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Response Properties of Vibrissa Units in Rat SI Somatosensory Neocortex

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SUMMARY AND CONCLUSIONS

1. Glass microelectrodes were used to record extracellular responses from 308 SI cortical neurons to deflections of the contralateral vibrissae in 21 unanesthetized, paralyzed rats. Controlled deflections of individual hairs were produced by means of an electromechanical stimulator. Fast green dye marks were made to aid histological reconstructions of electrode tracks.

2. Two types of spike potentials were observed. "Regular" cortical spikes (RS) were observed throughout layers II–VI; "fast" cortical spikes (FS) were less frequently encountered and largely restricted to layer IV. Although both types of potentials had similar negative-positive waveforms, FSs were distinguished from RSs by their comparatively rapid time course, about half that of RSs. RS units (RSU) discharged spontaneously at rates of <1–15/s, whereas FS units (FSU) displayed rates of 15–50/s. The amplitudes of FSs, which were generally smaller than those of RSs, often decreased during high-frequency discharges.

3. With sinusoidal oscillations of a vibrissa FSUs responded more reliably and over a broader range of frequencies (3 to at least 40 Hz) than did RSUs, particularly in layer IV. In addition, FSUs typically responded to whisker deflections over a range of 360°, whereas many RSUs in layer IV displayed sharp spatial-tuning characteristics, responding over a restricted range of <90°.

4. Of all units, 58% responded preferentially to stimulus transients (vibrissal movements), 32% displayed sustained responses to stimulus steady-states (fixed vibrissal displacements). For the remaining 10% of units the appropriate stimulus could not be specified; these units were particularly common in layer V.

5. Computation of quantitative stimulus-response relations showed that many units increased their rate of discharge with increasing stimulus intensities.

6. Most units were directionally selective, responding preferentially to deflections of a whisker in one or more of four quadrants.

7. In radial penetrations through the cortex there was a columnar pattern so that units were activated at least by the same (i.e., the "principal") whisker. In a number of cases these could be directly correlated with the barrels. Of all units, 55% responded to deflections of single vibrissa only, the remaining 45% to 2–12 adjacently situated vibrissae. For most multiple-whisker units the responses elicited by deflection of any one hair activating the neuron was qualitatively similar to those elicited by deflection of any other hair activating it. The principal whisker of the penetration was typically associated with the most vigorous responses.

8. In layer IV, 85% of neurons responded to deflections of one hair only, the remaining 15% to two or more hairs. In layers II and III 39% of units were activated by more than one vibrissa; in layers V and VI multiple-whisker units predominated (64%). Whisker configurations in the deep layers were larger than those in other layers.

9. These data are interpreted to mean that: *a*) cortical vibrissa-activated neurons are similar to those studied at other levels in the trigeminal system in that they

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was carefully drilled away until the vascular pattern on the surface of the hemisphere could be easily visualized. A small excavation (<1.0 mm^2) was then produced in the remaining bone overlying the cortex, which is associated with the longer, larger, and more accessible facial vibrissae. The dura was carefully opened to expose a small surface area of cortex, which was covered with warm saline. With this procedure the remaining thin layers of bone and meninges provided support adequate to prevent swelling and/or pulsation of the cerebral hemisphere.

Following surgery, the rats were allowed to recover from general anesthesia. Neuromuscular blockade was induced by intramuscular injection of *d*-tubocurarine (0.50 mg/kg) and maintained by subsequent injections at 20- to 30-min intervals. Positive-pressure respiration with 30–40% oxygen was provided (approximately 3.0 ml at 90–100 strokes/min), and all wound margins and injection sites were liberally and periodically infiltrated with a local anesthetic (Xylocaine). Rectal temperature was monitored and was maintained at 37–38°C by means of a DC heating pad. The condition of the animal was also assessed by observation of the ECG, the pupillary dilation, and the extent of vascularization of eyes, ears, and glabrous skin. End-tidal CO_2 was measured in several experiments and observed to be 4.0–5.0% of the expired air.

Unit recordings began 4–5 h after the initial induction of the barbiturate. By this time the rat's temperature and heart rate had stabilized at normal levels. Good preparations were studied for over 18 h. Glass microelectrodes filled with a saturated solution of fast green in 3 M KCl (≤1 μm tip diameter, 7–12 MΩ impedance) were oriented normal to the pia and advanced slowly through the cortical tissue by means of a hydraulic microdrive. In order to isolate units which were not spontaneously active, a large probe, controlled by an oscillograph unit (see below), was swept across the contralateral whisker field at one sweep per 3 s. Extracellular recordings were obtained from single cortical units as judged by impulse-discharge waveform and amplitude (36). Conventional methods were used for amplification, display, and tape recording of the potentials.

Stimulation

Some of the response properties of isolated units were determined by pushing, pulling, bending, stroking, etc., the contralateral vibrissae with a variety of small, hand-held probes. Quantitative information was obtained by examining unit responses to controlled deflections of single hairs. A whisker activating the unit was attached to a stimulator which transduces time-varying electrical waveforms into mechanical movements of a "wand." The stimulator consisted of the oscillograph unit from a polygraph instrument and its accompanying driver amplifier (Grass Instrument Co., Quincy, Mass.). Contact between the oscillograph and a hair was made by inserting the whisker into a hollow stainless steel tube attached to the arm of the galvanometer. The whisker was cut to a length of 12–13 mm and the wand was positioned over the cut end to a point 10 mm from the skin. To avoid pulling the hair during large-amplitude deflections, the whisker was left free to slide back and forth within the tube; for small deflections, the hair was rigidly attached to the wand with wax. The galvanommeter was mounted so that the wand could be aligned coincident with the axis of the hair and so that the stimulator could be rotated 360° about this axis.

The combined amplifier and oscillograph unit was calibrated "off-line" in several ways (50). For multiple-sinusoidal movements of the wand below 40 Hz, the frequency response was essentially linear for deflection amplitudes of 0.5–10.0 mm peak to peak; higher frequency stimuli could not be controlled precisely and, consequently, frequencies above 40 Hz were not routinely employed. There was inertia to the oscillograph. For stimuli which did not require abrupt changes in acceleration of the wand, the effect of the inertia was not appreciable. With higher velocity single-pulsed stimuli (e.g., ramps >25 mm/s) the input waveform was distorted by nonlinearities in acceleration and/or by overshoot of the wand tip at the termination of the intended displacement. Some noise was introduced by the stimulus-generating apparatus and, for this reason, it was impossible to precisely control stimuli at values approaching the thresholds of many units (i.e., deflections of <75 μm). Because of phase lag in the stimulator system, no attempt was made to specify in detail the phase angle or latency of the neural response. Data were analyzed with reference to the output of the function generator producing the stimulus waveform which was assumed to represent the movement of the wand tip and, thus, the end of the hair shaft.

Various stimulus waveforms (e.g., sinusoids, ramps, and sawtooths) were available from a Tektronix waveform generator. Time- and amplitude-varying parameters were controlled by means of digital attenuators and voltage-output ladders associated with a LINC computer, and interstimulus intervals were determined by means of external timing equip-

ment. The digital-to-analog converter on the LINC was also used to generate "trapezoid" or ramp-and-hold stimuli. With this system it was possible to obtain independent control of deflection amplitude, duration, onset velocity, and offset velocity. For movement velocities greater than 10 mm/s the ramp waveforms were essentially "smooth"; with slower movements, however, there was some "bumpiness" associated with the individual digital voltage steps comprising the "analog" signal.

Data collection and analysis

Information about various aspects of a unit's response properties made using hand-held probes included observations about whisker organization (single or multiple whisker), absence or presence and rate of spontaneous activity, type of response patterns (excitation or inhibition), preferred direction, if any, and most effective stimuli. Individual vibrissae were identified as follows: each row proceeding dorsal to ventral, A through E; each vibrissa in a row, proceeding caudal to rostral, 1 through 4–7; whiskers located between rows at the caudalmost limits of the mystacial pad, from dorsal to ventral, α, β, γ, and Δ (see figurine, Fig. 6). Quantitative data obtained with the mechanical stimulator were stored on FM magnetic tape for subsequent analysis with a LINC computer. The computer was also used for on-line data acquisition and analysis at the time of the experiments.

Histology

The point of entry of the electrode tip into the cortical tissue and the depth of unit-recording sites were noted directly from the microdrive. To facilitate estimation of the point of surface contact the excavation was carefully dried of fluids before the electrode was inserted into the tissue; once the electrode was in place and its relation to surface landmarks noted, the excavation was again bathed with warm saline. No dimpling of the cortex was observed. At the conclusion of an electrode penetration selected recording sites and/or the penetration's deepest point were marked with fast green (51) by passing 2- to 3-μA anodal current between the electrode tip and the surrounding extracellular tissue for 3–8 min.

