angle for stimulus onset. The distributions of these angles for all cells are shown in polar coordinates in Figure 4A. The length of each vector line from the origin indicates the number of cells responding maximally at that angle (i.e., the cell's "best" direction). Vectors are scaled proportionately to the longest line, which is at 45°. If two angles yielded the same maximal discharge, the best angle was determined by the lower standard deviation. For five cells (three rapidly adapting and two slowly adapting), maximal discharges and standard deviations were equal for two angles, and therefore both were tabulated as a maximal angle. Within the population, there appears to be an overall preference for whisker movements in upward directions of 45°, 90°, and 135°. This preference is due to a pronounced nonrandom distribution of maximal angles in favor of upward whisker deflections in the rapidly adapting (Fig. 4B) but not the slowly adapting (Fig. 4C) population. Overall, there was no systematic correlation between a cell's best angle and the magnitude of its ON response, except that slowly adapting cells preferring 90° deflections (but not movements at 45° or 135°) responded the most vigorously (data not shown). Also, chi-square tests failed to reveal any relationship between the location

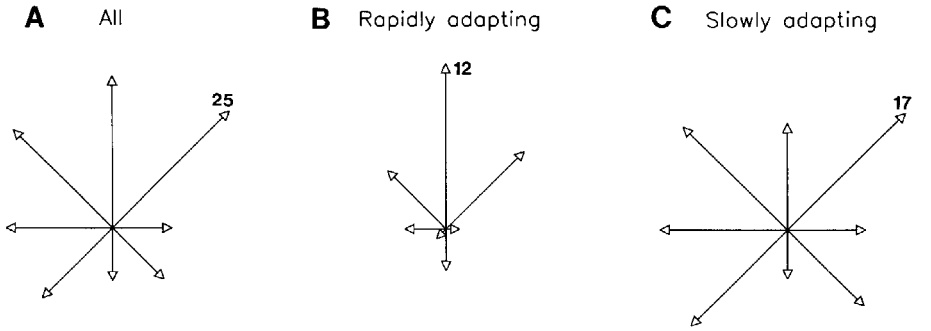

FIGURE 4. Distributions of maximally effective angles for stimulus onsets. The length of each vector line from the origin indicates the number of cells responding maximally at that angle (0° or caudal, right; 90° or dorsal, up; see inset in Fig. 1). Vectors are scaled proportionally to the longest line, and in each panel the number of units responding to that angle is indicated next to the longest vector. Panel A shows all cells; panels B and C display rapidly adapting and slowly adapting populations, respectively.

of a whisker within the mystacial pad and the preferred angles of its associated ganglion cells.

DIRECTIONAL SENSITIVITY

Most ganglion cells responded differentially to the angular direction in which the vibrissal hair was deflected. To quantify this, cells were classified into eight categories (see "Methods"). Category 0 represents the most poorly tuned cells, category 7 the best. For example, in terms of their ON responses, the units of Figures 1A and 1B are category 7 and category 6 cells. Figures 5A and 5B show angular tuning histograms for ON and OFF responses. For the former, most cells (81%) were well tuned, defined as categories 5–7. Only 3% were poorly tuned (categories 0–2). Similarly, for OFF responses, 74% were well tuned; only 8% were poorly tuned. For both ON and OFF responses, Kolmogorov–Smirnov tests showed no differences between rapidly and slowly adapting cells (p's > 0.05). Plateau responses of slowly adapting cells (Fig. 5C) were somewhat less well tuned than ON or OFF responses (categories 5–7, 72%; categories 0–2, 22%). Again, this could be due to the inclusion of some cells classified as slowly adapting that responded with exceptionally low discharge levels during the stimulus plateau.

