

MODALITY AND TOPOGRAPHIC PROPERTIES OF SINGLE NEURONS OF CAT'S SOMATIC SENSORY CORTEX¹

VERNON B. MOUNTCASTLE
*Department of Physiology, The Johns Hopkins University School of Medicine,
Baltimore, Maryland*

(Received for publication November 5, 1956)

INTRODUCTION

THE PRESENT PAPER describes some observations upon the modality and topographical attributes of single neurons of the first somatic sensory area of the cat's cerebral cortex, the analogue of the cortex of the postcentral gyrus in the primate brain. These data, together with others upon the response latencies of the cells of different layers of the cortex to peripheral stimuli, support an hypothesis of the functional organization of this cortical area. This is that the neurons which lie in narrow vertical columns, or cylinders, extending from layer II through layer VI make up an elementary unit of organization, for they are activated by stimulation of the same single class of peripheral receptors, from almost identical peripheral receptive fields, at latencies which are not significantly different for the cells of the various layers. It is emphasized that this pattern of organization obtains only for the early repetitive responses of cortical neurons to brief peripheral stimuli. These neurons may be related in quite different organization patterns when analyzed in terms of later discharges. A report of these experiments was made to the American Physiological Society in September, 1955 (10, 17).

METHODS

Data presented here were obtained from the 59 experiments on cats described in the preceding paper (19); for details, reference is made to its section on methods. Once the importance of the vertical module of cells was recognized, every effort was made to attach the recording chamber over the skull opening so that the microelectrode approached perpendicularly to the cortical surface. In two experiments the chamber was attached so that the microelectrode approached at a 45 degree angle of incidence to the cortical surface.

The frequency graphs which appear were made by counting the number of impulses in each short period of time, which is indicated in the legends, and plotting the averages for these periods. Our methods of indicating onset and release of steady pressure upon the skin, or the onset and cessation of joint movements, were so crude that we can make no statements about the latencies of the changes in discharge rates observed. However, that these changes were associated with the application of the stimuli was obvious.

RESULTS

I. MODALITY PROPERTIES OF NEURONS OF SOMATIC SENSORY CORTEX

A. Classification, and distribution of neurons between classes

All the neurons of the somatic cortex which could be driven by physiological stimuli delivered to the periphery of the body were activated by me-

¹ Aided by a grant (B-357) from the National Institutes of Health, United States Public Health Service, Department of Health, Education and Welfare.

chanical displacement of some tissue, and the divisions described hereafter indicate subgroups of this general broad modality. The first obvious division is between cells driven by the stimulation of the skin and those responsive to stimulation of the deep tissues. Neurons related to the skin were driven either by movements of hairs or by pressure upon the skin, and cells of these two groups showed different adaptation properties. Reasons for supposing that the third cutaneous subgroup indicated in Table 1 (NBD) does not represent a third submodality are given below. Of neurons related to deep receptors there are two subgroups, the first those activated by pressure upon the deep fascia and connective tissue, and the second those driven by joint rotation. An important point which we wish to emphasize is that *we have never observed cross activation between these groups, i.e., a given neuron is responsive to only one of the forms and locales of stimuli described.*

It will be seen in Table 1 that a very large percentage of the neurons encountered which could not be driven by peripheral stimuli were discharging initially positive spikes. Evidence has been presented in the preceding paper that neurons discharging such spikes are to be considered more damaged than those discharging initially negative spikes, and that when it occurs this damage is first signalled by a loss of driveability from the periphery. For this reason, and because such a very high per cent (93 per cent) of cells discharging initially negative spikes were responsive to peripheral stimuli, we conclude that there is not sufficient evidence to establish that there exists in this cortical area a group of cells functionally independent of its thalamo-cortical inflow.

B. Response properties of cortical neurons of the different modality subgroups

1. Neurons related to cutaneous receptors. (a) Those activated by movements of hairs. The data of Table 1 indicate that about 60 per cent of all neu-

Table 1. Classification of 685 neurons by their modality subgroups, and by initial sign of their spike discharges

	Cutaneous				Deep		Un-drive-able	Totals
	Hair	Press.	NBD	Sub-total	Joint	Fascia		
Units discharging initially negative spikes	162	40	60	262	68	27	26	383
Units discharging initially positive spikes	40	22	19	81	37	20	164	302
Totals	202	62	79	343	105	47	190	685

A table showing distribution of all units observed between the various modality subgroups. Note especially high proportion of "undriveable" neurons that discharged initially positive spikes. Evidence that this loss of driveability is due to damage is given in preceding paper (19). Term NBD indicates neurons activated by stimulation of skin, for which more complete identifications were not made.

rons of the cutaneous group were activated by stimulation of the hairs. Such units are exquisitely sensitive to bending of the hairs of the skin—so much so that they are optimally driven by short weak jets of air delivered against the hairs. Their response patterns to single and repetitive brief stimuli are described in the preceding paper. They are driven also by direct stimulation of the skin at the base of the hairs. They are, however, strikingly different from the skin pressure class, described below, in the property of adaptation. When a few hairs are quickly depressed and held in a steady position these neurons respond with a brief discharge; they remain silent or discharge at their spontaneous rate during steady depression of the hairs, and discharge a brief train once again upon their release. Their receptive fields are small, and vary in size directly with the distance of that field from the tip of the limb (see section II, and Figs. 7, 8, 9).

(b) *Those activated by pressure upon skin.* Neurons of this type make up 18 per cent of the cutaneous group. They differ from the preceding subgroup in two ways. Firstly, they are optimally driven by direct pressure upon the skin, although the threshold is so low that pulls of the hairs within their receptive fields will drive them also. There can be little doubt that the receptors concerned lie within the skin or the subadjacently attached connective tissue, for the response of units of this class to pressure is unchanged when the skin containing their receptive fields is surgically elevated from the deep tissues, its innervation remaining intact. Secondly, while their response patterns to single and repetitive brief stimuli differ in no way from those of neurons related to the hairs, their adaptation properties differ markedly. An example is given in Fig. 1. The records and the graph of changes in impulse frequency show that with application of steady pressure upon the skin there was a rapid rise in frequency to a very high rate, an *onset transient*. In less than a second the frequency of discharge declined slightly to a more or less *steady state*, at which rate the discharge continued during steady application of the pressure. Upon removal of the stimulus the rate dropped suddenly, and a short poststimulus period of depression intervened for 1 sec. or so before the spontaneous discharge began again.

This general type of adaptation curve has held uniformly for all the skin pressure units we have studied. Some of its variations are shown in Fig. 2. The curve for SC I 24-4 resembles closely that shown in Fig. 1, and here the arrows signal with some accuracy the onset and release of the pressure. The curve for unit SC I 5-2 shows the dead-beat onset and cessation of the response of a unit which was silent in the absence of stimulation. The curve for SC I 27-3 is that of a unit with a high rate of spontaneous discharge; in this case the onset transient reached a very high level, but the steady state rate of discharge was only slightly above the spontaneous level. This is the only response curve of this type observed.

In general, no difficulty arises in identifying a cortical neuron as either skin hair or skin pressure by the form and locus of the optimal driving stimulus. The most reliable criterion, however, is the type of adaptation to a

steady stimulus. Whenever doubt as to modality type has arisen, which happens only rarely, this last has been the deciding factor in classifying the particular neuron under study.