At the end of each experiment the animal was deeply anesthetized with sodium pentobarbital and perfused through the aorta with 0.9% saline followed by 10% formalin solution. The dorsal and lateral aspects of the cranium were removed and the head replaced in the recording apparatus. The perfused brain was then blocked in the plane of the electrode track(s) by means of a scalpel blade attached to the electrode carrier. Frozen sections were cut in a variety of planes (e.g., ref 61), saved, and mounted. The dye marks were located in the unstained material and tracings were made of the cortical area using an overhead projector. These tracings were later referred to the sections after staining with cresyl violet or thionine.

RESULTS

General observations and definitions

The data are taken from 308 cortical units which were isolated in 32 penetrations within the vibrissa-SI cortex of 21 rats. An additional seven penetrations were located in cortex just outside the whisker projections, and in one experiment, three penetrations were unintentionally made near the most posterior boundary of the SI cortex. Vibrissa-activated neurons were distinguished on the basis of several properties. These include: *1*) impulse-discharge waveform, *2*) response to repetitive stimuli, *3*) response to velocity and amplitude of vibrissal deflection, *4*) directional selectivity, *5*) location of the unit in the cortical laminae, and *6*) the number and peripheral pattern of vibrissae activating a cell.

Traditionally, the term receptive field refers specifically to the areal extent of receptor surface, i.e., the skin, whose stimulation elicits responses from a neuron (2). Previously, investigators have described a vibrissal unit's "receptive field" in terms of the whisker, or whiskers, whose deflection activates a neuron. The mystacial pad is composed of discrete, punctate tactile organs, and the mechanoreceptors associated with the vibrissae are distributed about each hair shaft. Because of the leverlike action of the hair shaft (fulcrum probably at the skin surface), the population of receptors that is stimulated by deflection of a whisker is determined, in part, by the direction of hair displacement. These considerations suggest that a vibrissal unit's receptive field may be described by its directional sensitivity as well as by the individual whisker(s) that activates it.

In this report the individual vibrissae that activate a given neuron will be designated the unit's "whisker complement," and the spatial disposition of these hairs on the face pad will be termed its "whisker configuration." Relationships between the different properties of a neuron

decrease during these high-frequency trains even though the cells showed no signs of injury. The extent of the bioelectric fields was small, rarely exceeding several 10's of micrometers, and isolation of these potentials and maintenance of stable recordings during extended periods were difficult. FSUs were similar to RSUs in that they discharged injury potentials and could occasionally be inverted by careful advancement of the electrode. Similar observations have been made by Mountcastle et al. (37) who referred to these short-duration potentials as "thin" spikes.

Unit discharge characteristics

FSUS VERSUS RSUS. FSUs and RSUs could be distinguished functionally by their responses to sinusoidal oscillations of a whisker. Differences between these types of units are illustrated in Figs. 2, 3*B*, and 3*D*, which show a FSU being strongly entrained over a broader range of stimulus frequencies than a RSU. Similar differences are illustrated in Fig. 3*A* and *C*, in which the frequency-response properties of a number of units are compared.

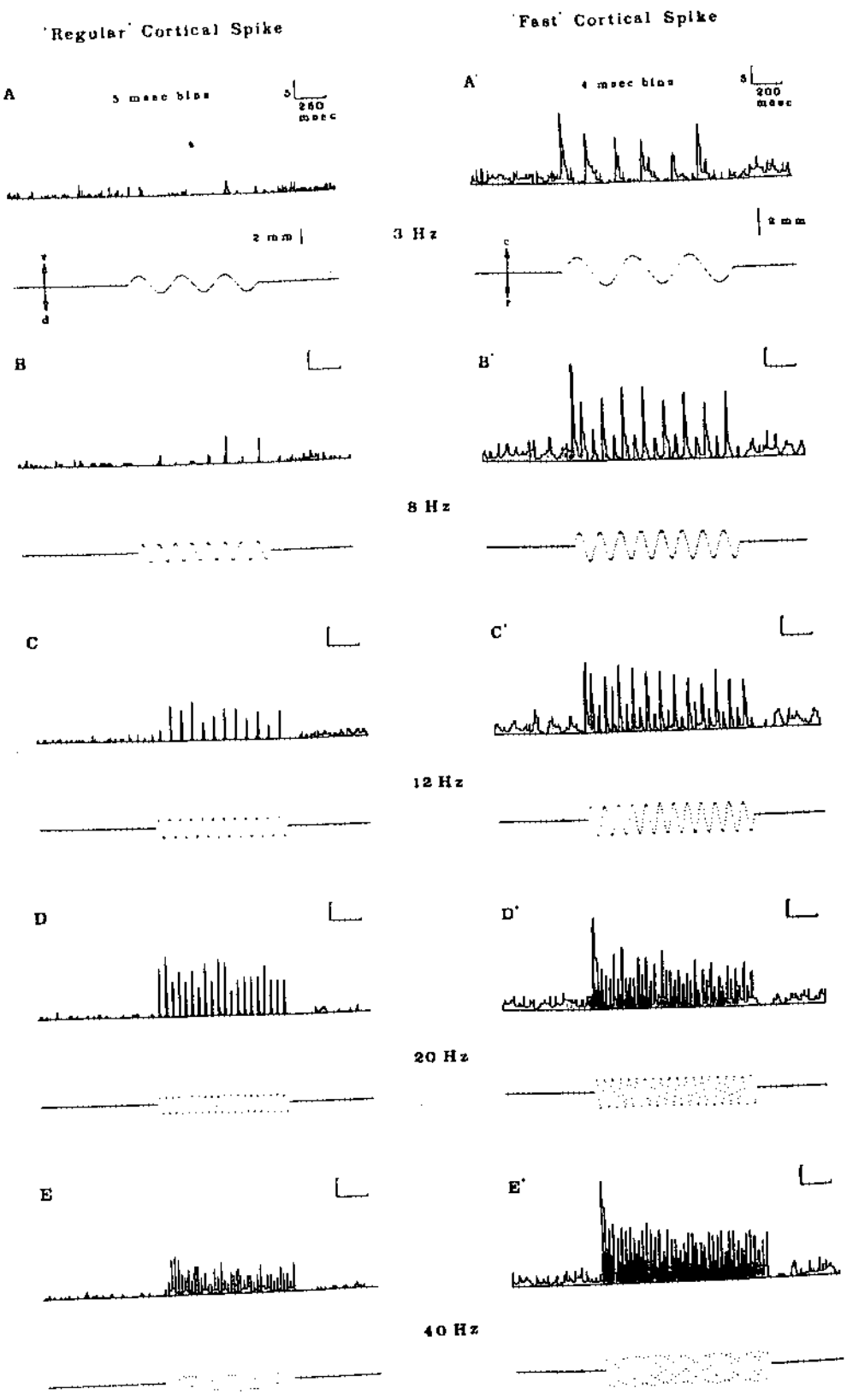
These comparisons were made by computing the probability that a discharge would occur for each cycle of the stimulus at different stimulus frequencies. This analysis was chosen in lieu of an interspike interval analysis (37) because it enables direct comparison of the RSUs, which typically discharge one spike per cycle, and FSUs, which typically discharge bursts of impulses during each cycle. The analysis assumes that when a discharge (or series of discharges) occurs, it does so in a phase-locked relation to the stimulus and, further, that within the midrange of suprathreshold amplitudes employed, there is minimal variability in a unit's frequency-response properties. The validity of these assumptions was verified for each unit by reference to stimulus-response or cycle-time histograms and by observations of the unit's responses to stimuli of different suprathreshold amplitudes. For the units in this analysis, amplitudes of 1.0–2.0 mm (2.0–4.0 mm peak to peak) were associated with the best overall responses with all frequencies tested. In Fig. 3, one-to-one entrainment at any given frequency is reflected by a probability value of 1.0, poorer entrainment by lower probability values.

The relative flatness of the curves in Fig. 3*A* illustrates that most FSUs responded vigorously and in a phase-locked manner to stimulus frequencies at least as high as 40 Hz. By contrast, RSUs displayed considerably more variability. Moreover, with few exceptions, FSUs were readily entrained by repetitive stimuli. On the other hand, many RSUs were not entrainable at all and would respond only to the first cycle of each stimulus, regardless of oscillation amplitude or frequency. The data presented in Fig. 3*C* represent some of the best examples of RSU entrainment, whereas the data presented in Fig. 3*A* are more typical of FSUs as a population.

TYPICAL RESPONSE PATTERNS. To determine if cortical neurons were differentially responsive to specific aspects of vibrissal deflection, stimulus-response histograms such as those shown in Fig. 4 were constructed. The unit in 4*A* and *B* is clearly responsive to the transient aspects of the stimulus, firing vigorously to deflections toward the animal's eye. Neurons displaying this type of response pattern commonly fired to whisker movements as small as 75 μm (0.42°). Velocity thresholds were distributed over a range from <1.0 mm/s (5.7°/s) to >100 mm/s (570°/s). Approximately 30% of all neurons displayed high-velocity thresholds (>75 mm/s); in general, these cells were not directionally sensitive (see below), and they rarely responded to deflections of more than two or three vibrissae.