A consistently observed difference between rapidly and slowly adapting cells is that the former often respond to many, or all, angles of initial whisker displacement, whereas the latter typically respond well to only a few onset angles, with little or no discharge to the others. For example, the rapidly adapting cell of Figure 1A discharged at least 1 spike/stimulus onset at all eight angles; the slowly adapting cell of Figure 1B failed to discharge any spikes for 10 repetitions at four of the eight angles. In the population profiles of Figures 2B and 2C, which sum responses for all eight deflection angles, this is demonstrated by the larger ON (and OFF) responses of the rapidly adapting units. Figure 6 plots the proportions of rapidly and slowly adapting cells displaying different numbers of null angles. Approximately 50% of the slowly adapting cells (45 of 92) had at least one null angle, compared to only 13% (4 of 31) of rapidly adapting cells. Also, slowly adapting cells discharged 8.64 times

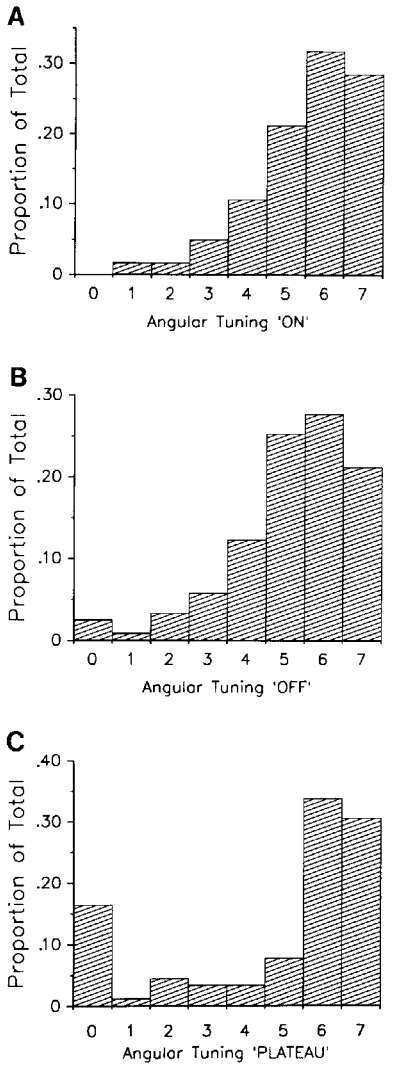

FIGURE 5. Angular tuning. Panels A and B show distributions of angular tuning categories for the whisker's ON and OFF responses, respectively (n = 123). Each cell was categorized on the basis of how many angles evoked a statistically smaller response than that produced by the cell's maximally activating angle. Category 0 represents nontuned cells (all angles equivalent), category 7 the most highly selective (see text). Panel C shows distributions of angular tuning categories for the plateau responses of slowly adapting cells (n = 92).

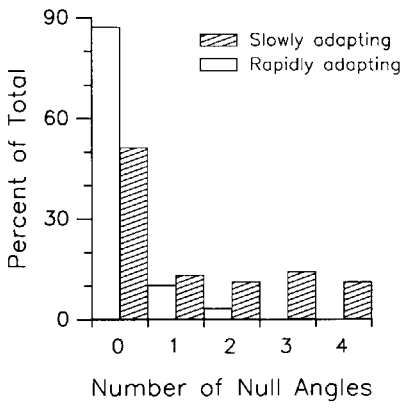

FIGURE 6. Relative frequencies of null directions in rapidly and slowly adapting units. A null response is defined as the complete absence of stimulus-evoked discharges for 10 stimulus onsets.

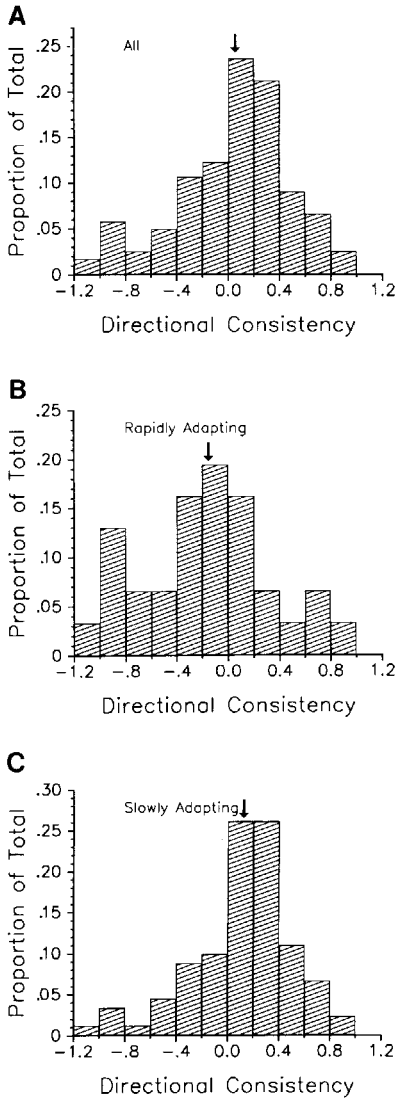

FIGURE 7. Directional consistency. Panel A plots the distributions of an index related to the directional consistency of each cell's response to whisker movements in opposite directions. More positive values indicate greater selectivity for whisker movement in a particular direction, regardless of the initial position of the hair (see text). The distributions for rapidly adapting (n = 31) and slowly adapting cells (n = 92) are shown in panels B and C, respectively. Arrows denote means.