(c) *Those neurons classified as skin, NBD.* The remaining 22 per cent of the neurons driven by skin stimulation are listed in Table 1 under this heading. A review of all the protocols revealed this number of neurons classified

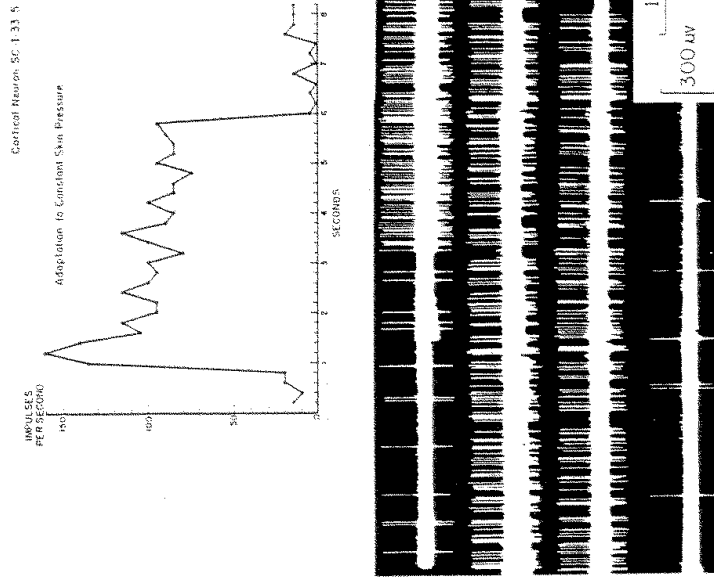


FIG. 1. Records of impulse discharges of unit SC I 33-5 in response to steady pressure applied to peripheral receptive area, with a small blunt instrument. Neuron was driven by light pressure upon a 1×2 cm.² receptive area of skin upon contralateral elbow. Signals of onset and release of pressure were inexact, and are not shown, but the causal relation of frequency changes to application and withdrawal of stimulus was repeatedly observed. Graph plots continuously average frequency during each 200 msec. Observed for 20 min. at a depth within cortex of 645 μ . V_0 of spike amplitudes = 4.2%, short time constant recording.

as skin, without further notation. All were driven by mechanical stimulation of the skin, but a careful examination to determine more accurately the modality subtype of each was not made. It seems likely that they do not make up a separate subgroup, but would upon more detailed study have divided between the two cutaneous subgroups already described.

2. *Neurons related to receptors located in deep tissues.* (a) *Neurons driven*

by movement of joints. A distinct class of neurons in the somatic cortex has been observed which responds to the rotation of joints. We have observed a total of 105 such units, and have made extensive photographic records of the discharges of 21 of them. These neurons may be entirely silent but usually discharge at a low spontaneous rate when the joint to which they are related rests in its neutral position. Their impulse frequency accelerates rapidly when the joint is rotated in an optimal direction, and they discharge at a

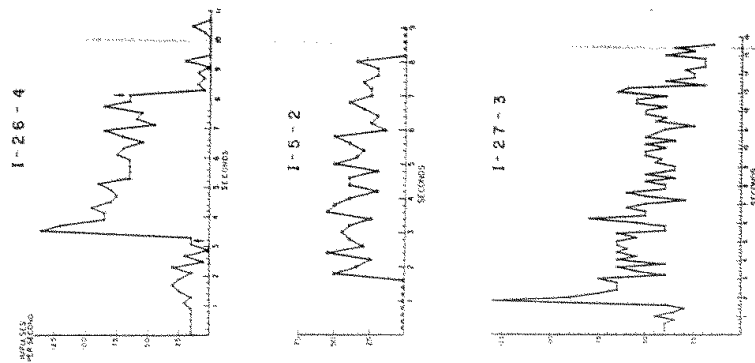


FIG. 2. Impulse frequency graphs for three other skin pressure units responding steadily to steady stimuli. Graphs plot continuously the average frequency of discharge in each 200 msec. I-26-4—Arrows indicate accurately onset and release of pressure to peripheral receptive zone, which lay in contralateral cubital fossa, and measured 1 cm. in diameter. Duration of observation not recorded. Depth 1330 μ . I-5-2—Adaptation curve of a neuron completely silent in absence of any stimulus. Receptive zone restricted to skin between 2nd and 3rd digits of contralateral forepaw. Observed for 1 hr. 5 min. at depth of 1027 μ . I-27-3—Adaptation curve for a neuron with a very high rate of spontaneous discharge. Receptive zone confined to volar surface of contralateral wrist. Observed for 1 hr. 40 min., at a depth of 860 μ . V_0 of spike amplitudes = 1.4%. See text.

The records of Fig. 3 show the transient change in discharge rate of neuron SC I 39-1, produced by extension of the contralateral elbow. The discharge ceased completely upon flexion of the joint. Our attempts to determine how rapidly a joint may be moved in alternating directions and the related neurons still give frequency peaks upon each excitatory movement are incomplete, but we have observed clear peaks at rotation rates up to 4 or 5

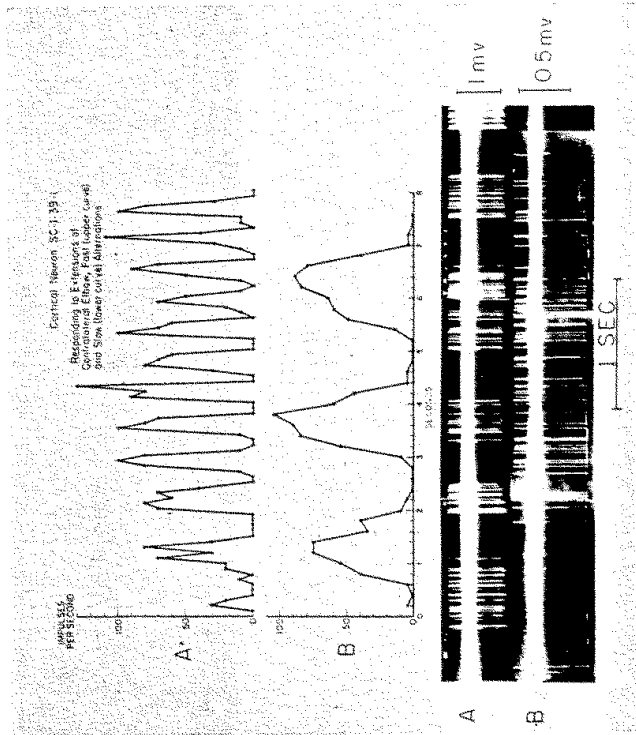


FIG. 3. Records of impulse discharge of unit SC I 39-1, a neuron responding to extension of contralateral elbow. Sample of records below, and complete impulse frequency graphs above for (A) rapid joint rotation, and (B) slower joint rotation. Graphs plot average frequency in each 200 msec. period. Unit observed for 46 min. at depth in cortex of 980 μ . V_0 of spike amplitudes = 3.5%; short time constant recording.

per sec. This gives some idea of the capacity of the system to transmit information concerning phasic joint movement. Neurons of this class continue to discharge also when the joint to which they are related is held in a steady position, if that displacement from neutral is in the direction for activation of the neuron. The graph and records of SC I 24-1 are shown in Fig. 4, which illustrates the very slow rate of adaptation of these receptors and the related neurons of the afferent system. This is shown also at the end of the graphs in Figs. 5 and 6. Following return of the joint to its neutral position there was a short period during which the spontaneous rate of discharge was somewhat depressed.