The neurons in Fig. 4*C* and *D* illustrate quite a different type of response profile. Although the cells clearly fire to the onset transient, a continuous and vigorous discharge is maintained throughout the duration of the steady-state displacement. The strength of the response to the transient aspect of the stimulus varied among units of this type, and in some cases only the response to the steady-state displacement was present (see also ref 49). Both inhibitory and excitatory response patterns were observed. Alterations in unit discharge rates could be elicited by maintained whisker displacements as small as 0.125 mm (0.71°).

A number of units were responsive to both the transient and the steady-state aspects of whisker deflection. As Fig.


'Regular' Cortical Spike
'Fast' Cortical Spike
A
5 msec bins
5
250 msec
A'
4 msec bins
5
200 msec
2 mm
3 Hz
2 mm
B
B'
8 Hz
C
C'
12 Hz
D
D'
20 Hz
E
E'
40 Hz

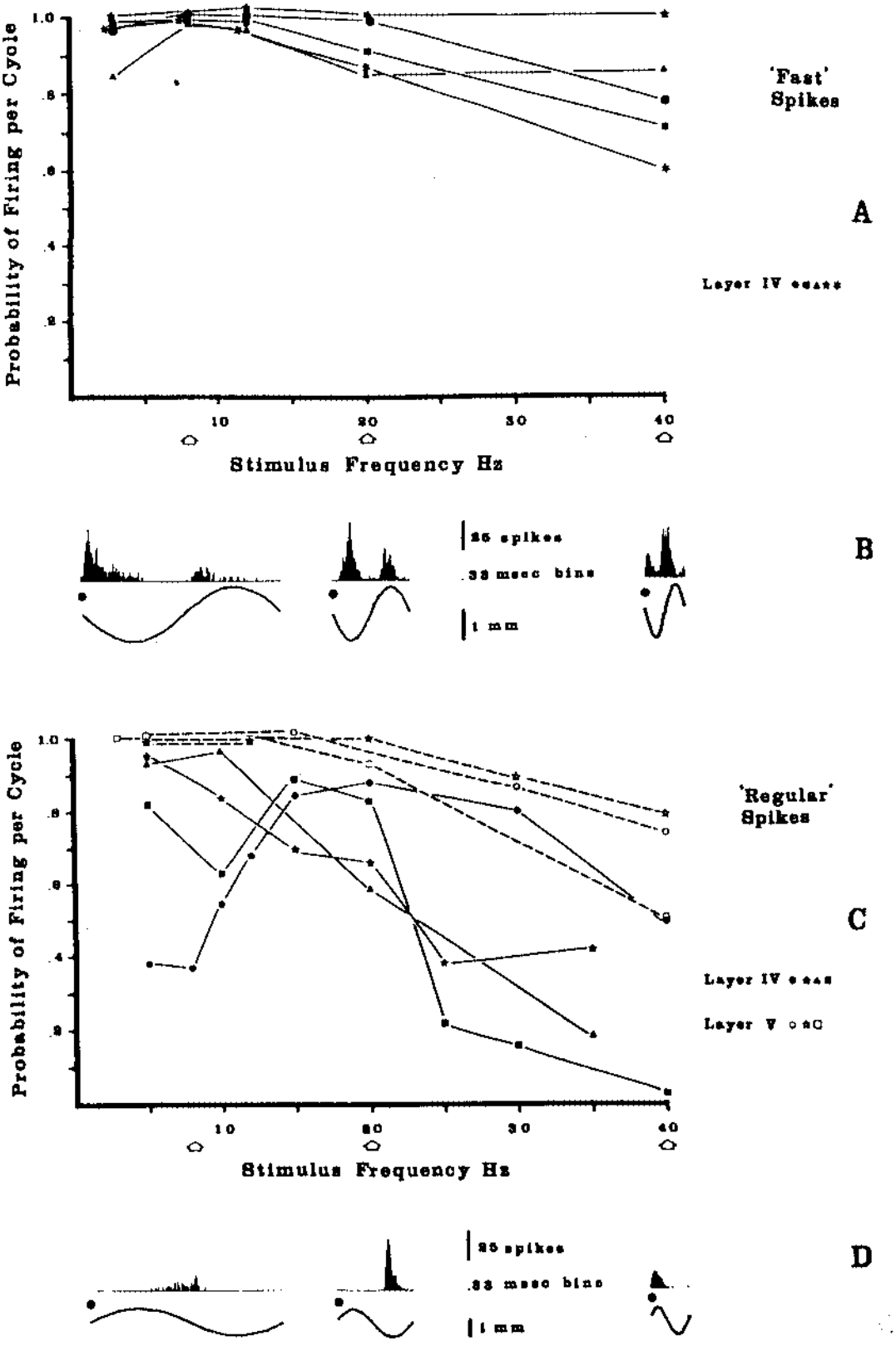
4*E* illustrates, the most pronounced component of these units' responses was to the stimulus transient, but there was also a component clearly related to the maintained displacement. A brief period of silence was frequently associated with the termination of the initial whisker movement (see Fig. 4*E*; 1-bin-wide silent periods are also present in Fig. 5*B* and *D* and are marked by small arrows; see also ref 6, 49). Clear patterns of excitation and inhibition characterized the responses of many FSUs to ramp-and-hold stimuli (Fig. 4*F*); patterns of alternating excitation and inhibition also characterized these units' responses to sinusoidal stimulation (see Fig. 2). For many neurons discharge rates were systematically related to the intensity of the eliciting stimulus. This property is illustrated by the unit in Fig. 5 which increased its initial rate of firing with increases in deflection velocity and its sustained rate of firing with increases in the amplitude of the fixed displacement (see also Fig. 8).

LAMINAR DISTRIBUTION. The possibility that there might be a laminar segregation of neurons as a function of the temporal pattern of evoked unit activity was investigated (see below). For these analyses units were arbitrarily categorized on the basis of their similarities to the above examples as follows: transient encoding units (58%); transient and steady-state or steady-state only encoding units (32%). Neurons in the latter category were distinguished by the presence of a distinct sustained response that could be observed on single stimulus sweeps (approximately a 10–20% change from prestimulus levels). Overall these two unit types were distributed evenly throughout the cortical depths. Nevertheless, certain transient encoding units discharging regular spikes were observed exclusively in the deeper aspects of the cortex. These cells displayed high spontaneous activity, which was briefly inhibited by high-velocity deflections of a single vibrissa. Temporally structured response patterns could be reliably elicited from these neurons even with long trains of closely spaced stimuli. These RSUs thus displayed functional properties similar to those associated with FSUs in layer IV. Ten percent of the cortical units did not fall into any of the above categories. Except for one FSU, all of these units discharged RSs. Many of these cells responded erratically, if at all, to whisker stimulation, and the relation between stimulus and response could not be defined. Others, however, responded vigorously and reliably to the "probe" stimulus, which deflected many hairs on each sweep (see METHODS) but could not be driven by deflections of individual hairs alone. Interestingly, "unclassifiable" cells were most common in layer V.

Spatial tuning

Most units preferentially responded to deflection of a hair in one or more of four quadrants, up and back, down and forward, up and forward, and down and back. This directional sensitivity assumed several forms (9; see Fig. 6). In most cases a neuron's directional preference was associated with one or two adjacent quadrants. Overall there were more units (approximately 70%) responding preferentially to whisker deflections in either up-and-back and down-and-forward directions than to deflections in the other quadrants. Apart from this general bias, directional preferences varied among units recorded in a radial penetration, but there was a strong tendency for units recorded

FIG. 2. Comparison of responses of a FSU and a RSU, both recorded in layer IV, to 1-s oscillations of a vibrissa at several different frequencies. The top trace in each stimulus-response histogram is a peristimulus time histogram based on 15 presentations of the stimulus whose waveform is shown in the bottom trace. Amplitude of oscillations is 2 mm (11.4°) peak to peak; the base line represents the resting or undeflected position of the vibrissa and arrows indicate the stimulus directions: v, ventral; d, dorsal; c, caudal; r, rostral. For each unit the different appearance of the stimulus waveforms at each frequency is due to the use of different time base and scaling factors. The vertical scales in the upper corners show the number of impulses per bin and the horizontal scales show time; bin widths are also indicated for the top histogram. For each unit these parameters at each frequency are the same as those shown for the uppermost histograms. Stimulus frequencies are indicated for each comparison.