more spikes at their maximally effective onset angle than at their minimally effective one. By contrast, the ratio of maximum angle discharge to minimum angle discharge was 3.48 for rapidly adapting units. Thus slowly adapting cells respond more selectively to deflection angle, in that they display more marked differences between responses to their "best" and "worst" angles.

Many slowly adapting units discharged vigorously to the onset of initial whisker displacements in one direction and responded almost equally well to stimulus offsets following initial movements in the opposite direction (see Fig. 1B). The angular selectivity of such cells is therefore *directionally consistent*. Correlation coefficients between ON and OFF responses at the eight different angles approach −1.0. To quantify this, a directional consistency index was computed (see "Methods). For example, the unit shown in Figure 1A has a directional consistency index of −0.06; that in Figure 1B has one of 0.12. Figure 7 plots

the distribution of these indices for all cells (Fig. 7A), for rapidly adapting cells (Fig. 7B), and for slowly adapting cells (Fig. 7C). The mean for all cells was 0.051; that for rapidly adapting cells was −0.158; and that for slowly adapting cells was 0.121. The difference between rapidly and slowly adapting cells was statistically significant (two-tailed t test, $p < 0.01$). Comparisons of directional consistency with angular tuning failed to reveal a statistically significant correlation between these two measures for either rapidly adapting ($r = 0.30$, $p = 0.107$) or slowly adapting ($r = 0.20$, $p = 0.055$) cells. Thus, these two indices appear to measure somewhat dissimilar aspects of unit responses to whisker movements in different directions.

UNIT RESPONSIVENESS AND DIRECTIONAL SENSITIVITY

Directionally sensitive cells responded more vigorously to whisker stimulation than cells lacking strong directional preferences. This relationship is illustrated in Figure 8, which plots spikes/stimulus onset at the maximally effective angle as a function of angular tuning category. Both rapidly and slowly adapting cells display monotonic increases in spike discharge with increasing selectivity for whisker movements at different angles. The function for slowly adapting cells, however, displays a steeper slope, and for categories 5–7 (i.e., well-tuned cells), they discharge significantly more spikes/stimulus onset at their best angle than rapidly adapting cells (t test, $p < 0.01$). Similar monotonic relationships are observed between angular tuning category and maximal-angle OFF responses, and between angular tuning category and maximal-angle plateau responses of slowly adapting units (data not shown). For slowly adapting cells, the magnitude of the maximal ON response was positively correlated with directional consistency ($r = 0.28$, $p < 0.01$), and the magnitude of the minimal ON response was negatively correlated ($r = -0.37$, $p < 0.01$). Statistically significant correlations were not found for either measure in the rapidly adapting population. Taken together, the findings indicate that cells that are most selective for displacement direction respond most vigorously to whisker stimulation.

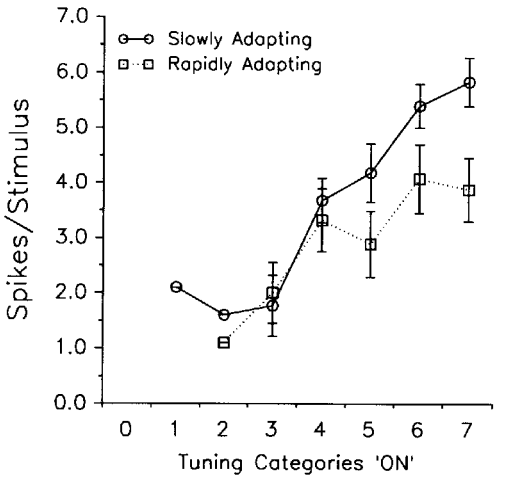

FIGURE 8. Angular tuning and unit responsiveness. The relationship of angular tuning category to maximal-angle discharge in spikes/stimulus onset is plotted. Rapidly adapting and slowly adapting populations are shown separately. Bars denote ±1 *SEM*.