Upon five occasions we have observed the discharges of pairs of cortical

steady rate if the joint is held in the new position. They usually become completely silent when the joint is rotated in a direction opposite to that which optimally causes their discharge. The inference that the receptors driving these neurons are located in the joint capsules and ligaments, the periosteum of the long bones, and about the tendon grooves (but not in the tendons or muscles) has been confirmed on several occasions by dissection of the limbs and direct location of the position of the receptors. Such dissections were, of course, done for only a few units, for the experiment is thereby terminated. Section of the tendons acting at a joint has no effect upon the driveability of the related neurons by rotation of that joint.

neurons present in the record at the same time, which discharged in a reciprocal fashion when the related joint was rotated. The frequency charts for a pair of such reciprocal units, SC I 21-1 and 21-2, are shown in Fig. 5. The first unit was driven by extension of the contralateral elbow, the second by its flexion. The graphs show that each neuron became completely silent when its reciprocal partner was maximally excited. At the end of the record

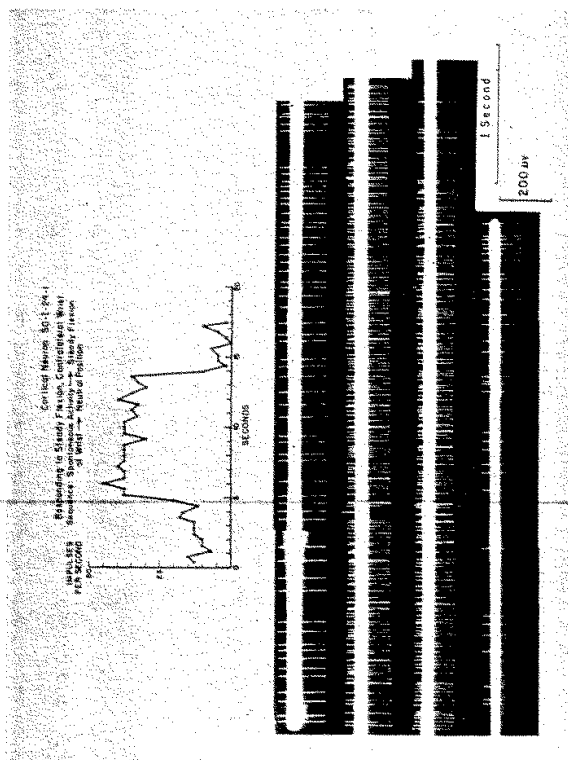


FIG. 4. Record below and impulse frequency graph above of unit SC I 24-1, a neuron responding steadily to steady flexion of wrist; receptors lay in joint capsule. No signal of joint movement given, but relation of frequency changes to joint movements was repeatedly observed. This record taken by chance during sudden shift in spike amplitude (cf. 19). At beginning, mean spike amplitude $252.6 \pm 11.8 \mu V$, $V_0 = 6.11\%$; at end of record mean spike amplitude $221 \pm 1.0 \mu V$, $V_0 = 3.4\%$. Spike amplitude dropped by 12% to a new level at which it was steady. Duration of observation not recorded; depth 160μ . Short time constant recording.

the elbow was held in steady flexion, which produced a continued steady discharge of the second unit and nearly complete silence of the first. Frequency charts of another such reciprocal pair, SC I 47-1 and 47-2, are shown in Fig. 6, together with a short strip of the record. These two units were activated, respectively, by protraction and retraction of the shoulder joint.

These observations indicate that some neurons closely adjacent within the cortex are activated reciprocally by reciprocal movements of the joints. It seems likely that this reciprocity results from alternating inputs from the peripheral receptors activated by the rotation of the joint in opposite directions. The possibility that alternation in cortical cell discharge results from a central reciprocal interaction between them will be considered in the dis-

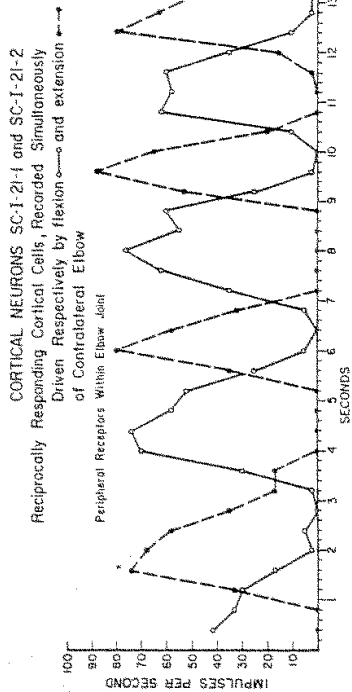


FIG. 5. Impulse frequency graphs of two units, SC I 21-1 and 2, observed simultaneously. Units responded reciprocally to alternating flexions and extensions of contralateral elbow. Records obtained were photographically too faint for reproduction. Graphs plot continuously average frequencies for each consecutive 400 msec. period. Impulse frequency reaches zero for each unit when joint reaches position maximally exciting the other unit. During 14th and 15th seconds joint held in steady extension, and extension unit fires steadily, while flexion unit is almost completely silent. Observed for 2 hrs., 5 min., at depth of 1112μ .

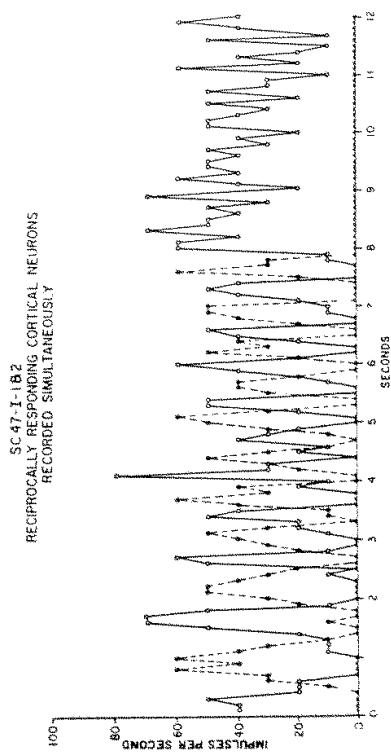


FIG. 6. Above, plot of impulse frequencies of two units, SC I 47-1 and 2, present simultaneously in record and responding reciprocally to alternating protraction and retraction of contralateral shoulder joint. Receptors in or near joint capsule. Alternations more rapid than for neurons illustrated in Fig. 5, but reciprocity of discharge is precise. From 8th second on joint held in steady protraction, causing continued discharge of neuron excited by protraction, and complete silence of neuron excited by retraction. Below, to left, short strip of record showing complete alternation of discharge of the two units during a joint cycle. Short time constant recording. To right, discharge of protraction unit (above) and retraction unit (below) evoked by appropriate joint positioning, here at long time constant recording. Time lines 40 c./sec. Units observed for 2 hrs. 9 min., at depth of 1800μ .

cussion, as will the role this group of receptors and their central connections may play in position sensibility.