Probability of Firing per Cycle
1.0
.8
.6
.4
.2
10
20
30
40
Stimulus Frequency Hz
'Fast' Spikes
A
Layer IV
B
25 spikes
33 msec bins
1 mm
'Regular' Spikes
C
Layer IV
Layer V
D

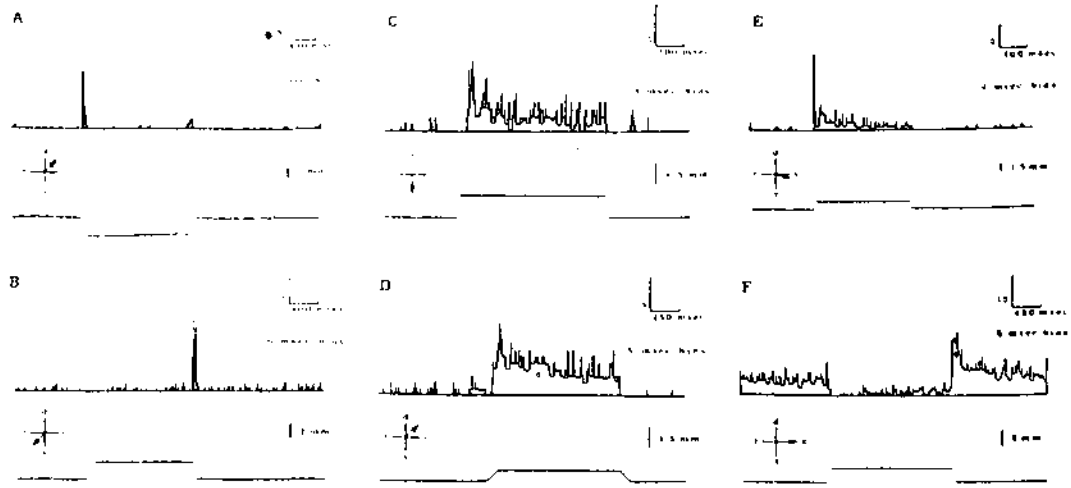


FIG. 4. Histograms illustrating commonly observed response profiles. Whisker movements (stimulus transients) evoked responses from all these units, but responses varied to fixed whisker displacements (stimulus steady states). *A* and *B* show the response (principally to transients) of a single unit to deflections in opposite directions. Units in *C* and *D* displayed vigorous responses to steady-state displacements, while the unit in *E* responded less vigorously to maintained displacements. *F* shows a FSU being inhibited during maintained displacements; all others are RSUs. Arrows indicate the direction of deflection; other scales as in Fig. 2. Each histogram was computed for 15 stimulus presentations. (For further details see text.)

near each other to display similar preferred directions.

For some units spatial tuning was assayed by using suprathreshold stimuli to deflect a hair in a number of directions relative to the axis of its horizontal row on the face (see figurine, Fig. 6). Figure 6*A*, *B*, and *C* illustrates the directional properties of FSUs in layer IV. The unit of Fig. 6*A* was excited by maintained displacements directed caudally and inhibited by displacements directed rostrally. When their responses to stimulus transients were assessed, FSUs were frequently observed to respond vigorously over a range of 360° (see Fig. 6*C*). The spatial tuning of FSUs in layer IV contrasts with the narrow tuning displayed by many RSUs in layer IV (see Fig. 6*D–F*). Figure 6*H* and *I* illustrates that these directional properties were also observed in laminae other than layer IV. The plot in Fig. 6*J* was constructed from a unit that responded to whisker movements directed rostrally and ventrally regardless of the hair's initial position (e.g., Fig. 4*A* and *B*). Figure 6*K* and *L* shows the directional properties of two units that responded to both stimulus transients and stimulus steady states and demonstrates that, for each unit, the directional preferences revealed by both stimuli are similar. The directional properties of a multiple-whisker unit, as revealed by whiskers D3 and D2, are illustrated in Fig. 6*G* (see below).

FIG. 3. Comparison of frequency-response properties of FSUs and RSUs. *B* and *D* are cycle-time histograms for the FSU (*B*) and RSU (*D*) whose responses are illustrated in Fig. 2. These represent the accumulated cycle-by-cycle response patterns for an equivalent number of stimulus cycles at 8, 20, and 40 Hz, indicated by the large arrows along the abscissa of each "probabilities" plot. To eliminate the contribution of the transient responses frequently associated with the initial movement of the hair (see Fig. 2*C'*), data for the first cycle of each stimulus are discarded. The total duration of each histogram equals the period of the sine wave and is measured in 300-μs bins. The phase shift at 40 Hz may be due to instrumentational and/or physiological factors (see METHODS). *A* and *C* show probability of discharge curves for five FSUs and seven RSUs, respectively (see text). In both graphs the solid circles represent data for the units whose responses are illustrated in Fig. 2 and 3*B*. *D*: closed symbols and solid lines are for units recorded in layer IV; open symbols and dashed lines for units in layer V. Stimulus frequencies greater than 40 Hz were not employed because of limitations in the stimulator (see METHODS). These data illustrate that FSUs responded more reliably and over a broader range of frequencies than RSUs (see text).

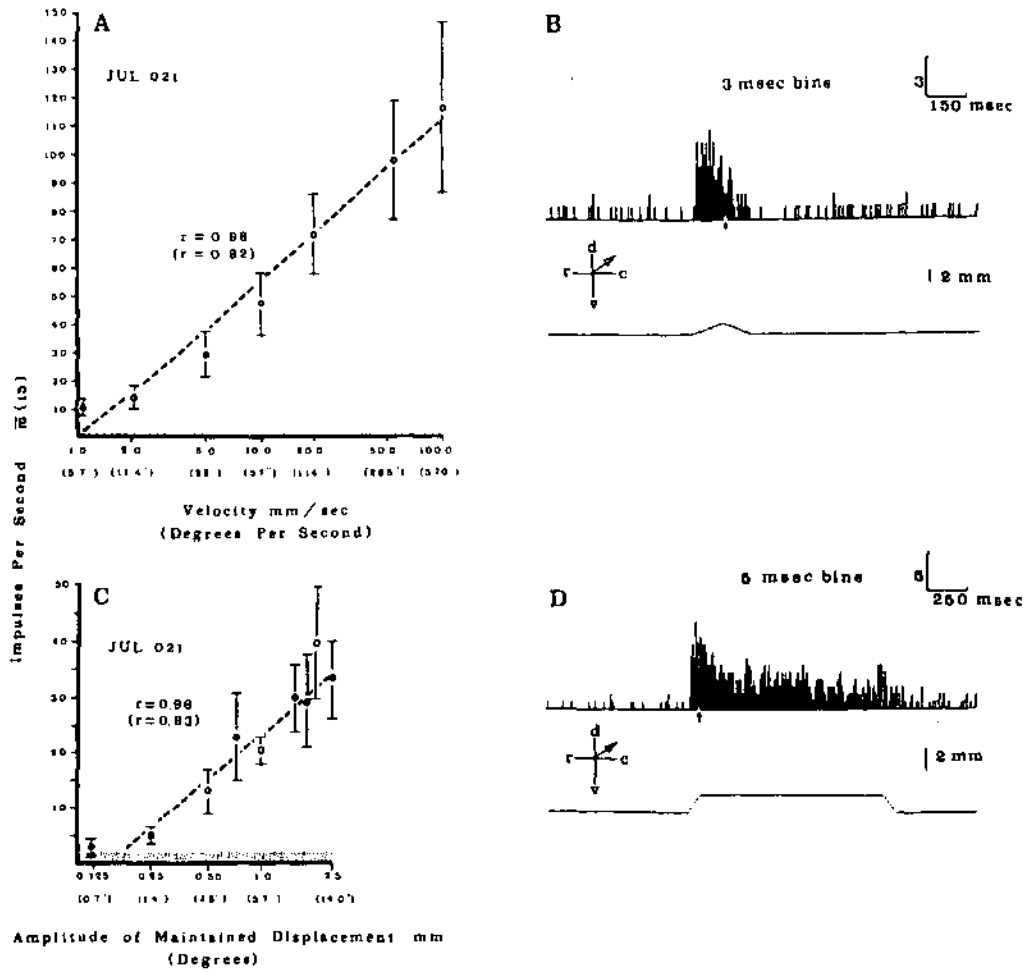


FIG. 5. Quantitative stimulus-response relations computed for a single RSU. The abscissa in each plot shows log-stimulus intensity, the ordinate shows spike frequency in linear coordinates. These latter values were obtained by dividing the mean number of spikes discharged during the appropriate phase of the stimulus (initial movement, 1 s fixed displacement) by its duration. Each data point was computed for 15 presentations of a stimulus whose waveform is shown in the stimulus-response histograms at the right of each graph. The correlation coefficients (r) were computed by a least-squares procedure (Pearson's r); values in parentheses show correlation coefficients based on linear-linear plots. Vertical lines at each data point bracket values within 1 standard deviation of the mean; stippling indicates the level of spontaneous activity. The small arrows in the response profiles indicate a brief period of silence (see text).

