Thalamocortical Response Transformation in the Rat Vibrissa/Barrel System

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SUMMARY AND CONCLUSIONS

1. Extracellular single-unit recordings and controlled whisker stimuli were used to compare response properties between cells in the “barrels” of the thalamic ventrobasal complex and those in the cytochrome oxidase-rich centers of the “barrels” in the first somatic sensory cortex. Individual vibrissae were deflected alone or in paired combination involving the neuron’s maximally excitatory whisker and an adjacent one in the same or neighboring whisker rows. Quantitative data were derived from 135 thalamocortical unit’s (TCUs), 242 “regular-spike” barrel units (RSUs), and 16 “fast-spike” barrel units (FSUs) recorded in 26 normal adult rats.

2. Compared with TCUs, RSUs displayed lower rates of spontaneous activity and responded less vigorously to whisker stimuli. Proportionally, more than twice as many TCUs as RSUs responded in slowly adapting fashion to at least one angular direction of whisker displacement. Discharges of slowly adapting TCUs were ~3.5 times greater than those of slowly adapting RSUs.

3. Proportionally, about twice as many TCUs than RSUs responded selectively to whisker movements in different angular directions.

4. Cells in the thalamus responded more vigorously to a larger number of whiskers than RSUs in the cortex. Depending on the stimulus conditions, two to three times more TCUs than RSUs were excited by two or more whiskers.

5. Following displacement of an adjacent whisker, unit discharges to subsequent deflections of the maximally excitatory whisker were reduced in a time-dependent fashion. The time course of response suppression was similar in TCUs and RSUs, but inhibitory interactions between adjacent whiskers were observed much less often in the thalamus. A cyclic pattern of stimulus-evoked excitation/inhibition characterizes responses in the cortical barrels but is considerably less pronounced in the thalamic barreloids.

6. The presence and/or degree of response suppression depended on which adjacent whisker was stimulated and on the angular direction of that whisker’s movement. For individual TCUs, some adjacent whiskers evoked inhibition, whereas others did not. The vast majority of RSUs displayed response suppression to all adjacent whiskers. Unlike receptive fields of TCUs, those of RSUs have small—i.e., single-whisker—excitatory centers with potent and symmetrical inhibitory surrounds.

7. Fast-spike units in the barrels displayed the greatest spontaneous and stimulus-evoked activities and were the least selective for whisker movements at different angular directions. FSUs had the largest excitatory receptive fields; 100% responded to two or more vibrissae.

8. Barrel circuitry transforms the thalamic signal into a spatial code that enhances contrast among inputs from adjacent whiskers and a temporal code that establishes a characteristic pattern of cortical excitation and inhibition.

INTRODUCTION

Anatomic and physiological evidence indicates that the rodent primary somatosensory cortex contains subsets of neurons that are linked together to form local networks that transform tactile information from the mystacial vibrissae, or whiskers, on the contralateral face (56). Thus the face area within this cortex contains identifiable clusters of layer IV cells, called barrels, that are related one-to-one to individual vibrissae (67). Barrels are thought to be morphological correlates in layer IV of functional cortical columns that extend throughout the thickness of the cortex (77). For example, within a vertical electrode penetration from pia to white matter, all driveable cells are activated by stimulation of the one vibrissa that corresponds anatomically to the layer IV barrel through which the electrode passes, and within the barrel most cells respond only, or best, to this columnar or “principal” whisker (PW) (1, 9, 53, 60). Receptive fields of cells in infragranular layers, and to a lesser extent in supragranular layers, typically encompass many more vibrissae. These findings suggest that the cortex operates to synthesize excitatory multi-whisker receptive fields.

Whisker displacements also evoke inhibition within the barrel cortex (8, 55). Following movement of a vibrissa, cortical unit discharges to subsequent deflections of the same or adjacent whiskers are reduced in a time-dependent fashion. The columnar whisker consistently evokes the strongest inhibition, whereas adjacent whiskers elicit variable or no inhibition. For some cells in the deeper layers, excitatory and inhibitory effects of adjacent, noncolumnar vibrissae are distributed asymmetrically around the principal whisker, yielding unit responses that appear to be selective for patterned whisker stimuli that mimic object movement in a particular direction across the mystacial pad.

Physiological studies thus indicate that an important function of the barrel cortex is to integrate information arising from the array of whiskers on the face. One hypothesis is that this integration involves neuronal interactions among cortical cells and is not simply a reflection of processing that has occurred at lower levels of the ascending sensory system (53, 55). This was supported indirectly by a number of physiological studies indicating that the large majority of cells in the thalamic ventrobasal complex (VB),...
ties than were previously used, an additional sample of conditions than those employed in our previous cortical data were obtained under slightly different experimental diversity of unit response properties. Because the thalamic "barrel" was known to be immediate presynaptic to thalamic cells that are thought to be immediately presynaptic to the cortical "barrel" (18), and VB in rats is largely devoid of inhibitory interneurons (20). Inhibition influences from cells in the latter nucleus are directed only over the barrel of interest. This procedure helped us to target VB. For cortical recording experiments, we wanted to sample units exclusively from the cytochrome oxidase-rich barrel centers in layer IV, which in rats occupy only part of the areal extent of the posteromedial barrel subfield (33). To maximize the likelihood of recording from a barrel center, the following triangulation procedure was used. The exposed skull was thinned by careful drilling, and a scaled drawing of the surface vasculature, which was visible through the remaining thickness of bone, was made. Two or three small openings were then produced over widely separated points of the barrel field, and under continuing barbiturate anesthesia tungsten microelectrodes were recorded and observed from a number of cytochrome oxidase-stained specimens. Using a best-match procedure, the approximate location of a given barrel could be determined with respect to the surface vasculature. A larger hole in the skull and dura (~0.5 mm^2) was then produced over the barrel of interest. This procedure helped us to target a barrel center in virtually all of the subsequent electrode penetrations. For both thalamic and cortical experiments, an acrylic dam was constructed around the skull excavation and was filled with warm saline. Incisions were sutured closed around the dam and cannulae.

Nineteen of the 26 rats were subsequently maintained in a lightly narcotized and sedated state by continuous intravenous infusion of lentan, a potent, synthetic opiate receptor agonist (Sublimaze, Janssen Pharmaceuticals; 5-10 µg/kg -1 h^-1). Barrel neurons recorded under these conditions are indistinguishable from those recorded in the absence of general anesthesia (57). This dosage range of fentanyl produces in rats that are not paralyzed but suspended in a torso sling (Harvard Apparatus) a behavioral state that can be characterized as tranquilization accompanied by mild hypogalasia; though sedated compared to unanesthetized animals, rats still display spontaneous movements, particularly of the vibrissae. To prevent such movement that would preclude the use of controlled whisker stimuli (see below), paralysis was induced and maintained by a mixture of gallamine triethiodide and pancuronium bromide; this was administered through an indwelling intraperitoneal cannula that consisted of a polyethylene tube connected to an infusion pump. Rats were artificially ventilated with a respirator that was adjusted to maintain measured end-tidal carbon dioxide levels at 3.5-4.5%. Core temperature was kept at 37°C by a servo-controlled heating blanket. Ophthalmic ointment was applied to prevent drying of the corneas. The condition of the rats was assessed by observation of the electroencephalogram, electrocardiogram, expired CO_2_ levels, pupillary reflexes, and capillary perfusion of glabrous skin. Ex-
Experiments were terminated by barbiturate overdose in any individual rat in which physiological conditions could not be maintained within normal ranges, e.g., abnormal EEG activity, increased or decreased expired CO2 levels.