(b) *Neurons whose receptive fields lie in deep fascia.* We have observed 47 neurons which were activated by stimulation of the deep fascia. They make up 31 per cent of all the deep units observed. Their receptive fields are in shape and size similar to those of skin units (see Figs. 7, 8). These units are

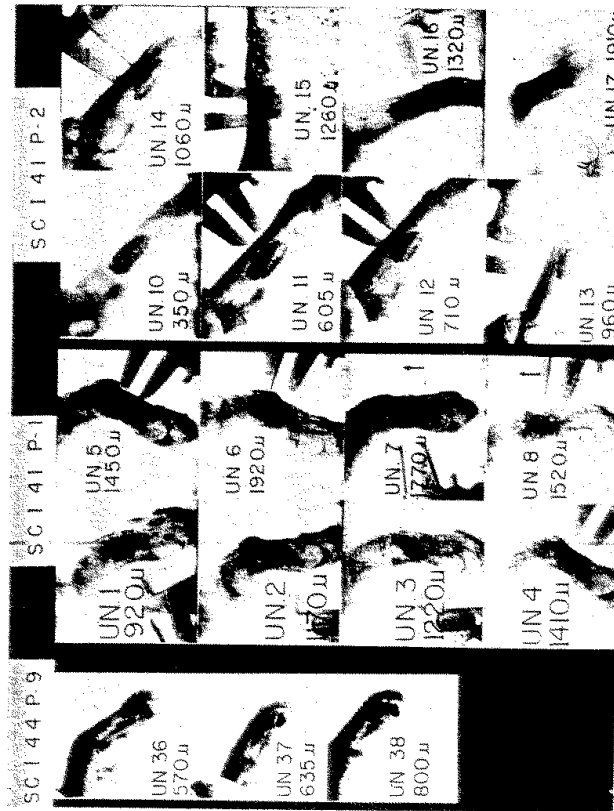


FIG. 7. Photographs of excitatory peripheral receptive fields on skin of contralateral foreleg of cat which play upon cortical neurons. Technique described in text. In ninth penetration of SC I-44 three units were isolated and eight were studied in first and eight in second penetrations of experiment SC I-41. Depths at which neurons isolated indicated. Caliper set at 1 cm. Photographs for SC I-44, P-9, are only ones retouched. Note (i) that receptive fields for neurons lying in vertical line of electrode's traverse have fields of almost identical size, shape, and position, and (ii) relation of size of receptive field to its distance from tip of limb (see Fig. 9).

driven by very light mechanical stimuli, so that even a small displacement of the overlying skin produces their discharge. They may also be driven by pressure changes occurring in the deep fascial compartments when the enclosed muscles contract. That the receptors concerned lie in the fascia and not in muscle or skin has been demonstrated by surgical dissection of the peripheral tissues, while observing continuously the response of the cortical neurons. The units of this group adapt only very slowly when constant pressure is applied against the fascia, resembling in this property the skin pressure units (see Figs. 1, 2). These properties suggest that this class of neurons

functions in an overall light tactile sensibility, for they respond to all but the very weakest stimuli impinging upon the skin surface overlying their own fascial receptive fields.

II. ANALYSIS OF TOPOGRAPHIC PATTERNS OF REPRESENTATION OF BODY SURFACE UPON CORTEX, IN TERMS OF SINGLE NEURONS

A. Excitatory peripheral receptive fields of cortical neurons

It has been possible by using weak mechanical stimuli to map with considerable accuracy the limits of the peripheral receptive fields of the cortical

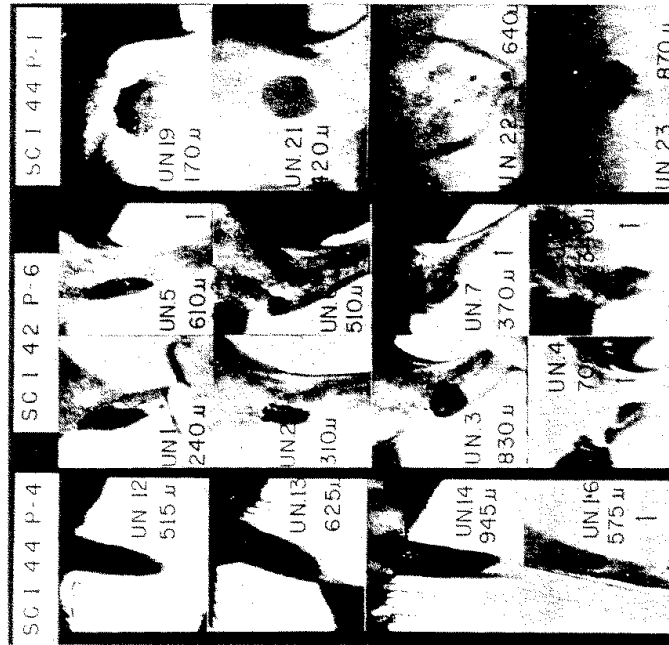


FIG. 8. Photographs of excitatory peripheral receptive fields of skin of contralateral body surface playing upon cortical neurons. Technique described in text. In fourth penetration of exp. SC I-44 four neurons were isolated, eight in sixth of SC I-42, and four in first of SC I-44. Fields of neurons isolated in the latter penetration show the great enlargement in size and increased variation for fields upon proximal portion of limb and upon thorax.

neurons belonging to the cutaneous subgroups. The procedure was as follows. Upon isolation of the discharges of a single neuron the peripheral field activating it was quickly located by mechanical stimulation of the body surface, and its modality type established. If of a cutaneous class, the fur was then clipped, and the receptive field mapped by stimulation of the skin with a small blunt rod. The field was marked with india ink and photographed,

together with a scale. The negatives were later projected to natural size, traced, and the area enclosed by the tracing measured with a polar planimeter. The error introduced by the planar projection of the curving limb surface cannot be accurately estimated, but is roughly of the same degree for different portions of the limbs. All the receptive fields were upon the side of the body contralateral to the cortical neurons studied. *We have never observed a single cortical neuron of the first somatic region to be activated by stimu-*

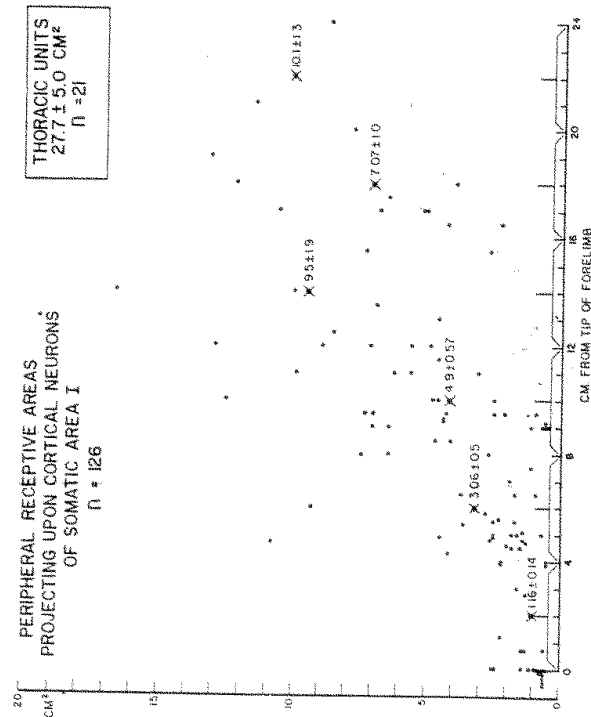


Fig. 9. Graph upon which each black dot relates the area in cm.² of excitatory peripheral receptive field for a given cortical neuron to distance of that field from tip of limb—contralateral foreleg. Crossed dots locate means for these fields when grouped into classes by 4 cm. distances from limb tip. Means and standard errors are given alongside. Relation is nearly linear for first 12 cm. up from limb tip; data insufficient to establish relation beyond that point.