Somatotopic and columnar organization

Within the PMBSF region neurons responded to small deflections of one or more whiskers on the contralateral face. Although units frequently responded to light tapping of the skin which immediately surrounds the base of the hair, no unit was activated by direct stimulation of the fine fur between the whiskers or of the common fur surrounding the mystacial pad. In radial penetrations, such as the one indicated in the photomicrograph of Fig. 7, there is a columnar pattern in which all units tend to be activated at least by the same whisker. In this penetration most of the cells responded at least to deflections of whisker B2 and the lesion is appropriately located within a row B barrel. Table 1 shows the whisker complements of neurons recorded in five penetrations. The principal (P) whisker is defined as the hair most likely to be included in the whisker complements of neurons encountered in a vertically oriented penetration. The di-

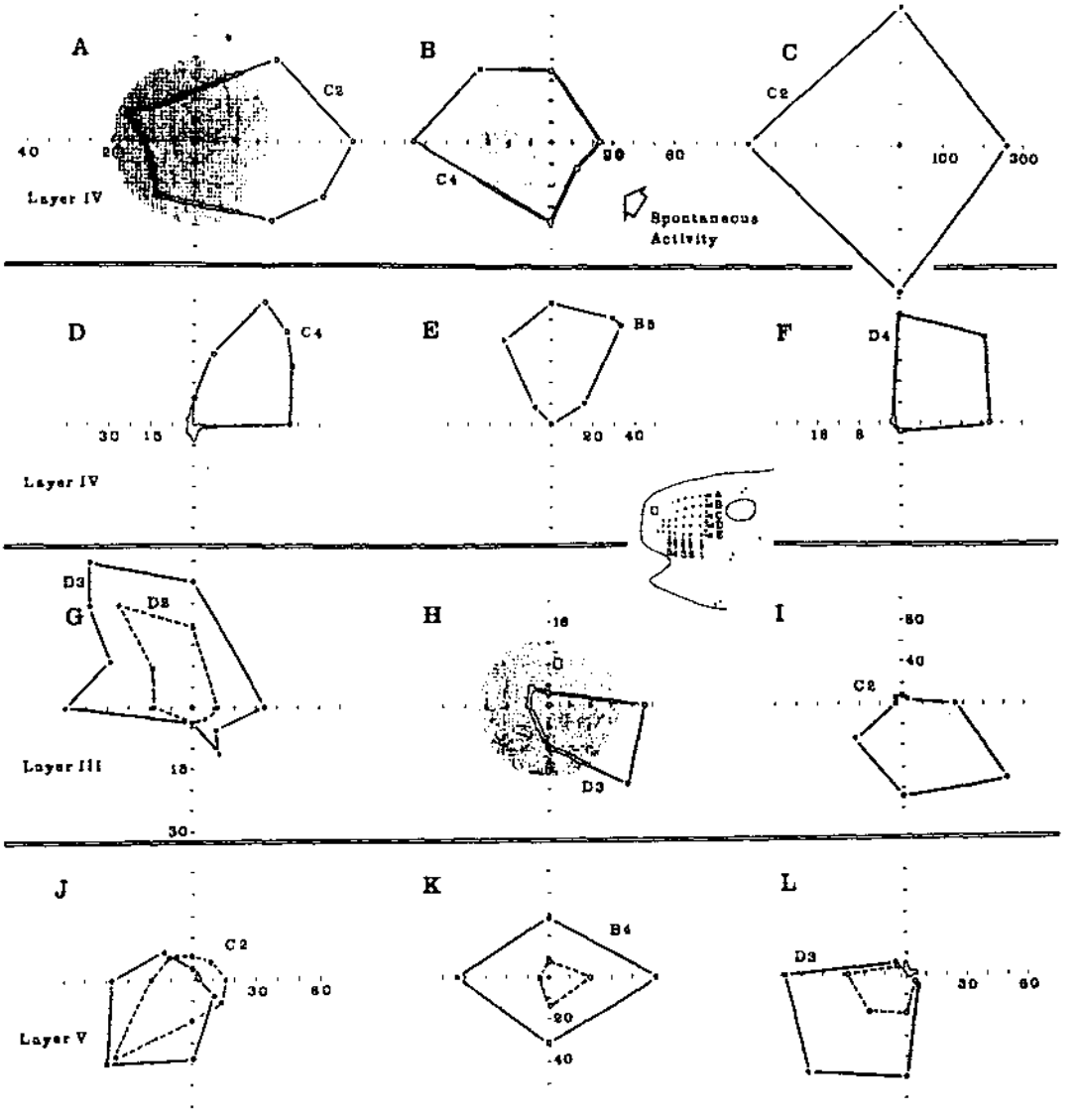


FIG. 6. Directional properties of 12 cortical units as illustrated by polar plots. For each direction tested the mean discharge rate, based on 15 stimulus presentations, is expressed as the distance from the plot's origin. Axes indicate discharge frequency. Lines connect each data point and stippling shows the level of spontaneous activity: lines and data points lying outside the stippling indicate an excitatory response; those inside the stippling indicate an inhibitory one. The vibrissa(e) for which each plot was constructed is indicated as is the cortical layer in which each unit was recorded. Solid circles denote responses to stimulus transients, circles enclosing open stars denote responses to stimulus steady states. All steady-state stimuli were 2 mm displacements for 1 s. Stimuli in plots *E*, *G*, *I*, *J*, *K*, and *L* were 2 mm transients at 60, 34, 67, 67, 60, and 16 mm/s, respectively; stimuli in *C* were 1 mm movements at 100 mm/s. The solids lines in *J* show effects of moving the hair away from its rest position; the dashed lines show the effects of moving it toward rest. See text for further explanation. In *G* note that individual deflections of two vibrissae which activated this multiple-whisker unit reveal qualitatively similar spatial tunings.

tribution of principal whiskers in the rostrocaudal and mediolateral planes was found to reflect the somatotopic organization of the mystacial pad described previously by others in rat and mouse (59, 69). Thus, vibrissae in the dorsal aspects of the mystacial pad were represented more laterally than those near the upper lip; caudal vibrissae projected to more posterior regions of the SI cortex than did whiskers

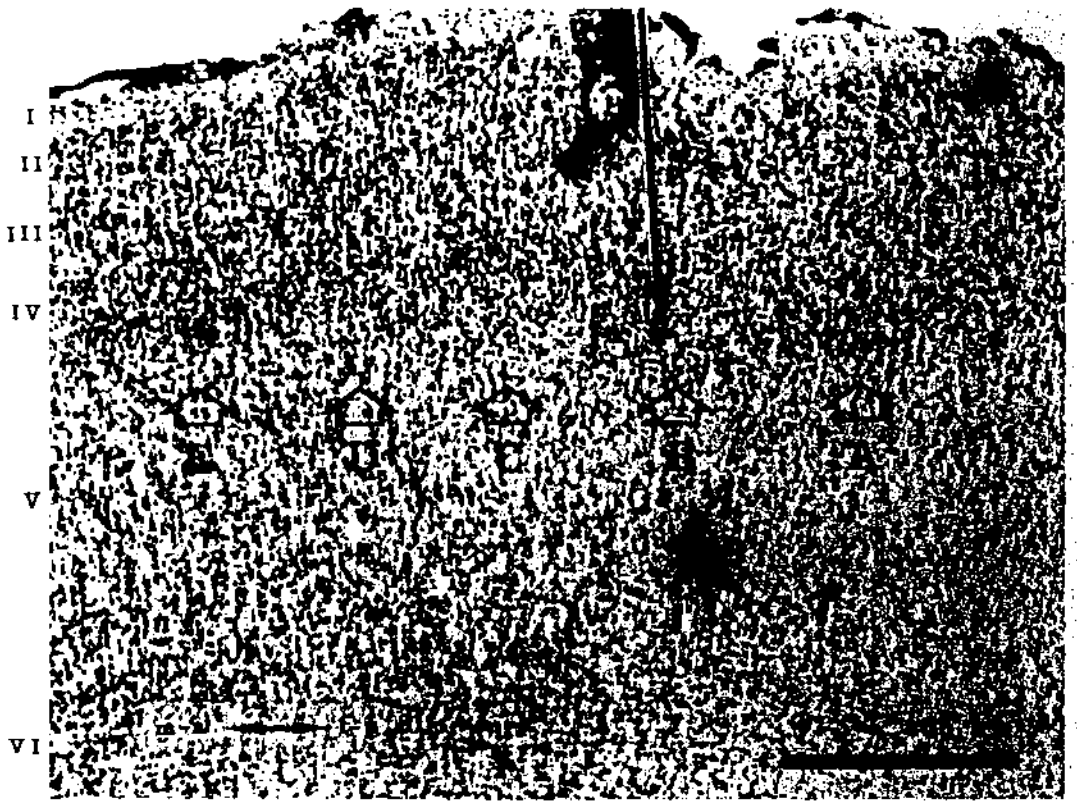


FIG. 7. Photomicrograph of a 30-μm section stained with thionine that was cut normal to the pia and across the long axis of the PMBSF. Five clusters of cells can be visualized in layer IV: these represent the five rows of barrels, labeled *A* through *E*, which correspond to the five horizontal rows of vibrissae on the mystacial pad (barrels are better seen in thicker sections, e.g., ref 61, Fig. 9). The dashed line shows the path of an electrode and the arrow points to a lesion produced at the electrode's tip (see text). In this penetration units responded at least to whisker B2 and the lesion is appropriately located in a row B barrel). Roman numerals indicate different laminae; m, medial; l, lateral; a, anterior; p, posterior.

near the nose. These relationships are illustrated in penetrations 7-1 and 7-12 in Table 1 (see table legend for further details). In addition to the columnar pattern of principal whiskers, the data in Table 1 reveal several other features of multiple-whisker units, namely that the other whiskers activating them are situated adjacently on the face and that whisker configurations become larger in deeper cortical layers. Moreover, for a given penetration the principal whisker is frequently the only hair that activates units recorded in layer IV.