All VB recordings and all of the cortical units studied with multi-whisker stimuli were obtained from rats receiving fentanyl. We also included in the analyses data from an earlier study that examined the effects of fentanyl on the response properties of barrel neurons using single-whisker stimuli (57). Among these were data from seven rats maintained during the recording sessions with local anesthetics only as described previously (55). Surgical preparation, maintenance, and monitoring of these animals were identical to the procedures described above except that fentanyl was not administered during the recording sessions, and 5% lidocaine or 0.5% bupivacaine was applied periodically to all wound margins. Again, experiments were terminated by barbiturate overdose if normative physiological conditions could not be maintained.

**Electrophysiological recordings**

Extracellular unit recordings were obtained with double-barreled glass microelectrodes (59). One barrel was filled with 3 M NaCl (~1-μm tip diameter; 6 to 12-MΩ impedance) and was used for unit recordings; the other barrel contained 10% horseradish peroxidase (HRP) in 0.5 M Tris·HCl that was iontophoretically ejected to mark individual recording sites and/or the termination of electrode tracks. For thalamic recordings, electrode penetrations passed through VB in the approximate dorsal/ventral plane of the Paxinos and Watson atlas. For cortex, electrodes were oriented perpendicular to the pial surface overlaying the barrel field. Electrodes were advanced in 3- to 4-μm steps by means of a hydraulic microdrive equipped with a digital counter. During advancement, whiskers on the contralateral (left) face were stimulated either manually or with electromechanical stimulators that deflected whiskers randomly in different directions (see below). Extracellular recordings were obtained from single units as determined from spike amplitude and waveform criteria. An analog delay line was used for visualizing the entire spike waveform, and an amplitude discriminator was used to digitize the impulse events.

Data were obtained almost exclusively from units discharging initially negative spikes. The polarity of these potentials often could be reversed with further advancement of the electrode; though larger in amplitude, such initially positive potentials often displayed signs of injury and on continued electrode advancement produced trains of injury discharges. In VB initially negative recordings were assumed to be somal spikes and were easily distinguished from presumed axon spikes because the latter were always initially positive, of shorter duration, and often characterized by exceptionally high levels of spontaneous activity. On impalement, these units disappeared almost immediately without prolonged injury discharges. In addition, the receptive fields of these units frequently were on vibrissae or sinus hairs located some distance away from those included in the receptive fields of presumed somal spikes recorded nearby. Finally, the electrode typically passed through zones of ~150-250 μm in which somal spikes were observed commonly, separated by narrower regions in which the predominant activity was axonlike. In VB, vibrissal-related aggregates of neurons, called barreloids, are separated by dense fiber plexuses containing axons projecting to or from more remote barreloids (34, 65). We therefore attribute the initially negative, longer-duration spikes to discharges of barreloid neurons. Because all barreloid cells in rats are thought to project to the barrel cortex (see DISCUSSION), somal-type spikes recorded in VB are presumed to be thalamocortical units (TCUs). Axonlike recordings were not observed in the cortical barrels using the glass micropipettes. In terms of spike waveform characteristics, barrel units were classified on the basis of the duration of their action potentials. Fast-spike units (FSUs) have action potentials with initially negative waves of ~150 μs, whereas those of “regular-spike” units (RSUs) last 350–500 μs. Compared to RSUs, FSUs are more difficult to isolate and study for long periods of time (see also Ref. 40).

At the conclusion of the recording sessions, rats were deeply anesthetized with pentobarbital sodium and perfused for HRP and cytochrome oxidase histochemistry (59). For cortical experiments, the right hemisphere was cut tangential to the pial surface overlaying the barrel field. Thalami were cut in the coronal plane. Using microdrive readings and HRP spots, all electrode tracks were reconstructed. Data are reported only for units recorded in the cytochrome oxidase rich barrel centers in layer IV and lower layer III or in the medial aspect of VB where the barreloids are located. Because the plane of section for visualizing barreloids in adult rats differs considerably from the plane of the VB electrode penetrations, no attempt was made to reconstruct thalamic penetrations with respect to individual barreloids.

**Stimulation**

Individual whiskers were deflected using multiangular electromechanical stimulators (54). The stimulators were constructed from two sets of piezoelectric bimorph benders (Vernitron Piezoelectric, Bedford, OH) that are cemented together so that their planes of movement are orthogonal to each other. Separate driving signals 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. Stimulus waveforms were ramp-and-hold trapezoids that produced ~1-mm whisker displacements of 200 ms duration; onset and offset velocities were ~135 mm/s. Stimulus waveforms were filtered to reduce mechanical ringing of the piezoelectric devices. The stimulators were controlled by a laboratory computer (LSI 11/3, Digital Equipment Corp.), and for a given battery of stimuli (see below) stimulus parameters were randomized and delivered at stimulus intervals of at least 2 s. The computer was used also to simultaneously acquire and store the unit data. Spike interevent times were measured with a resolution of 100 μs and retained in a format that allowed complete reconstruction of the spike discharge pattern for each stimulus presentation. Data were collected for a period of 300 ms that bracketed the whisker stimulus.

Individual vibrissae were specified by row (A through E, proceeding dorsal to ventral) and arc (1 through 4, proceeding caudal to rostral; see inset, Fig. 2). Whiskers were deflected individually, either alone or in paired combinations involving the “principal” whisker and one immediately adjacent vibrissa. The principal whisker, or PW, was defined during the experiment as the vibrissa that typically elicited the most vigorous responses from units recorded in close succession. In the cortex, the PW was found to correspond invariably to the barrel in which the cell was recorded. In VB, the topographical representation of PWs was consistent with previous anatomic and physiological descriptions of the vibrissa representation in rats (34, 64).

**Experimental procedures**

Whisker stimuli were designed to yield quantitative information about excitatory and inhibitory components of unit receptive fields. Data were obtained using three protocols.

**PROTOCOL 1.** The PW was deflected in 8 different angular directions, i.e., in 45° increments relative to the horizontal align-
RESULTS.

The initial step in all of the analyses was to convert the raw data, consisting of individual spike trains, into peristimulus time histograms (PSTHs) having 1-ms bins. The mean and variance of spike discharges during selected time epochs were computed from the individual spike trains. Because ON responses of most cells averaged <2.0 spikes/stimulus, interspike interval analyses were not performed, and therefore spike-counts per unit time is the metric used for most of the data analyses. Data were analyzed with the LSI 11/73 or with an IBM PC/XT running the statistics

ment of the whisker rows. Stimuli were delivered randomly for each sequence of 8 angles, and this was repeated 10 times for a total of 80 stimulus presentations. The mean and variance of the spike discharge for a 20-ms period beginning 5 ms after the onset of the deflection were computed on-line. A visual representation of the cell’s angular preference for stimulus onset was displayed on a graphics terminal in the form of a polar plot. These data were used to identify the unit’s maximally activating or “best” angle in response to PW stimulation.

PROTOCOL 2. The PW and an adjacent whisker were deflected in a conditioning-test paradigm. Both whiskers were moved at the PW’s best angle as determined above. Deflections of the two whiskers were separated in time by conditioning-test intervals (hereafter referred to as interdeflection intervals) of 0, 2, 5, 10, 20, 50, and 100 ms (55). The spatial sequence of the whisker deflections was varied so that in one-half of the trials the PW was the conditioning stimulus (the first-deflected whisker) and in one-half of the trials the adjacent whisker was the conditioning stimulus. Each whisker was also deflected alone. An individual battery thus consisted of 15 different stimuli. All stimuli within each battery were randomized and repeated 10 times for a total of 150 stimulus presentations. Data obtained with this protocol were used to determine the magnitude and time course of cross-whisker inhibition.