lation of the ipsilateral body surface, though ipsilateral testing has been a standard procedure. The photographs shown in Figs. 7 and 8 illustrate the shape of these peripheral fields. They show also that these fields are very small near the tips of the extremities, become larger as the positions shift towards the base of the limbs, and are very large indeed upon the thorax and trunk. The area of the receptive field for each of the 124 neurons studied in this way is indicated by the solid dots on the graph of Fig. 9. The open circles and the figures beside them give the means, and the standard errors of the means, of these data, when they are grouped into 4 cm. classes by distance of the centers of the receptive fields from the tip of the limb. The points so marked are linear up to about 12 cm. distance from the limb tip. Beyond

that the number of observations is too small to determine whether the relation is linear or not. Nevertheless, it is obvious that the size of the field is related to its distance from limb tip, which suggests it varies inversely with peripheral innervation density. From such data it seems possible to make a clear definition of what is meant by the localized representation of cutaneous sensibility in the cortex. An attempt to do so is made in the discussion.

Another and most striking fact illustrated by the photographs of Figs. 7 and 8 is that the cells of vertical columns are related to peripheral fields which are very much alike in size and shape, and which occupy more or less the same peripheral area. The fields for eight units isolated in penetration 1 of SC I 41 (Fig. 7), for example, or the eight isolated in penetration 6 of SC I 42 (Fig. 8), show this very clearly. This identity of the peripheral fields of cells lying beneath one another in a vertical line traversing the successive layers of the cortex is the most precise when the microelectrode enters and traverses the cortex perpendicularly to its surface. On the other hand, when slanting penetrations (at a 45 degree angle of incidence to the cortical surface) are made, the receptive fields of neurons successively encountered shift gradually, in conformity with the surface pattern of representation directly above the successive positions of the electrode tip in the depths.

B. Afferent inhibition

We have observed peripheral sensory stimulation to have an inhibitory effect upon a cortical neuron in seven instances. In each of these cases such stimulation interrupted the spontaneous discharges of the cell. An example is given in Fig. 10, in which the spontaneous discharges of unit SC I 37-1 are shown to be held in abeyance by light pressure applied to the skin outside the excitatory peripheral receptive field of the unit. This neuron was activated by movement of a few hairs in a skin area near the elbow, which measured 1.5 cm. in diameter. The area of skin whose stimulation caused inhibition of the spontaneous discharge covered a much larger area of the arm, which completely surrounded the excitatory peripheral receptive field; its extent was not determined exactly. Stimulation elsewhere on the body surface had no effect. The threshold for inhibition was very low, for a light puff of air directed anywhere within the inhibitory field sufficed to interrupt the unit's discharge. In this case suppression of spontaneous discharge did not seem to affect the response of the unit to a specific stimulus delivered within its excitatory field. In another instance, however, we have observed that gentle mechanical stimulation of the skin surrounding the peripheral receptive field of a unit, SC I 30-1, prolonged the latency and reduced the number of spikes per response of the unit to stimuli delivered within that receptive field. Afferent inhibition is not limited to neurons serving cutaneous sensibilities, and the charts of Fig. 11 show the reduction in spontaneous discharge of two other units which were excited by stimulation of deep structures of the limb, and inhibited by stimulation of other deep structures near-

CORTICAL NEURON SC I-37-1
INHIBITION OF SPONTANEOUS ACTIVITY BY PHYSIOLOGICAL
STIMULATION OF SKIN SURROUNDING THE
PERIPHERAL RECEPTIVE ZONE

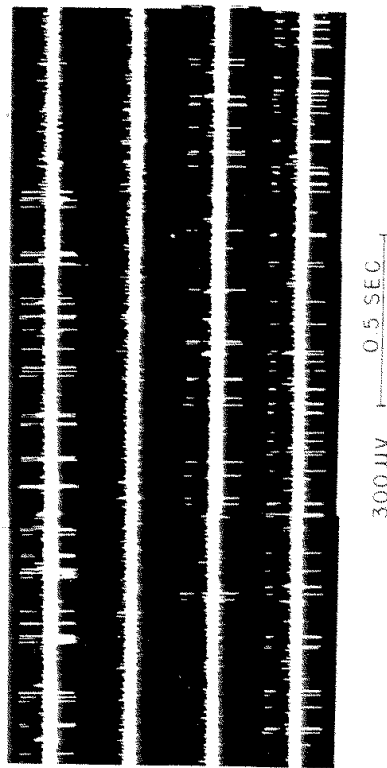


FIG. 10. Inhibition of spontaneous discharge of neuron SC I-37-1. Unit was driven from a 2 cm.² excitatory receptive zone of skin just below contralateral elbow. Stimulation within a much larger area, *surrounding* excitatory field prevented completely spontaneous discharge. In strip illustrated, inhibition produced by light pressure within peripheral inhibitory field; it was also produced by a steady faint stream of air directed against skin of same area. No signal of onset and removal of inhibitory stimulus given, but association repeatedly observed. Unit observed for 3 hrs., 39 min., at depth of 815 μ . V_0 of spike amplitudes = 3.2%. Short time constant recording.

Each of these seven instances was observed in animals under light Pentothal-d-tubocurarine anesthesia. In the case of unit SC I-37-1 a further inhibition for a period of about 15 minutes, at the end of which time the inhibition could once more be obtained, in as exquisite a form as ever. The injection affected in no way the driveability of the unit from its excitatory peripheral receptive field. This suggests that the afferent pathways responsible for the inhibition on the one hand and the excitation on the other are differently arranged, for they are differentially sensitive to anesthetic agents. While our observations upon afferent inhibition are few in number, they do confirm its existence, which was suggested by Amassian (2, 3) from experiments in which afferent nerve volleys were used as input. Some discussion of the role it may play in sensation is given below.

III. LOCATION IN CORTEX OF NEURONS OF MODALITY SUBGROUPS

A. Distribution in depth

The charts of Fig. 12 show the depths at which neurons of the various subgroups were encountered. Only neurons encountered in penetrations reaching 1500 μ in depth or more are tabulated, so that the number of cells in each class is somewhat smaller than those given in Table 1. The distribu-

tions for each modality extend throughout the cortex, and are not significantly different in any case from that for all neurons, shown in Fig. 12 of the preceding paper (19). It is concluded that neurons of each modality class are located in each of the cellular layers of the cortex, II through VI.