DISCUSSION

The present findings demonstrate that the majority of low-threshold mechanoreceptive afferent fibers innervating the mystacial vibrissae in rats respond in slowly adapting fashion to whisker movements in particular directions. Results are generally consistent with those from other studies, which have shown that first-order neurons in the vibrissa systems of a number of species encode a variety of specific parameters of whisker displacement (see below). These findings, together with behavioral data demonstrating remarkable tactile discrimination abilities by rats using only their vibrissae (Carvell and Simons, 1988), are consistent with the conclusion that the vibrissa–trigeminal system detects subtle variations in the surface features of objects in the animal's immediate environment. Comparisons of the response properties of peripheral and central neurons indicate, however, that the neural signal originating in the sensory periphery is not faithfully reproduced through the synaptic relays to the primary somatosensory cortex. Rather, the signal is progressively and substantially transformed by mechanisms that function to integrate information from different peripheral receptors and from different, individual vibrissae.

OTHER STUDIES OF FIRST-ORDER VIBRISSA NEURONS

In all species studied to date, individual peripheral nerves have been reported to respond to low-threshold mechanical stimulation of a single vibrissa only (Fitzgerald, 1940; Kerr and Lysak, 1964; Zucker and Welker, 1969; Hahn, 1971; Gottschaldt et al., 1973; Pubols et al., 1973; Gibson and Welker, 1983a; Jacquin et al., 1986; see also Nilsson, 1969). Unit responses to two or more whiskers can be elicited with whisker deflections large enough to deform the mystacial pad (see Simons, 1985). In the absence of specific stimulation, most cells in our sample were virtually silent. Reports of the incidence and rates of spontaneous activity in vibrissal afferents vary considerably, however. In rat trigeminal ganglion, Zucker and Welker (1969) observed spontaneous discharges in only 6.5% of the cells; and Gibson and Welker (1983a) attributed all of the observed spontaneous activity to nerve damage by the recording electrode, small movements of the vibrissae, and/or hysteresis of the hair shaft. We too observed hysteresis effects following either manual or controlled whisker deflections (see also Gottschaldt et al., 1973). By contrast, Dykes (1975) reported cells having exceptionally high rates of spontaneous activity in cats and seals, although other investigations of cats have reported considerably lower rates (Hahn, 1971; Gottschaldt et al., 1973). Perhaps the elastic properties of the skin surrounding the follicle or of tissues within the follicle contribute to the generation of spontaneous activity. Regardless of whether the peripheral nerves are active in the absence of experimentally applied stimuli, the exceptional sensitivity of many of the receptors makes it unlikely that the adult trigeminal ganglion is ever silent in a natural setting.

In our sample of ganglion cells, 75% were classified as slowly adapting. Two other studies in rats reported 60% (Zucker and Welker, 1969) and 45% (Gibson and Welker, 1983a). Even more widely discrepant findings have been reported in cats: Dykes (1975) reported only 21.5% slowly adapting cells; Gottschaldt and his colleagues 67% (Gottschaldt et al., 1973) and 64% (Schultz et al., 1976); and Fitzgerald 100% (1940). A value of 53% was reported for the opossum (Pubols et al., 1973), and 84% for the cat and monkey (Kerr

and Lysak, 1964). Our estimate is on the upper end of the reported range and probably reflects (1) the statistical procedure used to classify the cells quantitatively and (2) the systematic testing of responses at eight different deflection angles spanning a full 360°. Also, the relatively low incidence of rapidly adapting cells may reflect the fact that we limited our analyses to units that could be driven by our stimulators; excluded cells having large-amplitude, high-velocity thresholds were rapidly adapting, as judged qualitatively by manual stimulation. We did not attempt to subclassify slowly adapting cells on the basis of the regularity of their sustained discharges, as Gottschaldt et al. (1973) did. Nevertheless, we did observe that some units discharged in a clearly regular fashion. Gibson and Welker (1983a) studied this property of ganglion cells in detail and concluded that the interspike interval profiles of slowly adapting vibrissa afferents in rats represent a continuum that is not distributed into two distinct populations.