PROTOCOL 3. An adjacent whisker was moved at 8 different angular directions followed in each case by deflection of the PW at its best angle. A 20-ms interdeflection interval was used because cross-whisker inhibition is maximal at this time (see below). The PW was also deflected alone. The protocol thus consisted of 9 different randomly delivered stimuli that were repeated 10 times for a total of 90 stimulus presentations. Because adjacent whiskers were deflected over a range of 360°, data obtained with this protocol provided a comprehensive assessment of the excitatory and inhibitory contributions of the adjacent whisker.

For all units single-whisker polar plots (protocol 1) were obtained first. The two multi-whisker protocols were applied variably. In initial VB experiments, protocol 2 was used most often so that the time period of maximal cross-whisker inhibition could be identified. In almost all cases, the PW was paired with each of the (two) adjacent whiskers in the same row. When it became apparent that more cells than expected had multi-whisker receptive fields and that the best excitatory angle for a given adjacent whisker was not necessarily the same as the best angle for the PW, protocol 3 was used more often. An attempt was made to pair the PW with adjacent whiskers both in the same and in the neighboring rows, a procedure that required attachment of stimulators to five whiskers. Because in VB an individual electrode track typically passed through several barreloids, stimulators had to be continually repositioned, thus somewhat limiting our ability to consistently pair the PW with both within- and across-row neighbors. This problem was not encountered in the barrel recordings because all penetrations during an individual experiment could be placed in the same barrel. The number of units and types of whisker pairings studied using the different protocols will be specified in RESULTS.

Data analysis

The initial step in all of the analyses was to convert the raw data, consisting of individual spike trains, into peristimulus time histograms (PSTHs) having 1-ms bins. The mean and variance of spike discharges during selected time epochs were computed from the individual spike trains. Because ON responses of most cells averaged <2.0 spikes/stimulus, interspike interval analyses were not performed, and therefore spike-counts per unit time is the metric used for most of the data analyses. Data were analyzed with the LSI 11/73 or with an IBM PC/XT running the statistics

FIG. 1. Histological localization of electrode tracks. A: 40-μm thick, frozen, coronal section through the thalamus processed for horseradish peroxidase (HRP) histochemistry and counterstained with thionin. An electrode track passing dorsoventrally through the thalamic ventrobasal complex (VB) is clearly visible, and a spot of reaction product marks the location of units responding maximally to the C1 whisker. Orientation: dorsal, up; lateral, right. The section is ~3.5 mm caudal to bregma (see Ref. 42). B: 60-μm cytochrome oxidase- (CO) stained, tangential section through the barrel field in layer IV of the somatosensory cortex. Arc 1 barrels in rows B, C, and D are indicated. Unit recordings were obtained from the CO-rich center of the C3 barrel. HRP spots (open arrows) in C were made deep to recording sites in the barrel, which are denoted by arrowheads in the C3 barrel of B. Note that the electrode tracks reduced the intensity of the CO stain. Spots in layer V were made ~500 μm below the deepest recording sites in layer IV and were found in the eighth section below the bottom of the layer IV barrel. Arrows in B and C denote corresponding blood vessels. Scale in B applies also to C. Receptive-field properties of a “fast-spike” barrel unit (FSU) recorded in the marked penetration closest to the C2 barrel are illustrated in Fig. 12. Orientation of sections: medial, up; anterior, right.
package from SPSS, Inc. Because different analytic procedures were used to derive quantitative measures of unit response properties obtained with the various stimulus protocols, specific details of these analyses will be presented in the appropriate part of RESULTS. Distributions of these measures in the TCU and RSU populations were often quite dissimilar. Therefore, two-tailed nonparametric K-S tests (Kolmogorov-Smirnov) were used for making statistical comparisons between the two populations (52). Differences between TCUs and RSUs were judged to be significant if the probability level was \( \leq 0.05 \).

RESULTS

Thalamic data were obtained from 135 TCUs recorded during 11 experiments in which rats were maintained during recording sessions with fentanyl. Findings are reported also for 242 barrel RSUs recorded during 15 experiments. One hundred four of these, from 8 experiments, were obtained from animals receiving fentanyl infusions identical to those used for the 11 thalamic experiments. The remaining RSUs from 7 animals were obtained from rats maintained without fentanyl; in these experiments only single-whisker stimuli were used. Findings from 16 FSUs will be presented separately below. Electrode track reconstructions verified that all of the data to be reported here were from cells recorded in the medial division of the thalamic ventrobasal complex or in the cytochrome oxidase-rich barrel centers of the cortex (see Fig. 1).

Some important and consistently observed differences between the receptive field properties of TCUs and RSUs are illustrated qualitatively in Fig. 2. In each panel the central peristimulus time histogram (PSTH) shows responses evoked from a single cell by deflecting the PW at its best angle. Surrounding PSTHs show the same cell's response to paired deflections of the PW and each of the immediately adjacent vibrissae. Adjacent whiskers were deflected randomly in eight angular directions, and each deflection was followed 20 ms later by movement of the PW at its best angle, i.e., protocol 3. Although the excitatory and inhibitory effects of a given adjacent whisker often depend on the angular direction of that whisker's displacement (see below), in Fig. 2 adjacent whisker responses are summed across all eight angles to illustrate the pronounced differences between the receptive fields of TCUs and RSUs in terms of the overall contributions of non-PW vibrissae. The size of the excitatory receptive field (RF) is illustrated by the presence or absence of ON responses to the initial movements of the four adjacent whiskers (open arrows). Thus the TCU (panel A) responded

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**FIG. 2.** Peristimulus time histograms (PSTHs) illustrating excitatory and inhibitory components of receptive fields of a thalamocortical unit (TCU) (A) and a "regular-spike" barrel unit (RSU) (B). In each panel the central PSTH shows responses from 40 repetitions evoked by deflecting the principal whisker (PW) at its maximally excitatory angle. Surrounding PSTHs show responses to paired whisker stimuli involving the indicated adjacent whisker and the PW. Adjacent whiskers were deflected randomly in 8 different angular directions, and each deflection was followed 70 ms later by movement of the PW at its "best" angle. Each of these PSTHs is also based on 40 stimulus repetitions (8 angles x 5 presentations). Binwidth, 2 ms. Arrows denote stimulus onsets and offsets: closed symbols, PW; open symbols, adjacent. Note that all of the PSTHs in both panels are plotted at the same scale. Whisker nomenclature and polar coordinates for deflection angle are shown in figurine.
vigorously to all four adjacent vibrissae, in addition to the PW, whereas the RSU responded well to the PW only. Inhibitory components of the RFs can be appreciated by comparing the PW “alone” responses observed in each of the central PSTHs with the changes produced in them by the adjacent whisker-conditioning stimuli. Inhibition is weak in the TCU in which deflections of only one of the four adjacent whiskers produced a substantial reduction in the PW response. Inhibitory effects of adjacent whiskers are considerably more pronounced in the barrel cell, and all adjacent vibrissae evoked PW response suppression. A difference in the two units’ levels of spontaneous activity also is readily apparent.