Whisker organization

Fifty-five percent of units were activated by deflection of one whisker, only while the remainder responded to deflections of from 2 to a maximum of 12 hairs. The hairs in a multiple-whisker configuration were always contiguously located on the face. Many belonged to the same horizontal row of sinus hairs, while others were associated with two, three or, rarely, four rows.

These data are based on observations of cells which responded to deflections of identified, individual whiskers. Neurons were only designated multiple whisker if at least two hairs could be definitely shown to elicit responses from the unit; borderline cases, where one whisker's effects were clear but others' were doubtful, were assigned to the single-whisker category. Thus, the number of single-whisker units may be overestimated and the size of multiple-whisker configurations may be underestimated. Also, with this criterion it is unlikely that multiple-whisker configurations were artifacts caused by mechanical spread of

the stimulus through the skin to neighboring hair follicles.

For a majority of multiple-whisker units, the response pattern elicited by deflection of any one whisker activating the neuron was qualitatively similar to the response pattern elicited by deflection of any other whisker activating it. The plot in Fig. 6*G* illustrates this response similarity with respect to spatial properties and shows that the responses elicited by deflections of different hairs in a multiple-whisker complement are related quantitatively. This is further illustrated in Fig. 8, which presents data obtained from a unit that responded to stimulus transients applied to whiskers D3, D2, and C3. For most, but not all, multiple-whisker neurons the whisker producing the most pronounced responses was the principal whisker, and in large whisker configurations the "stronger" hairs tended to be situated nearer the principal one (see also ref 21). In addition, observations using hand-held probes suggest that concurrent deflections of two or more hairs activating a neuron may elicit quantifiably different responses than deflection of either whisker alone. These fine details of multiple-whisker organization were not studied systematically because of limitations in the stimulator.

Functional cytoarchitecture

In addition to depth readings from the microdrive, three procedures were employed in reconstructing the electrode tracks. In the first, these readings were referred to the green dye marks or, in several instances, to small lesions which were unintentionally produced at the electrode tip (see Fig. 7). The depth of 110 units recorded in 12 penetrations was

TABLE 1. *Whisker organization within individual cortical electrode penetrations*

Penetration	5–12		6–21		9–8		7–2		7–12	
Cortical Layers	P	O	P	O	P	O	P	O	P	O
II, III	—	D4	C3	D3	B1	—	—	C5,4	—	B3,4
	D3	D4	—	D3,E2	B1	B2	—	C5,4	—	B3
	D3	D4	C3	C2,D2,3	B1	B2	—	D5	—	B3
	D3	—							—	B3,4
									—	B3,4
IV	D3	—	C3	—	—	B2			B2	—
	D3	C2	C3	—	B1	—			B2	—
			C3	—	B1	—			B2	C2,3
									B2	—
V, VI	D3	—	C3	—	B1	B2	D3	—	B2	B1,3,4,5, A1–5
	D3	D2	C3	D3,2	—	B2	D3	D2,4, C3,2		
	D3	D1,2,4,5	C3	C4,D3	B1	β,B2, α,A1,2, γ,C1,2	D3	—		
	D3	D4	C3	C2,4, D2–4, E1–3	B1	B2,C1,2				
	D3	D1,2,4,5	C3	C4						
	—	E3								

Whisker complements of neurons recorded in five penetrations that were histologically reconstructed with the aid of green dye marks. Each unit's whisker complement is shown in the order in which the unit was recorded during advancement of the electrode; the layer(s) in which the units were recorded is also indicated. Whiskers under the P headings are the principal whiskers of the penetrations (see text); those under the O headings are "other" vibrissae which activated the particular unit. Dashed lines indicate that either principal or other whiskers did not activate the particular unit. With the exception of 7–2 and 7–12, all penetrations are normal to the pial surface. In 7–2 the electrode passed in a slightly lateral to medial fashion, and in 7–12 there was a slight anterior to posterior bias. The designation of the principal whisker in these two penetrations is arbitrary.

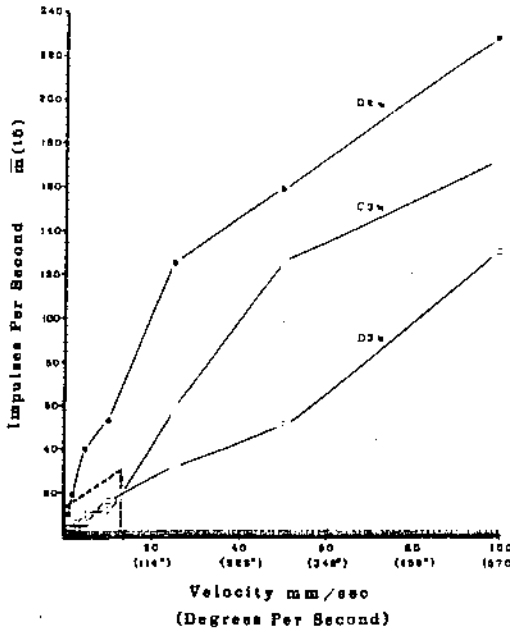


FIG. 8. Quantitative stimulus-response relations for a multiple-whisker unit. Data were obtained by individually deflecting whiskers D3, D2, and C3 at different movement velocities. Amplitude of movement was 1.0 mm. Discharge frequencies were computed as in Fig. 5 and all data points are based on 15 stimulus presentations. Since the responses to the 100 mm/s stimuli occurred with latencies of 10–13 ms, the responses did not begin until after the termination of the stimulus, which had a rise time of 10 ms. In these cases the discharge rate was computed on the basis of the mean number of spikes discharged from the beginning of the response to the time of the peak response (which typically occurred at a latency of 15 ms); this value was then divided by the stimulus rise time of 10 ms. The marked parallelism of the plots between the 50 and 100 mm/s data points may be an artifact of this procedure. Statistical analyses (t tests) revealed that, with the exception of the data points close to the origin that are bracketed by the dashed line, at each velocity the differences in the discharge rates elicited by each whisker were greater than chance values ($P < 0.05$, one tail).

directly determined by reference to these marks. The location of an additional 52 units recorded in six penetrations that were adjacent and parallel to the marked tracks could also be determined. A third procedure involved estimating the cortical depth of 47 units in four experiments in which marks were not made. This was done by noting changes in electrical activity associated with piercing the pia, increases in background activity on entry into layer II, and the de novo appearance of initially positive impulses which typically accompanied passage of the electrode into the underlying white matter.

The graph on the left side of Fig. 9 shows the results of these analyses. The parallel relationship displayed in the plots indicates that the depth distributions revealed by the three procedures are similar and, further, that histological data obtained from different penetrations in the same and/or in different preparations are highly comparable. The photomicrograph of a section cut normal to the pia, as shown at the right in Fig. 9, illustrates the packing density of neurons in this cortex which is reflected in the distribution of the recorded units, especially in regard to lower layer III through layer VI. The relative paucity of units recorded more superficially is probably attributable to several factors, including tissue damage and the small size of neurons in the superficial layers.

Single- and multiple-whisker units were unevenly distributed throughout the thickness of the cortex. Figure 9 shows that layers V and VI contain many multiple-whisker units. This difference is clearly illustrated in the upper histogram of Fig. 10: 85% of all neurons in layer IV (91% of RSUs, 64% of FSUs) responded to deflections of one hair only, the remaining 15% to deflections of two or more hairs. In layers II and III there is an increase in the percentage of multiple-whisker units (39%), and in the deeper layers multiple-whisker units predominate (64%).

The vertical distributions of two features of multiple-whisker units are also illustrated in Fig. 10. Apparent in both are differences between the supra- and infragranular layers. In comparison to multiple-whisker units in layers V and VI, those in the superficial layers tend to be activated by fewer whiskers, independent of "rowness" (for a definition see legend to Fig. 10), and their whisker complements tend to include hairs which belong to the same horizontal row, independent of whisker number. Further analyses indicate that in both infra- and supragranular layers these two features are highly related. Thus, as Fig. 11 illustrates, compared to multiple-whisker configurations in layers II and III, those in layers V and VI are larger with respect to both the number of whiskers and the number of horizontal rows involved.