B. Neurons of vertically oriented groups are related to same single submodality

In our early experiments it was evident that the neurons lying more or less directly over one another in a direction parallel to the transverse axis (*i.e.*, the axis penetrating the cortex) of the cortex were similar in their mo-

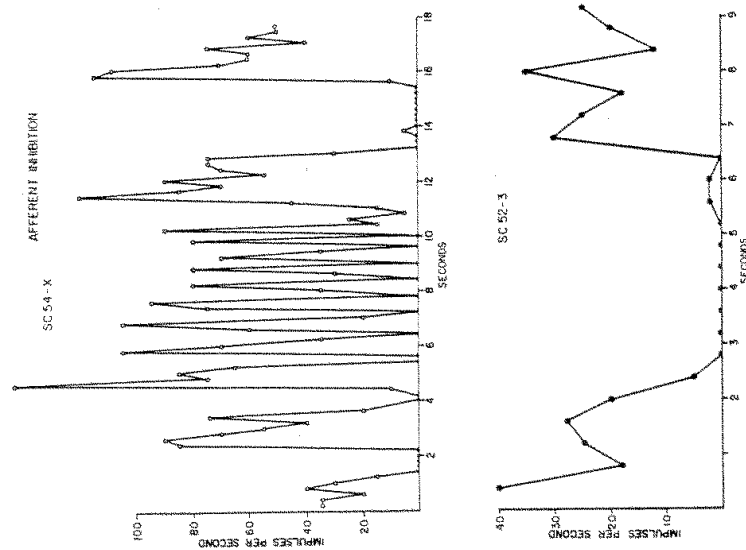


FIG. 11. Frequency of impulse discharge of two other units showing afferent inhibition. SC I-54-x, above, was a deep unit driven by rotation of elbow joint. Here its high spontaneous rate of discharge is intermittently inhibited by rapid squeezes of paw. Stimulation of skin of paw did not affect spontaneous rate. During 13th and 14th seconds paw was steadily squeezed, producing almost complete inhibition, with rebound to high rate of spontaneous firing upon release. Stimuli to paw did not change angle of elbow joint. Unit observed for 55 min., at depth of 1750 μ . SC I-52-3 was a "deep" unit driven by extension of first digit of contralateral forepaw. Receptors lay in small joints of paw, not in muscles. Spontaneous rate here (in lower graph) completely inhibited by squeezing 3rd and 4th digits. Light tactile stimulation of skin of paw did not inhibit. Unit observed for 33 min., at depth of 825 μ .

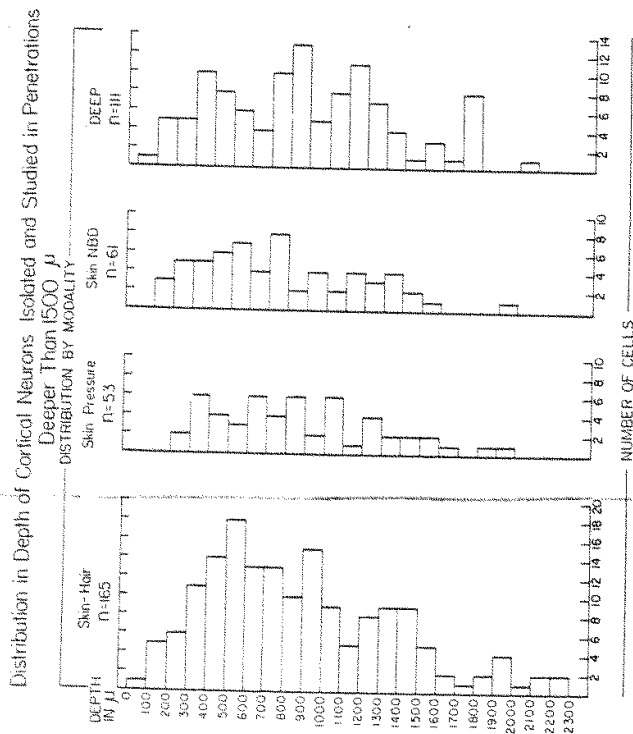


FIG. 12. Distribution in depth of cortical neurons, by modality subclass. Only neurons encountered in penetrations of 1500 μ or more enter these populations, so totals are slightly less than those of Table 1. Charts show that neurons of each type are found in all cellular layers of cortex.

ality properties. Thereafter an effort was made in each experiment to orient the chamber on the skull in such a way that the electrode approached perpendicularly to the cortical surface. We estimate that this was achieved within a range of 10 degrees. Further, we chose to concentrate our penetrations in the foreleg region of the first somatic area, where the cortex is flat over a considerable distance. The rolling of the cortex on banks of sulci makes perpendicular traverses impossible there, for the angle between the electrode path and the transverse axis of the cortex changes continuously as the electrode is advanced.

Making penetrations as nearly perpendicular as possible, we found that in the large majority of cases the cells whose discharges were observed at successive depths through the cortex belonged to the same modality subgroup. Examples are shown in Fig. 7, where the units isolated in penetrations 1 and 2 of Exp. 41 are used to illustrate the peripheral receptive fields. In each case, all the units isolated in a penetration belonged to the skin hair subgroup, and units of other subgroups were not observed. The distribution among the various subgroups of all the penetrations is given in Table 2. Very stringent criteria were used in making this classification. (i) For a penetration to be classed with one or another of the modality subtypes, all the units isolated in the traverse must belong to the same subgroup. (ii) In addition, all the

units observed in multiple unit recordings must belong to the same modality subgroups. (iii) Whenever any suspicion of mixing exists, the penetration was classed as mixed, even when the definite modality identifications establishing the mixing were not made.

In view of these rather rigid criteria, it is an impressive fact that 84 per cent of the 119 penetrations were "modality-pure," in that they could be listed as of either the cutaneous or deep subgroups. This is especially so in view of the considerable error in placing the chamber so that the microelectrode approached the cortex perpendicularly. Moreover, there is a strong suggestion that the vertical columns of cells activated from the cutaneous

Table 2. Classification of penetrations by modality subgroups

Subgroup	Number	Per Cent
Deep	31	26.0
Skin-Hair	30	25.5
Skin-Pressure	9	7.0
Skin-Mixed	30	25.5
	(Hair-Pressure-11) (Hair-NBD-11) (Pressure-NBD-3) (NBD only-5)	
Skin-Deep Mixed	19	16.0
Totals	119	100%

Classification of penetrations by modality subgroups of neurons encountered during perpendicular traverse of electrode through cortex. Criteria used to make classifications of penetrations given in text.

receptors belong exclusively to one or another of the skin subgroups. Of the 30 penetrations classified in Table 2 as skin-mixed (43 per cent of penetrations classed in the cutaneous groups), positive evidence for the mixing was found in only 11. Of the remainder there are 14 penetrations in which units for which modality identification of skin were made without further examination (NBD) and five in which the only information available is that the units encountered were driven from the skin. It is likely that if more complete identifications had been made a considerable number of these 19 penetrations could have been classed with one or the other of the two cutaneous subgroups. In summary, the evidence is clear for the separation of deep and cutaneous groups in this way, and it is highly suggestive that even the two groups of cutaneous units are separately arranged in vertical columns.