Response dynamics

As a population, TCUs were more active spontaneously and in response to whisker stimuli. Several measures of unit responsiveness are plotted in Figs. 3 and 4. These data are derived from the discharges of 135 TCUs and 242 RSUs evoked by each cell’s PW (protocol 1). Figure 3 plots the distributions of spontaneous activities in the two populations. For each cell, the frequency of spontaneous discharges in spikes/s was computed from 80 100-ms time epochs of prestimulus activity. Spontaneous activities of TCUs were approximately 7 times greater than those of RSUs [7.89 ± 6.77 (SD) versus 1.09 ± 1.53 spikes/stimulus; K-S test; P < 0.001]. Approximately one-third of the TCUs discharged spontaneously ≥10 spikes/s, whereas none of the RSUs displayed spontaneous discharges in that range. Conversely, 62% of RSUs but only 6% of TCUs displayed little or no spontaneous activity, i.e., ≤1.0 spikes/s. Figure 4 demonstrates that stimulus-evoked responses also are greater for TCUs. Data in panel A are based on responses elicited by deflecting each cell’s PW at its best angle; ON responses in the form of spike count averages were computed for a 20-ms epoch following the initial movement of the vibrissa. These were significantly larger in TCUs (1.72 ± 0.78 versus 1.46 ± 0.47 spikes/stimulus; K-S test, P = 0.03). Differences are apparent even disregarding relatively unresponsive cells, which were observed more often in the cortex. For example, only 2.5% of RSUs discharged ≥2.5 spikes/stimulus, whereas 17.8% of TCUs responded within that range. Differences between the magnitudes of stimulus-evoked responses are more pronounced for OFF responses (Fig. 4B). Responses of TCUs to their best angle of stimulus offset were two times larger than those of RSUs (1.58 ± 0.79 versus 0.82 ± 0.44; K-S test, P < 0.001).

TCUs were more likely than RSUs to respond with elevated discharge rates during the plateau phase of the stimulus. Quantitative criteria were used to classify cells as either slowly adapting or rapidly adapting. For each unit, polar plots obtained with PW stimulation were examined to identify the deflection angle that elicited the maximal response during the middle 100 ms of the stimulus plateau. Two-tailed t tests were used to compare the number of spikes during the plateau response to the number of spikes during equivalent periods of prestimulus activity, and a cell was classified as slowly adapting if the evoked response was significantly greater than spontaneous activity (P < 0.025). By default the remaining cells were classified as rapidly adapting. Thirty-seven percent of TCUs and 15% of RSUs were slowly adapting. Chi-squared tests for two independent samples that compared the numbers of slowly and rapidly adapting units in the two populations revealed a significant difference (P < 0.001). Figure 4C plots the distributions of plateau responses for slowly adapting TCUs and RSUs. Each cell’s spontaneous activity was subtracted from its evoked response. Plateau discharge rates in spikes/s of slowly adapting TCUs were on average 3.5 times greater than those of slowly adapting RSUs (23.74 ± 18.86 versus 6.77 ± 6.81 K-S test, P < 0.001).

Angular selectivity

Like the first-order afferents in the trigeminal ganglion (54, 78), cells in VB and in the cortex may respond differentially to the angular direction in which the vibrissal hair is deflected. Figure 5 illustrates the angular selectivities of two well-tuned TCUs. PSTHs show the accumulated responses of each neuron to 10 deflections of its PW at 8 different angles; the bottom panel shows the magnitudes of the ON responses plotted in polar coordinates. The cell in panel A responded selectively to initial movements of the C1 whisker in downward directions, i.e., 225, 270, and
315° (see inset in Fig. 2). Maximal discharges (2.90 ± 1.29 spikes/stimulus onset) were evoked by 270° deflections. Plateau responses also were maximal at these angles, and the unit’s discharge activity was suppressed at the reciprocal angles. Sustained discharges followed the OFF responses for initially upward deflection angles, i.e., return movements in downward directions. Panel B shows responses of a rapidly adapting TCU that responded maximally to initial whisker movements in upward directions. OFF responses were similarly vigorous, provided that the return movement of the whisker to its resting or neutral position was in an upward direction, e.g., initial movements at 270°.

As a population, TCUs are more selective for deflection angle than RSUs. Figure 6A shows angular tuning histograms for the two populations. Cells were classified into eight categories on the basis of how many angles elicited ON responses that were statistically smaller than those at the maximally activating angle (t tests, Ps < 0.05, one-tail). Category 0 represents the least tuned cells, category 7 the most. For example, the units in Fig. 5 are both category 5 cells. There was a significant difference between TCUs and RSUs on this measure (K-S test, P = 0.03). Overall differences between the populations are due primarily to the greater percentage of well-tuned cells (categories 5–7) in VB (TCUs: 31.1%, RSUs: 15.7%). For both TCUs and RSUs, well-tuned cells discharged more spikes/stimulus to their best angle than poorly tuned (categories 0-2) cells (TCUs: 2.15 ± 0.95 versus 1.45 ± 0.55; RSUs: 1.84 ± 0.52 versus 1.30 ± 0.37). As shown in panel B OFF responses of TCUs also were more angularly selective than those of RSUs (K-S test, P < 0.001), and as in the case of response magnitudes, differences between the populations were more pronounced for OFF than ON responses.
Many TCUs displayed strikingly directional responses. As illustrated in Fig. 5B, such units discharged vigorously to the onset of initial whisker displacements in one direction and responded almost equally well to stimulus offsets of initial movements in the opposite direction. The angular selectivity of such cells is therefore directionally consistent. For example, the unit of Fig. 5B responded to upward deflections from the whisker's neutral position (ON responses with initial deflections at 0°) and to upward deflections from its downward-deflected state back to its resting position (OFF responses following initial deflections at 270°). For such a cell, correlation coefficients between ON and OFF responses at the eight different angles approached -1.0. These properties were seldom observed in the barrels. Many cells there had negative correlations between ON and OFF responses, but these were due to the fact that such units typically responded better to stimulus onsets than offsets at all or most angles. To quantify these differences between TCUs and RSUs, a Directional Consistency Index was computed as follows

\[
\text{Directional Consistency Index} = \frac{\text{MAXOFF}}{\text{MAXON}} \times \rho \times (-1)
\]

where MAXOFF is the largest OFF response in spikes/stimulus, MAXON is the largest ON response, and \( \rho \) is the correlation coefficient between ON and OFF responses at the eight different deflection angles. Thus a cell that responds equivalently well to a stimulus onset and a stimulus offset and that displays a large negative correlation between ON and OFF responses at the eight angles will have a relatively large positive index. For example, the unit of Fig. 5A has a Directional Consistency Index of 0.06, that of Fig. 5B, 0.61. Figure 6C plots the distributions of these indices for the two populations. RSU values cluster closely about 0.0, whereas those of TCUs are skewed toward positive values. Differences between the two groups were statistically significant (TCU: \( x^2 = +0.186 \pm 0.428 \); RSU: \( x^2 = +0.010 \pm 0.224 \); K-S test, \( P < 0.001 \)). Taken together with the angular tuning data of Fig. 6, A and B, the findings demonstrate that TCUs respond more selectively to whisker movements in different angular directions.

**Multi-whisker receptive fields**

Protocols 2 and 3 involved independently deflecting adjacent and principal whiskers. These protocols were designed to examine inhibitory interactions between pairs of whiskers, but the paradigms also permit an assessment of excitatory receptive-field characteristics of adjacent whiskers. Data obtained with protocol 2 were examined quantitatively to determine whether deflections of the adjacent whisker by itself evoked a statistically significant excitatory response. The mean and variance of the spike discharge during a 20-ms period following the onset of the adjacent whisker “alone” deflection was computed, and
Angular Tuning 'ON'

Angular Tuning 'OFF'

Directional Consistency

Directional Consistency

FIG. 6. Angular tuning of 135 TCU's (left) and 242 RSU's (right). A and B: distributions of angular tuning categories for PW ON and OFF responses. 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). C plots the distributions of an index related to the directional consistency of each cell's response to PW movements in opposite directions (see text). For the purpose of comparing the 2 distributions, the dotted lines indicate 0.0, and arrowheads denote means.

tests were used to compare the ON response to an equivalent period of prestimulus activity. The evoked discharge, if present, was identified as a response if it was greater than the spontaneous activity at a 0.975 confidence level. Ninety-three adjacent whiskers from 51 TCU's and 70 adjacent whiskers from 33 RSU's were examined. Significant excitatory responses were observed for 18% of the VB cases but only 5.7% of the barrel cases. In terms of individual units, twice as many TCU's responded to at least 1 adjacent whisker (23.5% versus 12.0%).