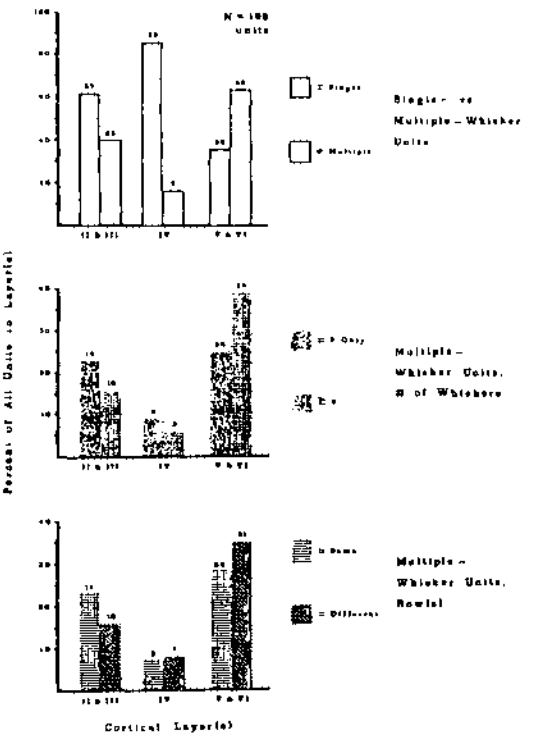


FIG. 10. Histograms showing how the number or spatial arrangement of vibrissae that activate a given cortical unit varies as a function of cortical depth. In the upper histogram numbers of single- and multiple-whisker units are expressed as percentages of all units recorded at each of three cortical depths. In the middle histogram the population of multiple-whisker units is subdivided into units that were activated by deflections of two individual vibrissae only and those that were activated by deflections of three or more vibrissae. The lower histogram illustrates the property of rowness: the multiple-whisker population is subdivided into units that responded to vibrissae located in the same, i.e., one, horizontal row of whiskers on the face and those that responded to vibrissae located in different, i.e., two or more, horizontal rows. The number above each bar is the actual number of units from which the percentage was computed.

laterally revealed units with comparatively small receptive fields located on the nose, near the midline.

DISCUSSION

Comparisons with other investigations

The response properties of cortical vibrissa units as revealed in the present study are similar in many respects to those previously described at various levels of the vibrissa-trigeminal system. Approximately 30% of the neurons are activated only by high-velocity whisker deflections and display properties comparable to the vast majority of units observed in SI cortex and ventrobasal thalamus of anesthetized rats (58, 59). Nearly one-third of cortical neurons give sustained responses to fixed vibrissal displacements. This value corresponds to 37% tonic units in rat trigeminal nucleus (48) and 39% tonic units in the cortex of lightly anesthetized cats (49). Directional selectivity is observed at all levels of the ascending vibrissa system (48, 58, 72) and is probably due, in large measure, to nonneural mechanisms associated with the sinus hair follicle (e.g., ref 3, 56). None of the data in rat or in other species (cf. ref 13) indicate a correlation between a whisker's location on the mystacial pad and the directional preferences of its associated neurons (e.g., ref 14). There may, however, be a general bias in favor of deflections directed in the up-and-back and/or down-and-forward quadrants, as observed here and in the brain stem (48). This coincides with the axis of whisker movements during whisking behavior and may be related to the use the animal makes of the vibrissae in palpating objects while simultaneously manipulating and exploring them with the mouth and forepaws.

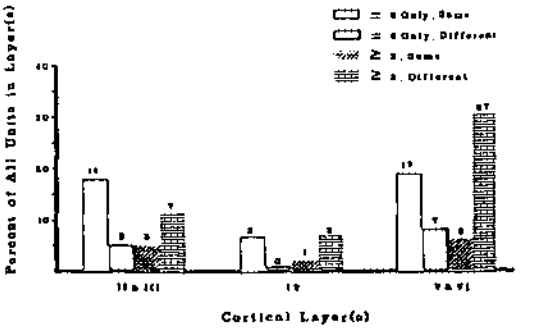


FIG. 11. Histogram showing how the number and spatial arrangement of vibrissae that activate a given multiple-whisker unit varies as a function of cortical depth. The population of multiple-whisker units is subdivided into four groups: units that responded to two vibrissae only, both located in the same horizontal row; units that responded to two vibrissae only, each located in different horizontal rows; units that responded to three or more vibrissae, all of which were located in the same horizontal row; and units that responded to three or more vibrissae, which were located in different, i.e., two or more, horizontal rows. The number above each bar is the actual number of units from which the percentage was computed.

Where quantitative comparisons can be made it appears that the range of sensitivities displayed by cortical neurons may be similar to that of first- (16) and second-order (48) afferents. Velocity thresholds are distributed over a range of at least two orders of magnitude, and the data suggest that some cortical cells are capable of detecting hair displacements at least as small as a few 10's of micrometers delivered 10 mm from the skin surface. Stimulus-response relationships can, in many cases, be described by monotonic functions, and in this respect cortical neurons are also similar to those at other levels of the rat vibrissa system (16, 48, 58, 72). Taken together, the data demonstrate that vibrissa-activated cortical neurons encode information concerning stimulus amplitude, velocity, and direction. Moreover, the findings suggest a marked fidelity in the transmission of information from periphery to cortex, a conclusion consistent with those from studies of other somatosensory systems in various species (34).

In the behaving rat neurons may respond not only to whisker deflections produced when the moving vibrissae contact objects (8, 72) but also to self-initiated whisker movements, which occur at rates of 5–11/s (62). It is not known, however, what stimulus features in the time domain are salient to the animals or to what extent they may be reflected in the frequency-response properties of cortical neurons. The decreased responsiveness of most units with whisker oscillations greater than 20–25 Hz (see Fig. 3) suggests that, as a population, cortical vibrissa neurons are limited in their ability to follow high-frequency stimulation. Similarly, in cat vibrissa cortex neurons are unable to follow electrical stimulation of the afferent nerves at frequencies greater than 30–50/s (21). By contrast, lower order afferents follow stimuli of several hundred hertz (e.g., ref 13, 19, 30; see also ref 48). A "low-pass" effect is also seen in the transmission of vibratory information from skin through cortex in monkeys where regular cortical spikes cannot be entrained by vibrations over 100/s. Lower order afferents and, of particular interest to the present findings, thin cortical spikes follow vibratory stimuli as high as 300/s (37).

Correlation of physiology and morphology in layer IV

Using microelectrodes, Welker (59, 60) demonstrated that the projections of individual sinus hairs are associated with specific, discrete cellular aggregates in layer IV, called barrels by Woolsey and Van der Loos (71). In Golgi preparations all of the neurons in the barrels of mice can be assigned to two groups of equal number according to both qualitative and quantitative criteria (39, 70). Class I cells have spiny dendrites and comparatively small somata; by contrast, the dendrites of class II cells are smooth with beads and their somata are larger. For a majority of neurons (85%) of both classes, the dendritic fields are restricted to a single barrel, whereas the remaining 15% distribute their dendrites to two or more adjacent barrels. On the basis of their observations, Woolsey et al. (70) predicted that two classes of barrel neurons could be distinguished physiologically and that with ideal electrodes, neurons of both classes would be found with equal probability. In this context it is particularly interesting that two types of action potentials, RS and FS, can be recorded extracellularly in the PMBSF of rats. Brief-duration potentials similar to FSs have also been observed in monkey somatosensory cortex (37, 66). Unfortunately, the technique of extracellular recording does not permit one to specify the neural element(s) from which recordings are obtained (43), and the issue of the origin of FSs (i.e., somata of cortical neurons versus terminals of thalamocortical fibers) and their exact position in the neuronal chain from periphery through cortex remains to be resolved.

Nevertheless, it is tempting to assume an identity between FSUs and class I neurons. The greater difficulty in isolating FSs may be attributable to the comparatively small somal size of class I neurons, the rapid rates of spontaneous discharge to extensive synaptic activity formed by incoming thalamocortical afferents which terminate on their spinous dendrites (65), and the comparatively brief time course of the extracellularly recorded potential perhaps to soma-dendrite configurations or to somal membrane properties. By this line of reasoning, RSs in layer IV would be identified

with class II neurons or with small pyramidal cells. Although technically difficult, the method of intracellular recording and staining of individual neurons may eventually provide a means of testing this hypothesis (22, 27). In addition, the functional differences displayed by FSUs and RSUs in layer IV suggest that an initial transformation of incoming information occurs within the barrels and that these transformations are mediated in part by synaptic linkages provided by FSUs. Parametric studies of large samples of barrel neurons may clarify these issues. That such connectivity is at least possible, however, is suggested by LeVay's (31) investigation of synaptic patterns in visual cortex of cat and monkey (see also ref 70).