DIRECTIONAL SENSITIVITY AND VIBRISSAL MORPHOLOGY

All of the aforementioned studies have reported qualitatively that some vibrissal afferents respond differentially to the direction in which the whisker is moved. In the present study, directional sensitivity was quantified from data obtained using standardized deflections of whiskers in different directions. When displaced 1 mm from a static position (resting or deflected), more than 70% of the cells responded more vigorously (at a 95% confidence level) to movements in one to three of eight cardinal directions than to the other angles. Since in almost all cases the most effective angles are contiguous, the data show that most low-threshold vibrissal afferents in the rat display a preference for whisker movement within an arc of 45–135°. Such preferences are manifested differently by rapidly and slowly adapting cells. The former often discharge spikes to most or all deflection angles, with the largest response at one, two, or three adjacent ones. By contrast, slowly adapting cells are more likely to discharge action potentials at some deflection angles but not others; not only do they frequently display "null" directions, but the difference in magnitudes of the response to the "best" versus the "worst" direction is greater than for rapidly adapting cells. Differences between the two unit types are observed also in terms of directional consistency. Compared to rapidly adapting afferents, slowly adapting ones more often respond to whisker movement in a specific direction, regardless of the initial position of the hair (neutral or deflected). Some investigators (Gottschaldt et al., 1973; Schultz et al., 1976) have regarded this property as the defining characteristic of directional sensitivity.

We interpret our findings to indicate that slowly adapting vibrissal afferents respond more selectively to whisker movements in particular directions than do rapidly adapting units. Despite the qualitative nature of most previous investigations of the directional properties of first-order vibrissa neurons, a consistent finding in those studies where comparisons can be made (Fitzgerald, 1940; Gottschaldt et al., 1973; Pubols et al., 1973; Jacquin et al., 1986; see also Nilsson, 1969) is that slowly adapting afferents are more directional than rapidly adapting ones.

The differential directional sensitivities of rapidly and slowly adapting units appear to parallel differences between their putative mechanoreceptive endings and the relationships between those endings and the follicle's structure. Merkel cell endings are thought to be slowly adapting mechanoreceptors in sinus hair follicles (Gottschaldt and Vahle-Hinz, 1981).

These endings are located in the superficial half of the follicle, where they are distributed in the external sheath and interposed between the relatively rigid glassy membrane and the hair shaft (see Rice et al., 1986). Gottschaldt et al. (1973) studied the mechanism of directional sensitivity of slowly adapting cells by comparing the directional preferences of individual afferent axons to whisker movement with responses evoked by direct mechanical stimulation of the isolated, microdissected follicle. Units were excited by stimulating the superficial half of the excised follicle on the side *opposite* to the most effective bending direction. The hair itself is anchored to the base of the follicle (see Vincent, 1913). Thus, for a slowly adapting cell, the effective stimulus appears to be compression of the Merkel cell ending by the bowing action of the hair shaft, which, upon deflection of its distal end in one direction, exerts pressure on the opposite side of the follicle.

Gottschaldt et al. (1973) were the first to speculate that lanceolate-like endings are associated with low-velocity-threshold rapidly adapting afferents in sinus hairs; the larger proportion of rapidly adapting afferents, which had higher velocity thresholds, were attributed to Golgi–Mazzoni corpuscles. Rice et al. (1986) did not identify Golgi–Mazzoni endings in rat vibrissal follicles. They proposed that lanceolate endings mediate rapidly adapting responses and that these endings are activated best by stretch, not compression. These endings are arranged in vertically oriented palisades parallel to the long axis of the hair shaft and are embedded in a mesenchymal sheath. Rice et al. proposed further that the blood sinus, ringwulst, and mesenchymal sheath constitute an "accessory structure" that translates movement of the distal end of the hair into a stretching of the mesenchymal sheath, thus activating the lanceolate endings embedded therein. According to the model of Rice et al., stretch would be effective on all sides of the hair shaft *except* that opposite to the deflection of the distal end; in the latter case, the lanceolate endings would be compressed and thus would be relatively inactive. They hypothesize therefore that (1) rapidly adapting vibrissal afferents should respond over a wide range of deflection angles, and (2) a null direction should be evident. Our findings support the former hypothesis, because rapidly adapting units were observed consistently to discharge at least some action potentials with most or all onset deflection angles. Similarly, the finding that these cells respond to most or all angles of stimulus offset is consistent with the speculation of Rice et al. that the inertial and elastic properties of the ringwulst and mesenchymal sheath, respectively, would effectively activate lanceolate endings upon return of the deflected whisker to its neutral state. The present results accord with this, since OFF responses of rapidly adapting cells were observed for most stimulus angles and their maximal OFF responses were almost as large as their maximal ON responses. Our finding that only a small percentage of rapidly adapting units display the predicted null direction is probably due to our use of relatively large-amplitude stimuli that would produce rather widespread distortions in the elastic tissue in which the lanceolate endings are embedded.