In protocol 2 the adjacent whisker was deflected in only one angular direction, the best angle for the cell's PW. Protocol 3 provides a more comprehensive evaluation of adjacent whisker responses because the whisker was deflected at 8 angles spanning a full 360°. ON responses independent of the paired PW response could be computed because the duration of the former rarely exceeded 20 ms, and the PW was not deflected until 20 ms after the onset of the adjacent whisker stimulus. Statistical tests as above were applied to the responses evoked by the best angle for the adjacent whisker. Fifty-six adjacent whiskers for 21 TCU's and 56 adjacent whiskers for 17 RSU's were tested. Significant excitatory responses were identified for 58.9% of the TCU cases and 12.5% of the RSU cases. In terms of individual units, 71% of the TCU's but only 23.5% of the RSU's had RFs in which at least one adjacent whisker elicited a response. Numbers of single- and multi-whisker units differed significantly between the 2 populations (x² test, P < 0.01), despite the fact that slightly more whiskers/unit were examined for the RSU's. Comparison of the findings obtained with the 2 stimulation protocols suggest that the best angle for the adjacent whisker does not necessarily correspond to the best angle for the PW, the discrepancy being more pronounced in the thalamus.

Receptive-field sizes were derived from those units for which all 4 vibrissae surrounding the PW were studied.
using protocol 3. Four of 12 RSUs had multi-whisker RFs, and the average number of responsive adjacent whiskers was 1.75. For all 12 units the average receptive-field size (including the PW) was 1.58 (with respect to a maximum of 5.0). Nine of 10 TCUs had multi-whisker RFs (average of 2.55 responsive adjacent whiskers); for all 10 units the average RF size, inclusive of the PW, was 3.30.

Adjacent whisker responses were more vigorous for TCUs than RSUs. Mean discharge/stimulus onset at the best adjacent whisker angle was $1.51 \pm 0.61$ spikes for the 33 TCU cases compared with $1.03 \pm 0.31$ spikes/stimulus for the 7 RSU cases. Because PW responses were generally more vigorous in the thalamus (see above), adjacent whisker responses were normalized with respect to the response evoked by the respective PW. This was done by dividing the former by the latter. Normalized adjacent whisker responses also were somewhat larger in the barreloids than in the barrels $(0.73 \pm 0.26$ versus $0.59 \pm 0.12)$. Taken together the data demonstrate that compared to RSUs, TCUs are much more likely to be multi-whisker and that such cells display larger receptive fields having somewhat more vigorous discharges to non-PW vibrissae.

Cross-whisker inhibition: temporal factors

Protocol 2 was used to examine the effects of an adjacent whisker deflection (the conditioning stimulus) on the responses evoked by subsequent movements of the PW (test stimulus) at seven interdeflection intervals. Because the

![Figure 7. Time course of suppression of PW response by prior deflection of an adjacent whisker. Paired whisker stimuli were used to quantify the effects of deflecting an adjacent whisker on the responses of individual neurons to subsequent movements of the PW at the indicated interdeflection intervals; data are computed for ON responses only. The observed PW response was divided by the response that would be expected to occur if there was no effect of the preceding adjacent whisker deflection (see text). Values $< 1.0$ represent proportional reductions in the PW response. Data are derived from 94 whisker pairings in 51 TCUs and 70 pairings in 33 RSUs. Error bars for TCUs show $\pm 1.0$ SD, for RSUs $-1.0$ SD.](image1)

![Figure 8. Relative frequency of statistically significant reductions in PW responses as a function of the time interval between PW deflections and prior deflections of an adjacent whisker. Percentages are based on the numbers of TCU and RSU whisker pairs tested, which are the same as those plotted in Fig. 7. Hatched bars, TCUs; shaded bars, RSUs.](image2)
basis of chance fluctuations in the data. Consequently, computation of the expected response was performed on a trial-by-trial basis to obtain its mean and variance over the 10 stimulus presentations. Mean and variance values for the observed and the computed expected responses were then compared using two-tailed \( t \) tests. An observed test response was identified as reflecting "statistically significant inhibition" if it was smaller than the expected response at a criterion level of \( \leq 0.025 \). Figure 8 plots the percentages of inhibitory interactions at the 7 interdeflection intervals. Following the adjacent whisker deflection, statistically significant decrements in the PW response become progressively more frequent and are observed somewhat more often at the shorter interdeflection intervals in TCUs than in RSUs. For both populations inhibitory interactions occur most frequently with 10- and 20-ms interdeflection intervals. Differences between TCUs and RSUs are most pronounced at 20-ms intervals in which the numbers of significant versus nonsignificant inhibitory interactions would be expected to occur by chance less than once in 100 samples (\( \chi^2 \) test). For those pairings in which inhibition was observed at 10-ms intervals, 83% of RSUs and 61% of TCUs displayed inhibition also at 20-ms intervals. An important finding is that when statistically significant inhibition is observed at 20-ms intervals, the average response suppression values for the 2 populations are equivalent (TCUs: 0.16 \( \pm \) 0.18; RSUs: 0.11 \( \pm \) 0.10; K-S test, \( P > 0.05 \)).

Inspection of response suppression curves for individual whisker pairings suggested that fewer TCUs displayed inhibition at any of the seven tested intervals. Quantitative analyses confirmed this. Thus in VB 43% of adjacent whiskers failed to evoke statistically significant inhibition at any interdeflection interval compared with 20% in the barrels. A \( \chi^2 \) test comparing the number of pairings with and without inhibition at any interdeflection interval showed a significant difference between TCUs and RSUs (\( P < 0.02 \)).

For 8 of 94 TCU pairs, test responses were \( \geq 1.0 \) at all 7 intervals, whereas only 1 of 70 whisker pairs in the barrels displayed all 7 test responses \( > 1.0 \). These findings indicate that facilitation is observed more often in VB, though statistically significant increases in test responses (i.e., positive \( t \) values with \( P < 0.025 \)) were rare in both populations. Interestingly, however, in both groups statistically significant facilitation was observed most often at 50-ms interdeflection intervals (TCUs: 2.1%, RSUs: 2.9%; see also Ref. 55).

**Angular inhibition**

Protocol 3 was used to determine whether the angular direction of the adjacent whisker deflection was an impor-

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**FIG. 9.** Effects of adjacent whisker stimulus angle on PW response suppression in 2 TCUs. In each panel the top PSTH shows the accumulated response of the cell to 10 PW deflections at its best onset angle, indicated at the left; the PW was deflected by itself, i.e., "alone." Remaining PSTHs show responses to paired deflections of an adjacent whisker and the PW. Adjacent whiskers were moved in 8 initial angles, as indicated, followed 20 ms later by PW deflections at its best onset angle. Stimulus onsets and offsets are indicated by arrows (open, adjacent; solid, PW). A: deflection of B2 suppressed the cell's ON responses to subsequent C2 deflections most strongly at 90, 135, and 180°. The unit also responded in excitatory fashion to B2 onset movements at these angles. B: prior deflections of C1 inhibited the cell's responses to subsequent deflection of D1 at all C1 stimulus onset angles, regardless of whether C1 itself evoked an excitatory ON response. Note that the C1 response has a directionally consistent characteristic. Conventions as in Fig. 5.
tant factor in PW response suppression. Figure 9A illustrates a multi-whisker TCU for which initially up-and-forward deflections of an adjacent whisker (B2 at 90, 135, and 180°) selectively inhibited PW ON responses; other B2 deflection angles evoked less, or no, inhibition. Note that B2-evoked inhibition occurred with the same deflection angles that also produced an excitatory B2 response. A different inhibitory relationship is illustrated for the TCU in panel B. Prior movement of the adjacent whisker (C1) completely suppressed the PW (D1) response at all eight deflection angles. Here, inhibition is observed whether or not the adjacent whisker elicits an excitatory response. Conversely, as illustrated in Fig. 2A above, excitatory responses by adjacent whisksers could be followed by a vigorous PW response. Thus the presence of an adjacent whisker response is neither necessary nor sufficient to produce inhibition. Also, in at least some cases, deflection angle is an important determinant of cross-whisker inhibition.