Columnar organization

On the basis of single-unit studies of cat SI cortex Mountcastle (33) proposed that, at least for the initial evoked activity, the cortex is composed of functional "columns" which are oriented perpendicular to the pial surface. To date a functional "columnar" organization has been described in all of the known sensory and motor areas of the cortex (i.e., ref 1, 5, 23, 25, 42), including the vibrissa cortices of adult cats (49) and 7-day-old rats (4). In the present study the columnar pattern was represented by the principal whisker. Most cells in layer IV responded solely to deflections of the principal whisker and in several cases these were found to be associated with appropriate barrels (see Fig. 7). These findings are consistent with the idea that the barrels are morphologically recognizable correlates of the functional cell columns (71) which have now been directly demonstrated using metabolic indicators of neuronal activity (12). In future studies it may be interesting to investigate whether certain unit properties, e.g., directional selectivity, vary in any systematic fashion within a column's horizontal dimensions and to see how these variations may be related to the barrel structure, i.e., sides versus hollows.

Laminar distribution of response properties

The size of whisker configurations clearly varies as a function of cortical depth, being smallest in layer IV and largest in layers V and VI. Further, the percentage of unclassifiable units is greatest in the deeper laminae; many of these cells appear to respond to concurrent deflection of several whiskers but not to deflections of individual hairs alone. Correlations between different functional properties of cortical neurons and laminar patterns have been extensively documented in the visual cortices of cats and especially monkeys (23, 24, 47). In the somatosensory cortex of monkeys, directionally selective "cutaneous" neurons are observed in layers III and V, but infrequently in layer IV (66). In all of these studies—visual, cutaneous, vibrissal—correlations between functional properties of cortical neurons and laminar patterns were revealed by stimulation of related but spatially different portions of the receptor periphery, i.e., by moving bars of light, moving probes, deflection of adjacent vibrissae.

Because of the vibrissa-barrel arrangement, the source of input, i.e., individual sinus hairs, can be accurately identified and the cortical context in which recordings are made can be determined. Thus interactions that may occur among inputs from different vibrissae can be readily recognized as involving different spatial areas of the mystacial pad. These distinctions are more difficult to make in the study of cutaneous somatosensory function since, for any given region of the body surface, the cortex receives overlapping projections from first-order neurons with overlapping receptive fields. These considerations suggest the importance of manipulating the spatiotemporal aspects of cutaneous stimuli (e.g., ref 15, 66) and may, in part, account for the failure to observe substantial laminar differences in the functional properties of cortical cells when single punctate stimuli are applied to the skin surface (but see ref 35).

Hierarchical organization and sequential processing

A hierarchical organization based on a sequential manipulation of sensory information has been proposed to account for laminar differences in the distribution of cortical neurons with different functional properties (23, 24, 66). At the risk of oversimplification, I propose that single-

and multiple-whisker units comprise a functional hierarchy within the vibrissa cortex of rats. Multiple-whisker organization is elaborated by the sequential transformation of information about progressively larger whisker configurations. In the cortex this process originates in layer IV, and perhaps lower layer III as well, and then proceeds to more superficial areas, and finally to the deep laminae.

1. Available evidence suggests that layer IV functions as an input stage of information processing in the vibrissa cortex and in other sensory cortices as well (cf. ref 71). In the present study, 85% of units recorded in the PMBSF responded to deflections of single hairs only. Single-whisker units also predominate in lower levels of the ascending system (48, 57, 72) where the projections of individual vibrissae can be correlated with morphological aggregations of axon terminals (28, see also ref 53). Single-whisker neurons in layer IV thus more closely resemble neurons at lower levels of the trigeminal system than do multiple-whisker units which are found mainly in the infra- and supragranular layers (for visual system see ref 23, 24).

2. Barrels, in layer IV, may constitute single-whisker "modules" from which large whisker organizations are constructed. Multiple-whisker organization could also result, however, from convergence of thalamocortical fibers onto individual neurons whose somata lie superficial or deep to layer IV. Thalamocortical afferents are known to form synapses with dendritic spines in the barrels (65), but it is not known whether these spines belong to dendrites of layer IV "stellate" cells or to apical dendrites of pyramidal cells deep to layer IV (64; see also ref 26, 31). Determination of whether or to what extent afferents terminate on dendrites of cells outside layer IV is critical; at present these issues are unresolved.

3. Available anatomical evidence in rat and other species indicates an important output function for the deeper laminae, particularly layers V and VI (e.g., ref 7, 18, 67).

4. The functional differences between neurons in layer IV and those in deep layers are consistent with the anatomically defined roles of these regions as input and output, respectively.

5. If a sequential processing of information does occur, it would be expected that response latencies would increase in a systematic fashion from middle-to-superficial-to-deep areas. Studies of somatosensory cortex have demonstrated that the shortest latencies are observed in middle layers, the longest ones in deep layers (35).

6. The numbers of single- and multiple-whisker units in layer II and upper layer III are roughly equivalent. Examination of multiple-whisker configurations suggests that those in superficial layers represent a transition from small configurations, which are most numerous in layer IV, to large ones, which are common in layers V and VI.

7. There is a greater proportion of unclassifiable units in deep layers. To the extent that a number of stimulus features must be present to activate these units, they may represent a higher order of integration (e.g., ref 23).

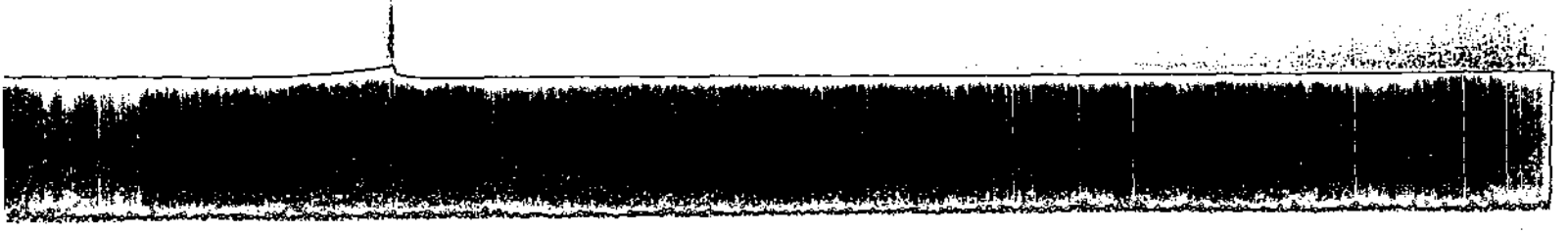
8. Each barrel in layer IV contains many neurons that respond to deflection of the same whisker and each occupies a finite amount of cortical space. Therefore, multiple-whisker configurations in superficial and deep layers will depend on a horizontal spread of information above and below the barrels, the size of the configurations being determined by the spatial extent of horizontal connectivity.[1]

9. Available functional and morphological evidence suggests several additional mechanisms whereby sensory information may be manipulated within the vibrissa-SI cortex (cf. ref 50). First, a number of alternate routes or "shortcuts" may be available, i.e., layer IV direct to layer V. Second, there are parallel inputs from the thalamus to deep portions of the cortex (11, 67). These projections may account for the observed similarities between FSUs in layer IV and stimulus transient-inhibited neurons which were found only in the deeper aspects of the cortex (for visual cortex, see ref (17, 23, 32). Third, the efferent projections of the vibrissa cortex do not arise solely from the deep layers (45, 67), suggesting that the origin and content of outgoing information may be quite varied.

Principles of cortical organization

The findings in this and other investigations of vibrissa cortex in rodents are

[1] There is some limited supporting evidence for point *8*. First, following lesions restricted to the supragranular layers, terminal degeneration is observed over a uniform field in layer V. The simplest explanation of these findings is that the vertical connectivity within the vibrissa cortex is not characterized by the marked segregation of fibers associated with the thalamocortical input to the barrels (45). Second, in tangential sections the distance between adjacent rows of barrels appears greater than the distance between adjoining barrels in the same row (61). Compared to multiple-whisker configurations in deep layers, those in superficial layers were observed here to be more likely to involve vibrissae from the same horizontal row. These findings are compatible with the hypothesis that a horizontal spread of information from individual barrels increases progressively from supra- to infragranular layers.



compatible with some general findings concerning cortical organization. Thus, evidence available at present indicates that the cerebral cortex can be differentiated on anatomical as well as on functional grounds and suggests that some correlation exists between function that can be revealed by available physiological techniques and structure that can be readily recognized (e.g., ref 10, 68). Further, the results from the present study and those from a variety of other single-unit studies of cortical function suggest two possible principles of intrinsic cortical organization. The first is a vertical organization characterized by interconnections among cells at different depths from the pial surface which preserves certain features of a peripheral stimulus, for example, which vibrissa is stimulated. The second is a horizontal organization correlated with the laminar pattern which allows stimulus information to be progressively manipulated and transformed. These two forms of organization are superimposed on each other and for any given region of the sensory projection they will be replicated many times. Presumably this arrangement achieves an economy of intracortical connectivity whereby inputs from nonneighboring cells or groups of cells that share similar response properties can converge on specific neurons (e.g., ref 23, 25). Moreover, similar sets of "instructions" may thus be performed by all of the functional units, or columns, which comprise the cortex. Future investigations of the rodent vibrissa system may provide answers to some general questions about cortical structure and function as some of the system's anatomical, physiological, and behavioral properties render it particularly amenable to investigation by available techniques.

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