From these data it is concluded that the neurons which lie in vertical columns extending across the cellular layers belong usually to one and the same modality type. The data presented in Section II indicate that these columns of cells are related to peripheral receptive fields which are almost identical. An important confirmation of this fact has been obtained in two experiments in which slanting penetrations at an incident angle of 45 degrees were made. In these the electrode passed from one to another group of cells of first one and then another modality subgroup. An important point upon

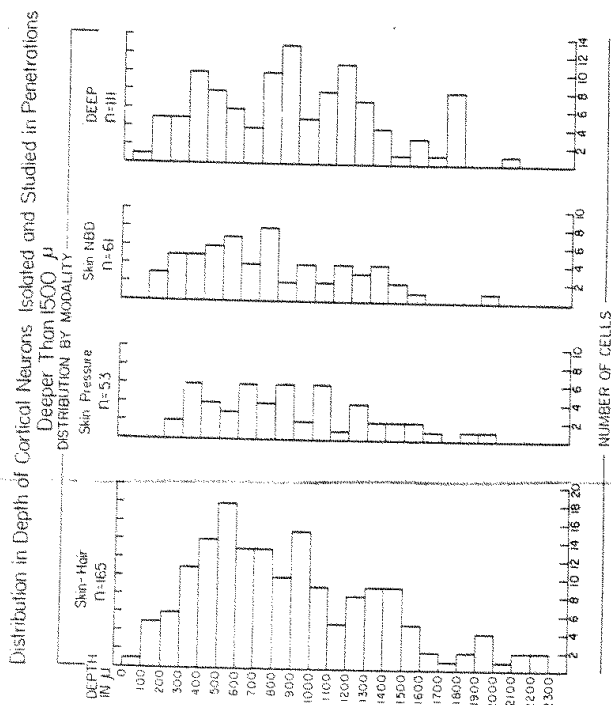


FIG. 12. Distribution in depth of cortical neurons, by modality subclass. Only neurons encountered in penetrations of 1500 μ or more enter these populations, so totals are slightly less than those of Table 1. Charts show that neurons of each type are found in all cellular layers of cortex.

dality properties. Thereafter an effort was made in each experiment to orient the chamber on the skull in such a way that the electrode approached perpendicularly to the cortical surface. We estimate that this was achieved within a range of 10 degrees. Further, we chose to concentrate our penetrations in the foreleg region of the first somatic area, where the cortex is flat over a considerable distance. The rolling of the cortex on banks of sulci makes perpendicular traverses impossible there, for the angle between the electrode path and the transverse axis of the cortex changes continuously as the electrode is advanced.

Making penetrations as nearly perpendicular as possible, we found that in the large majority of cases the cells whose discharges were observed at successive depths through the cortex belonged to the same modality subgroup. Examples are shown in Fig. 7, where the units isolated in penetrations 1 and 2 of Exp. 41 are used to illustrate the peripheral receptive fields. In each case, all the units isolated in a penetration belonged to the skin hair subgroup, and units of other subgroups were not observed. The distribution among the various subgroups of all the penetrations is given in Table 2. Very stringent criteria were used in making this classification. (i) For a penetration to be classed with one or another of the modality subtypes, all the units isolated in the traverse must belong to the same subgroup. (ii) In addition, all the

units observed in multiple unit recordings must belong to the same modality subgroups. (iii) Whenever any suspicion of mixing exists, the penetration was classed as mixed, even when the definite modality identifications establishing the mixing were not made.

In view of these rather rigid criteria, it is an impressive fact that 84 per cent of the 119 penetrations were "modality-pure," in that they could be listed as of either the cutaneous or deep subgroups. This is especially so in view of the considerable error in placing the chamber so that the microelectrode approached the cortex perpendicularly. Moreover, there is a strong suggestion that the vertical columns of cells activated from the cutaneous

Table 2. Classification of penetrations by modality subgroups

Subgroup	Number	Per Cent
Deep	31	26.0
Skin-Hair	30	25.5
Skin-Pressure	9	7.0
Skin-Mixed	30	25.5
	(Hair-Pressure-11) (Hair-NBD-11) (Pressure-NBD-3) (NBD only-5)	
Skin-Deep Mixed	19	16.0
Totals	119	100%

Classification of penetrations by modality subgroups of neurons encountered during perpendicular traverse of electrode through cortex. Criteria used to make classifications of penetrations given in text.

receptors belong exclusively to one or another of the skin subgroups. Of the 30 penetrations classified in Table 2 as skin-mixed (43 per cent of penetrations classed in the cutaneous groups), positive evidence for the mixing was found in only 11. Of the remainder there are 14 penetrations in which units for which modality identification of skin were made without further examination (NBD) and five in which the only information available is that the units encountered were driven from the skin. It is likely that if more complete identifications had been made a considerable number of these 19 penetrations could have been classified with one or the other of the two cutaneous subgroups. In summary, the evidence is clear for the separation of deep and cutaneous groups in this way, and it is highly suggestive that even the two groups of cutaneous units are separately arranged in vertical columns.

From these data it is concluded that the neurons which lie in vertical columns extending across the cellular layers belong usually to one and the same modality type. The data presented in Section II indicate that these columns of cells are related to peripheral receptive fields which are almost identical. An important confirmation of this fact has been obtained in two experiments in which slanting penetrations at an incident angle of 45 degrees were made. In these the electrode passed from one to another group of cells of first one and then another modality subgroup. An important point upon

30). Their general import is emphatically *not* that a small area of skin is represented at a cortical point, and only there. The figurine maps published show that stimulation of a small spot on the skin evokes intense activity at a limited cortical locus, and less intense activity over a considerable surround. It follows, reciprocally, and was shown (30), that a given cortical locus can be excited to some degree from a considerable area of skin, which is smaller for some and larger for other parts of the topographical pattern. As the peripheral spot stimulated is shifted across the skin, the peak activity shifts across the cortical surface. Similar patterns exist in the thalamic relay nuclei of the system (20). The exquisitely developed capacity of the waking animal or man to localize a peripheral stimulus can *not* very readily be explained in terms of a sensory mosaic of groups of receptors which project centrally along more or less insulated pathways to the cerebral cortex. The problem is to understand how finely developed capacities for two-point discrimination and for pattern and contour recognition are possible, using neural networks which, while precisely arranged, show a "point-to-area" relation between periphery and cortex. An attempt will be made to do so in terms of the action of single neural elements of the system.

A. *Mechanisms for localizing a single stimulus*

In the present experiments some direct measurements were made of the peripheral receptive fields which play upon cortical neurons (Figs. 7, 8, 9). The important fact is that these zones are comparable in area to those projecting upon thalamic neurons (21), and indeed are of the same order as those of the primary dorsal root afferent fibers (31). This is true in spite of the cascaded divergence which seems likely to occur at each successive synaptic relay, and suggests that the entire constellation of neurons receiving presynaptic activity does not discharge, but that successful synaptic action is limited to a central discharge zone of neurons, those upon which sufficient convergence occurs to bring them to threshold firing levels. Within this discharge zone a gradient in the intensity of response exists, a smooth variation in latency, number, and frequency of impulses evoked by a brief stimulus (19) from a maximum at the center of the field to a minimum at its junction with the surrounding subliminally excited zone of neurons. Thus at each successive relay the number of cells discharged is successively restricted. Reciprocal considerations explain the limited peripheral receptive field for each cortical cell. It is assumed that in some way such a limited zone of cortical activity of abrupt onset is perceived as a local peripheral event. The afferent inhibition discussed below will limit still further the lateral extent of the cortical activity evoked by a single stimulus.