Data obtained with this protocol provide a more conservative assessment of cross-whisker inhibition because the adjacent whisker is deflected at 8 angles spanning 360°. For analysis of these data the PW alone response was compared directly to the observed PW test response. Expected test responses (as above) were not computed since spike trains for adjacent whisker alone responses were not available; this was not deemed to be a serious problem because 20-ms interdeflection intervals were used and conditioning and test responses did not overlap in time. For each data file the number of angles that elicited a statistically significant reduction in the PW test response was computed (t tests, Ps < 0.025). Category 0 represents pairings in which inhibition was not observed at any angle; category 8 represents pairings in which all 8 conditioning stimuli elicited inhibition. For example, the unit of Fig. 9A is a category 3 cell, that of Fig. 9B a category 8 cell. Results from 56 whisker pairings for 21 TCUs and 56 pairings for 17 RSUs are plotted in Fig. 10. TCUs and RSUs differ most in terms of the proportion of pairings in which the adjacent whisker deflection failed to evoke inhibition regardless of deflection angle, i.e., category 0. For TCUs about one-half of the pairings evoked no inhibition compared to 20% of RSUs. The numbers of not-inhibited (category 0) versus inhibited (categories 1–8) cases differed significantly between the two populations (χ² test, P < 0.001). Moreover, the proportion of cases showing inhibition at all 8 angles (category 8) was more than 2 times larger for the barrel population.

Taken together with the above findings, the data demonstrate that: 1) in the thalamus and in the cortex inhibition is strongest 20 ms following deflection of an adjacent whisker; 2) when observed, the strength of inhibition at this time is equivalent in TCUs and RSUs, but; 3) inhibitory interactions are observed less frequently for the former than the latter. Thus PW responses of TCUs are less likely to be effected by prior deflection of an adjacent whisker.

Receptive field organization

A previous study (55) indicated that receptive fields of cortical neurons can be distinguished on the basis of the relative strengths of inhibition evoked by whiskers on either side of the PW. Therefore, we compared the effects of deflections of adjacent rostral versus caudal (within-row) or dorsal versus ventral (across-row) whiskers on each cell's response to subsequent deflections of the PW. For these analyses data obtained using protocol 3 were examined to identify the deflection angle of each adjacent whisker that evoked the strongest inhibition of the PW response. T tests were used to determine whether the test response differed significantly from the PW alone response (two-tail, Ps ≤ 0.05); statistically significant inhibition was defined as the former being smaller than the latter at a 0.975 confidence level. Data were available from 27 pairs of adjacent whiskers in 15 RSUs and 20 pairs in 11 TCUs. For 27 of the RSU pairs (81.5%) both adjacent whisksers evoked significant inhibition of the PW response, a finding consistent with our previous study showing that 85% of middle-depth neurons have symmetrically inhibitory receptive fields.
Importantly, symmetrical inhibition was observed for only 3 of 20 TCU pairings (15%).

Receptive-field organization in TCUs and RSUs is illustrated in the scatterplots of Fig. 11. In panel A the PW condition-test ratio evoked by the adjacent whisker rostral to the PW is plotted with respect to that evoked by the caudally adjacent one; open symbols denote pairings in which at least one of the two adjacent whiskers elicited a statistically significant excitatory response (see above). Panel B shows pairings for whiskers dorsal and ventral to the PW. The scatterplots clearly demonstrate that RSUs (circles) are strongly inhibited by both adjacent whiskers and that the large majority have single-whisker receptive fields. TCUs (squares) display considerably less inhibition, despite the fact that in 90% of the pairings at least one adjacent whisker elicits an excitatory response. In addition, correlation coefficients for rostral/caudal and dorsal/ventral response suppression values were statistically significant for RSUs ($P \leq 0.001$) but not for TCUs ($P > 0.05$). Thus RSUs are more likely than TCUs to have small, focused excitatory centers with potent and symmetrical inhibitory surrounds.

An interesting aspect of the scatterplots for RSUs is that the data points are skewed above a line representing a slope of 1.0 (line not shown). Thus rostral and dorsal whiskers evoke somewhat less inhibition than their caudal and ventral counterparts. Paired $t$ tests showed these differences to be statistically significant ($P \leq 0.01$, two-tail). Bar histograms to the right of each scatterplot show the average response suppression values for the indicated adjacent whiskers. For RSUs caudal whiskers yield the strongest inhibition, dorsal whiskers the weakest. Significant differences between TCU pairs were not observed ($P > 0.05$). Qualitatively similar findings were obtained when response suppression values were averaged over all eight deflection angles of the adjacent whiskers.

**Fast-spike units**

Our sample of barrel neurons includes 16 fast-spike units (FSUs). These units are distinguished by the rapid time
FIG. 12. RF properties of a "fast-spike" barrel neuron. Conventions as in Fig. 2. The penetration in which this cell was recorded is shown in Fig. 1. It is highly unlikely that the excitatory responses from C2, C4, and D3 reflect the extension of the cell's dendrites into these barrels that are at least several hundred μm distant from the recording site in the C3 barrel (see also DISCUSSION).

FIG. 13. Summary of observed differences among 135 TCUs, 16 FSUs, and 242 RSUs. A: mean spontaneous activities in spikes/s and stimulus-evoked discharges in spikes/stimulus for PW deflections at the maximally activating onset and offset angles. B: characteristics of the stimulus plateau responses. At the left the relative frequency of slowly adapting cells is plotted; at the right sustained activity measures are based on net plateau responses obtained by subtraction of spontaneous activity. C: relative frequencies of poorly tuned (angular tuning categories 0–2) and well-tuned (categories 5–7) cells for stimulus onsets and offsets. For A–C, data are from PW deflections. D: relative frequencies of multi-whisker RFs and the average number of spikes/stimulus onset evoked by excitatory adjacent whiskers. Data were obtained using protocol 3. Error bars in A, B, and D denote 1.0 standard error of the mean. Hatched bars, TCUs; shaded bars, RSUs; open bars, FSUs.
course of their action potentials and are thought to be non-spinous or smooth barrel cells that function as GABAergic inhibitory interneurons (see DISCUSSION). The dynamic responses and receptive field properties of FSUs are also distinctive. This is illustrated qualitatively in Fig. 12, which shows PSTHs in a format identical to that of Fig. 2 above. This unit displayed a high level of spontaneous activity and discharged vigorously to both the onset and termination of C3 displacements. Three of the four immediately adjacent whiskers (C2, C4, and D3) evoked excitatory ON responses. Displacement of these same three whiskers moderately suppressed the C3 test response; B3 had no excitatory or inhibitory effects.

Figure 13 summarizes some of the observed differences among FSUs, TCUs, and RSUs. FSUs have the highest rates of spontaneous activity and the most vigorous ON and OFF responses (panel A). They are also the most likely to display slowly adapting responses, which have the highest net rates of sustained activity during the stimulus plateau (panel B). For all of these measures, values for RSUs are lowest and those of TCUs intermediate. Panel C shows that ON and OFF responses of FSUs are least likely to be well-tuned for deflection angle.