An interesting and unexpected finding is the marked preference of rapidly adapting but not slowly adapting units for upward whisker deflections. If, as suggested above, the directional preference of a vibrissal hair afferent is determined by the circumferential location of its mechanoreceptive ending in the hair follicle, we predict that Merkel cell endings and lanceolate endings are not similarly distributed around the hair shaft. Specifically, Merkel cells should be uniformly positioned around the follicle, whereas lanceolate endings should be concentrated in its dorsal aspect, where they are stretched upon upward (90°) deflections of the distal end

of the hair shaft. Another possibility is a circumferential nonuniformity in the accessory structure in which the lanceolate endings are embedded.

RESPONSE TRANSFORMATION IN THE WHISKER–BARREL SYSTEM

Our recent study of vibrissa neurons in the ventrobasal thalamus showed that only 37% of the cells there are slowly adapting, according to the same criterion used in the present study (Simons and Carvell, 1989; see also Ito, 1988). It is unlikely that this pronounced difference is due to a preferential projection of rapidly adapting inputs from the periphery through the brainstem and then to the thalamus. Reasons for this are twofold. First, there is no strong bias for upward whisker deflections in the thalamus (Simons and Carvell, unpublished observations), which would be expected if rapidly adapting receptors were the major source of peripheral input. Second, many thalamic neurons have positive directional consistency indices, and indeed the mean value for this measure for all units in the thalamus is more nearly comparable to the mean for slowly adapting ganglion cells than for rapidly adapting ones. Thus it appears that inputs from slowly adapting ganglion cells do project to the ventrobasal thalamus, but that dynamic components of the response profiles are altered in the brainstem and/or at the level of the thalamus itself. We propose that this change is effected in large part by inhibitory mechanisms within the central nervous system that produce a stimulus-evoked, time-dependent suppression of neural activity. As a result, surround or cross-whisker inhibition is observed in the thalamus but not in the trigeminal ganglion (Simons, 1985; Simons and Carvell, 1989). In addition, the population profile of cells in the thalamus but not in the ganglion is characterized by a marked suppression of activity following the ON response (compare present Fig. 2 with Fig. 15 in Simons and Carvell, 1989). Cross-whisker inhibition and postexcitatory inhibition are even more pronounced in layer IV of the barrel cortex, which, unlike the vibrissa thalamus, contains numerous local inhibitory neurons (see Lin et al., 1985; Harris and Hendrickson, 1987).

An important finding in the present study is that most trigeminal ganglion cells respond selectively to whisker movements in different directions. By contrast, 32% of thalamic cells and only 15% of cortical barrel cells are categorized as well-tuned for deflection angle, according to identical quantitative criteria (Simons and Carvell, 1989). Conversely, thalamic and cortical cells respond to more deflection angles than do the primary afferent fibers. A parallel observation is that, unlike ganglion cells, these central neurons have excitatory and/or inhibitory receptive fields that encompass more than one whisker. Together, these findings indicate a central convergence of information arising from different peripheral axons innervating the same hair follicle, as well as convergence from afferents innervating different follicles. The former can account for the broader angular tuning of central neurons, whereas the latter can explain their larger excitatory and/or inhibitory receptive fields. The extent to which convergent mechanisms exist in the brainstem remains to be determined (see Gottschaldt and Young, 1977a,b). Moreover, it is unlikely that all neurons in the whisker–barrel pathway receive extensively convergent inputs from relay cells. The indirect evidence for this is that well-tuned cells in the trigeminal ganglion, thalamic barreloids, and cortical barrels share a common property of being the most strongly driven units (see also Simons and Carvell, 1989). Nevertheless, within the barrels, strongly driven, well-tuned cells constitute only a

small minority of the population, suggesting that convergence is a fundamental mechanism of information transfer in the vibrissa–trigeminal system.

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