Six FSUs were studied with multi-whisker stimuli in which a total of 22 adjacent whiskers were deflected at all 8 deflection angles (protocol 3). For 5 of these cells, recordings were stable enough to examine responses from all 4 adjacent whiskers. An important finding is that all FSUs responded to at least 1 adjacent whisker in addition to the PW (panel D, left). The average number of responsive adjacent whiskers was 2.83, and for these 5 units the average receptive field size inclusive of the PW was 4.20. Adjacent whiskers evoked 1.92 ± 0.58 spikes/stimulus onset (panel D, right); when normalized with respect to the discharge evoked by the PW, the mean adjacent whisker response was 0.84 ± 0.23. Thus FSUs have the largest and most vigorously driven receptive fields.

**Population profiles**

Differences among TCUs, RSUs, and FSUs are illustrated further by the population response profiles shown in Fig. 14. Each PSTH was constructed by a bin-by-bin accumulation of spike trains evoked by PW stimulation. Profiles are based on responses of 242 RSUs, 16 FSUs, and 135 TCUs to all 8 deflection angles; for each unit 80 spike trains were used (8 angles × 10 presentations). In terms of sponta-
neous activity and strength of ON responses, FSUs are clearly the most responsive, RSUs the least. Comparison of the magnitudes of ON and OFF responses indicate further that OFF responses are absolutely and relatively smallest for RSUs. Because inhibition is especially prominent in RSUs, the findings suggest that movement of the PW to a deflected state engages inhibitory mechanisms within the barrel that actively suppress unit discharges to the subsequent return movement of that whisker. The large OFF responses of FSUs is consistent with the finding noted above that these cells are poorly tuned for deflection angle. On the other hand, the relatively large TCU OFF response actually reflects the greater selectivity of these cells to PW movements in opposing directions, i.e., their larger directional consistency indices. This is obscured in the population profile because responses to all eight deflection angles are summed.

The temporal pattern of stimulus-evoked activity in barreloid and barrel cells is illustrated in Fig. 15. Panel A shows intracellularly recorded membrane potential changes of a single RSU averaged over 40 stimulus presentations (8 angles × 5 repetitions). Panels B–D are the population profiles from Fig. 14; here, the vertical axes have been greatly expanded to demonstrate the modulation of spike activity in each population. The profiles show that activity in TCUs and RSUs is sharply reduced immediately after the excitatory ON response, and over a period of 75 ms it gradually returns towards prestimulus levels. This pattern coincides with the time course of cross-whisker inhibition shown in Fig. 7 above. For TCUs, activity levels remain relatively constant throughout the remainder of the stimulus plateau, whereas activity in the RSU population is cyclic, having excitatory peaks that exceed prestimulus levels. Of particular interest is the presence during the later phase of the stimulus plateau of a second, and the beginning of a possible third, cycle of excitation/inhibition having a periodicity also of ~75 ms. Similar patterned activity follows the OFF response. Note that the summed activity of the population of extracellularly recorded RSUs closely reflects the fluctuation in the membrane potential of the single cell of panel A. The activity pattern of FSUs is qualitatively similar to that of RSUs. The relative heights of the peaks and troughs are smaller, however, and the second major peak following the ON response appears to occur somewhat earlier than in the RSUs. These subtle differences are due to the inclusion in the FSU population of four units whose activity profiles are reciprocal to that of RSUs and the other FSUs (see insert).

DISCUSSION

Distinguishing properties of barreloid and barrel neurons

The present study employed controlled whisker stimuli and quantitative analyses to compare response properties of neurons in the thalamic ventrobasal complex and two distinctive populations of cortical layer IV cells that are thought to be immediately postsynaptic to them. Thus anatomic studies have shown that all, or at least the overwhelming majority, of barreloid cells project to the barrel cortex (35, 44, 48) in which their terminal arbors are confined in almost all cases to the centers of their correspond-
could produce in RSUs an effective shunting inhibition of thalamocortical inputs onto dendritic spines located distally to the inhibitory synapses (31).

We found the receptive fields of cells in the barreloids to be quite diverse. This was unexpected because previous studies of the rat VB had shown a homogeneity of cell morphology (18), a virtual absence of interneurons (20, 38, 48), and an overwhelming predominance of single-whisker receptive fields. With respect to the latter for example, Waite reported that almost all VB cells had RFs restricted to a single vibrissa in deeply barbiturate-anesthetized rats, though multi-whisker RFs were observed more often with lighter levels of anesthesia (66; see also Refs. 50 and 62). Some recent studies have reported that as many as 25% of VB units in rats have multi-whisker RFs (47, 64). Our estimates of multi-whisker units suggest that well over one-half of the thalamic relay neurons respond to more than one whisker. Similarly, in cats studied under anesthetic conditions that yielded single-whisker RFs in ~80% of cortical neurons, 56% of presumed thalamocortical axons were found to be multi-whisker (22). Discrepant findings are probably due to the various types and levels of anesthesia that have been employed and to use in the present study of controlled multi-angular stimuli that maximize the identification of adjacent whisker responses.

TCUs in our sample varied considerably in terms of levels of spontaneous activity, adaptation, magnitudes of stimulus-evoked discharges, and angular selectivities. Again, early studies reported that the vast majority of VB cells had little or no spontaneous activity or sustained discharges to steady whisker displacements (7, 66). Results of recent studies, however, are more consistent with the present findings demonstrating a variety of unit properties (47, 50, 64). Our data also demonstrate a marked heterogeneity in terms of the presence or absence of inhibitory interactions between adjacent whiskers. These latter findings are generally consistent with a recent report of cross-whisker inhibition in the rat ventrobasal thalamus (62). This suggests that there is more diversity in the patterns of connectivity between cells in VB and those in the thalamic reticular nucleus than previously proposed (51).

In a number of important respects RSUs in the barrels are functionally more homogeneous. Though these cells display a range of spontaneous activities, stimulus-evoked discharge rates, angular selectivities, and velocity thresholds (23, 24, 53), differences among them are less striking than in VB. Thus most units are visually silent in the absence of stimulation, respond chiefly to stimulus transients, and are driven well only by the PW. In cat vibrissa cortex, most cells are rapidly adapting even though almost one-half of the thalamocortical afferents display slowly adapting properties (22).

The predominance of single-whisker RFs observed here for RSUs is consistent with our previous findings using hand-held probes under comparable physiological conditions (53, 60); also FSUs were observed previously to have larger RFs (53). These findings contrast with those of Armstrong-James and Fox (2) who recently reported that in the barrels of urethane-anesthetized rats >45% of the cells (presumed RSUs) responded to >2 whiskers with ±1.0 spikes/stimulus. Spontaneous activities of barrel neurons were larger by as much as fivefold relative to the conditions of the present study, and 64% of barrel cells responded with ±2.0 spikes/stimulus. By contrast only 11% of our sampled RSUs responded to PW deflections with ±2 spikes/stimulus, and a much lower proportion of cells had multi-whisker RFs. Although Armstrong-James and Fox measured ON responses for a period of 45 versus 20 ms in the present study, we observed little or no spike activity during the 25 ms following the ON response (see Fig. 15).

We attribute these discrepancies to differences in the overall level of excitability of the cortex under the different anesthetic conditions employed. We have recently found, for example, that microiontophoresis of a GABA antagonist, bicuculline methiodide, produces decreased magnitudes of responses of barrel cortex neurons to PW stimulation and the emergence of unit responses to deflections of previously ineffective adjacent whiskers (unpublished observations). We suggest that the numerous multi-whisker receptive fields observed by Armstrong-James and Fox reflect in part inputs from TCUs in the barreloids that respond to >2 vibrissae (see below). Even in urethane-anesthetized animals, as many as one-fourth of VB cells have been reported to have multi-whisker RFs (47, 64).

Another major characteristic shared by virtually all barrel RSUs is their inhibition by adjacent whiskers. Intracellular records, such as that shown in Fig. 15A, suggest additionally that most RSUs respond to whisker deflections with a stereotypic temporal pattern of recurring inhibition and excitation (see also Ref. 8). A clear exception to the functional homogeneity observed in the barrels is the pronounced difference between RSUs and FSUs. As discussed below, these cells represent identifiable subpopulations of barrel neurons that play distinctly different roles in the operations of the barrel circuitry.

**Thalamocortical response transformation**

Taken together the present findings suggest that thalamocortical response transformation normalizes the barrel response to functionally diverse inputs from the corresponding barreloid. We propose that the barrel, in layer IV, provides the basis for a remapping of vibrissal space onto cells in other cortical laminae. As a prerequisite, afferent information from the barreloids is transformed both temporally and spatially.

Barrel circuitry helps to establish a temporal code that underlies operations performed within the cortical column (see also Ref. 22). This is manifest in the characteristic pattern of barrel neuron excitability that regulates how cells in the column respond to successive displacements of the PW on adjacent vibrissae. Its time course parallels the limited ability of RSUs in layer IV to be entrained by whisker vibrations at frequencies greater than ~15 Hz (53); by contrast, thalamocortical afferents respond to vibratory stimuli of several hundred Hz (22, 64). A similar, limited frequency response of RSUs to repetitive peripheral stimuli has been observed in the somatic sensory systems of other, nonrodent species (15, 41). Temporal constraints are operative also in the response of somatosensory cortical neurons to multiple point cutaneous stimuli (16) and to objects moving smoothly across the skin surface (13).
Spatially, the barrel enhances contrast between inputs from neighboring whiskers. Thus the vast majority of RSUs discharge vigorously in response to movements of only the one vibrissa that corresponds anatomically to that barrel, and virtually all cells are strongly inhibited by deflections of adjacent vibrissae. These electrophysiological findings are entirely consistent with 2-deoxyglucose data obtained in freely moving animals (39). To use an analogy from visual system physiology, barrel RSUs display center-surround receptive fields characterized by small, focused excitatory centers and strong inhibitory surrounds (see also Ref. 22). Receptive fields of TCUs on the other hand are considerably less uniform in terms of both the size of the excitatory center and the organization of the inhibitory surround. The enhancement of spatial contrast in the barrel may provide a necessary condition for the synthesis in other cortical laminae of more complex, multi-whisker receptive fields (55). In this regard it may be significant that subtle asymmetries were observed in cross-whisker inhibition evoked by rostral/caudal and dorsal/ventral pairs of adjacent vibrissae. Similar asymmetries extending throughout the thickness of the cortical column have been reported recently in behaving mice (39).

Receptive-field properties: excitation

The differential responsiveness of FSUs and RSUs appears to parallel differences between the cell types in terms of receptive field size and degree of selectivity for whisker movements in different angular directions. To account for this, we propose that an individual barrel cell receives thalamocortical synapses from more than one cell in the corresponding thalamic barreloid and that the receptive field properties of FSUs display a synthesis of these barrelloid inputs that reflect TCU activity more faithfully than those of RSUs. Although there is as yet no direct evidence for or against convergence of thalamocortical inputs onto single barrel neurons, the assumption of at least some limited convergence is reasonable in light of the findings that each individual thalamocortical axon ramifies extensively throughout the barrel center (6, 26). The large receptive fields of FSUs could thus be explained by convergence of two or more TCUs, each of which responds to stimulation of the PW and to at least one of several, different adjacent whiskers. Similarly, the observation that FSUs respond to many angles of whisker deflection could reflect convergent inputs from several TCUs that have different preferred angles. In rabbit visual cortex, there is physiological evidence that synaptically activated cells discharging short-duration spikes receive convergent thalamic input and that these cells have exceptionally large receptive fields lacking orientation selectivity (63).

RSUs appear physiologically to be less strongly driven by thalamic input. Depolarization of spiny barrel neurons to threshold for action potential discharge might depend on activation by the axospinous thalamocortical inputs that are most numerous and synchronously active (49). Such inputs would be manifest in the response of RSUs to deflection of their barrel’s PW because all of the TCUs in the corresponding thalamic barreloid respond to it. Activation of RSUs by “inappropriate” whiskers is in fact present but so weak that it can be observed in our extracellular recordings only when responses are accumulated over many trials. With intracellular recordings from middle-depth neurons, they are observable as subthreshold EPSPs (8). In terms of angular selectivity, convergence of thalamocortical inputs having somewhat different preferred angles onto barrel neurons might produce a decrease in selectivity for both RSUs and FSUs relative to TCUs, and the differential responsiveness of the two cell types might result in somewhat greater selectivity for RSUs than for FSUs. This is in accord with our findings.

Receptive-field properties: inhibition

Cross-whisker inhibition is observed more often in the cortical barrels than in the thalamic barreloids. A parallel finding is that the temporal pattern of activation of barrel cells is characterized by cyclic alterations in unit excitability that are more pronounced than in the barreloids. The period of the oscillations corresponds to the time course of cross-whisker response suppression. It is unlikely that this patterned activity solely reflects intrinsic membrane properties of the barrel neurons because it, and other response properties, are markedly altered by chronic trimming of the vibrissae in young animals (58). Moreover, GABA antagonists abolish postexcitatory inhibition in other species (12). In contrast to the barrels, which contain a rich local inhibitory component (10, 11, 14, 29, 36), barreloids are virtually devoid of inhibitory inhibitory interneurons (3, 20, 32, 38, 46). Cross-whisker inhibition appears to be less pronounced than surround inhibition in the thalamus of species lacking inhibitory interneurons within VB (25).

Our hypothesis is that in a barrel cross whisker inhibition and the cyclic activity pattern depends on intrabarrel circuitry involving synaptic connections between spiny and smooth cells. Axons of smooth cells ramify profusely within the centers of their parent barrel (21) and make GABAergic symmetric synapses on both spiny and smooth cells (29). Thus activation of smooth cell/FSUs by non-PW whiskers could mediate cross-whisker inhibition of spiny cell/RSUs in the same barrel when that barrel’s PW is subsequently deflected. If the activation of FSUs by non-PW whiskers does in fact reflect direct multi-whisker inputs from TCUs in the corresponding barreloid as suggested above, inhibitory cross-whisker interactions in the layer IV barrel would not require extensive anatomic connections between adjacent cortical barrels or the columns of which they are a part.

A network of interconnected cells within a barrel also might form a local circuit that helps to establish a pronounced cyclic pattern of activity in response to stimulus-evoked discharges in TCUs. Light microscopic evidence is consistent with the idea that spiny and smooth barrel neurons are substantially interconnected within their parent barrel (21). Moreover, in spite of a paucity of electron microscopic data concerning synaptic connections among identified cell types in the cortex, White (70) has assembled an impressive body of evidence suggesting that any axon synapses on any cortical element capable of receiving that axon’s type of synapse. It remains to be determined whether synaptic interconnections among barrel cells are
restricted enough across and within cell types to generate a recurring pattern of excitation and inhibition.

**Implications for cortical function**

Regular spiking cells in the barrels have smaller excitatory receptive fields than neurons in the barrelrods that are presynaptic to them. Thus the presence of discrete cellular aggregates may not be a sufficient condition for the existence of single-whisker receptive fields. Even in a system in which somatotopy so closely reflects cytoarchitecture, physiological factors appear to regulate receptive field size and other response characteristics. Indeed, an essential feature of the organization that we have proposed is that it allows for substantial alterations in neuronal functional properties in the absence of neumorphological changes at the light microscopic level, i.e., axonal sprouting. Mechanisms normally inherent in the organization of adult sensory cortex may underlie functional abnormalities observed consequent to alterations in the sensory periphery, as well as the system’s response to moment-to-moment demands of the sensory environment (27, 74).

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