B. *Mechanisms for differentiating two adjacent stimuli*

In these experiments it was found that a slight transverse shift in the site of the electrode penetration of the cortex caused only a slight shift in the

position of the receptive fields of the neurons encountered, and that the fields of the neurons observed in two closely adjacent penetrations overlapped one another. For example, penetrations 1 and 2 of Exp. SC 41 (see Fig. 7) were more than 1.5 mm. apart on cortical surface, yet the receptive fields of neurons encountered in the two overlapped slightly. Thus, as two peripheral stimuli are brought towards one another the two discharge zones of cortical cells will overlap, resulting in a partial fusion of the two peaks of activity. This fusion will be furthered by the fact that the cells of the overlapped fringes will show mutual facilitation rather than refractoriness, which has been demonstrated experimentally. Thus, when recovery cycle studies are made for a cortical neuron driven by two equal successive submaximal stimuli delivered to the same locus in its peripheral receptive field, or by such stimuli delivered to two separate points near the edge of the receptive field, a summation of discharge occurs (spike-adding) rather than refractoriness. This mechanism would operate against the attainment of tactile acuity, especially for weak stimuli. In this regard, it would be of great interest to learn from experiments upon human subjects whether the fineness of two-point discrimination is a function of stimulus intensity. However, it is true that in species in which it can be tested the distance between two discriminable stimulated points is less, and often much less, than the diameter of the peripheral distributions of the dorsal root fibers. Quite obviously some other mechanism is required to maintain sharp peaks of cortical activity as the two points approach each other.

That mechanism is likely to be afferent inhibition. Our observations indicate the disposition of peripheral inhibitory fields for cortical cells which surround their excitatory fields. Thus a single stimulated point, producing a cortical cell discharge zone, will inhibit the surrounding cortical cells. As the two stimulated peripheral points approach each other the reciprocal overlap of their central inhibitory zones will sharpen and limit their discharge zones, contributing certainly to the double peaking of cortical activity, which is assumed to be necessary for two-point discrimination.

It is a common observation quickly confirmed that tactile sensation is more acute if the exploring finger pad moves lightly over the test surface than if held motionless against it—for example, in differentiating fine grades of sandpaper, in the finger movements of the blind in reading Braille, or in assaying the quality of cloth. Oscillatory movement of the sensory receptor sheet will produce sharper peaks in the grid of cortical activity, with steeper gradients between them. Temporal alternation in the activity of two widely overlapped groups of cells will accentuate the role of refractoriness of those cells common to both, rather than spatial facilitation, thus greatly steepening the gradients of activity between the two peaks.

These observations indicate that the functional organization patterns of the somatic afferent system follow principles similar to those already described for the visual system (16). A similar theoretical treatment of localization within the afferent system subserving pain was given by Tower (27).

II. MODALITY SPECIFICITY

The modality-specific groups of neurons encountered in the somatic cortex make up subgroups related to one overall modality, which might be termed that of mechanical deformation. While modality *per se* is an attribute of conscious perception, some implications of the functional neural correlates of that attribute derive from the present experiments. In the first place, it has been shown under carefully controlled conditions that individual cortical neurons are each uniquely sensitive to a certain form of peripheral stimulation. The implication is that such specificity requires that single types of sensory receptors be differentially responsive to these different forms of stimulation, and project upon specific groups of cells at central relay stations of the system. Such specificity at those stations has in fact been shown to exist (7, 21). However, some recent experiments (13, 23) correlating conscious perceptions of cutaneous stimuli in humans with histological studies of cutaneous nerve endings have brought into question the concept of the modality specificity of the various groups of afferent nerve fibers. It seems, nevertheless, a very remote possibility that the cortical neurons could possess such stimulus specificity and the peripheral nerve fibers lack any differential thresholds to the variety of impinging stimuli.

Some of our data do in fact support the view that the peripheral endings of sensory nerve fibers, whether encapsulated with or free of organized receptors, display different functional properties. For example, cortical neurons driven by pressure upon the skin adapt very slowly to steady stimuli, while those activated by movements of hairs do so very quickly. This same difference in discharge has been observed by Adrian (1) while recording from thalamocortical afferent fibers, in studies by Rose and Mountcastle of the neurons of the ventrobasal thalamic complex (21) for cells of the dorsal column nuclei (7), and indeed for the primary dorsal root afferent fibers themselves by Yamamoto *et al.* (31). It is reasonable to suppose that the discharge patterns of these two types are imposed upon the long polysynaptic chains finally impinging upon the cortical cells by the peripheral receptors. Some functional specificity resides at the nerve endings. The studies of cutaneous sensibility in man referred to (13, 23) do show, however, that this specificity is not necessarily due to the presence at those nerve endings of specific types of organized receptors.

Evidence has been presented that neurons of the somatic cortex are organized into vertical columns or cylinders which extend perpendicularly through the cortical layers. A major support for this idea is that in the large majority of perpendicular penetrations (see Table 3) all the neurons observed belonged to only one modality subgroup. Within a given topographical area these columns are closely mingled in an interdigitated mosaic. It should be emphasized, however, that in the normal waking animal the mechanical deformations of peripheral tissues which occur are not so discretely arranged as they are by the experimenter. Quite obviously rotation of a joint, for example, during walking or running, will cause pressure changes in nearby skin or fascia, and hairs bend and rub against one another as move-

ments proceed and alternate. Thus all the columns of cells topographically related to the moving peripheral part will be activated, to greater or lesser extent. Such multiple activation holds for all but the faintest of impinging stimuli. In normal function the isolated activation of specific groups of cells, achieved experimentally, is smeared in the widespread activity of all the modality subtypes. What complex interactions may then occur between them becomes a matter of interest and importance about which no experimental data are presently available.

III. A NEURAL BASIS FOR POSITION SENSE

A considerable number of the cortical neurons studied were activated by stimulation of the deep tissues. Many were driven by stimulation of deep connective tissue, deep fascia, the periosteum, or the interosseous membranes. Others were uniquely responsive to movement of joints, and peripheral dissection revealed that the receptors responsible lay in and about the joint capsules. We have never observed a neuron of this cortical area that was excited by muscle stretch, though contraction of muscle may excite a cortical neuron by mechanical deformation of other deep tissues. A neuron of this class not only responds to transient rotation of the joint, but continues to fire steadily when the related joint is held at angles other than the neutral one for the unit. They adapt very slowly. While no precise measurements of these angles have been made, it was clear that the steady state frequency of discharge varied progressively with the angle of the joint displacement from neutral, in the direction for excitation. The neutral positions were different for different units related to the same joint. Thus some elements of this group are active at any joint position, and phasic movements produce changes in cortical activity both by recruitment of additional neurons and by increasing the discharge frequency of some of those already active, and by decreasing the activity of still others. The overall activity of this group of neurons depicts the position of the joints to which they are related.

The structure and the functional properties of the joint receptors and their afferent fibers have been intensively studied in recent years. The discharge characteristics have been described in precise and quantitative terms by Boyd (8), Boyd and Roberts (9), Skoglund (24), Andrew (4), and by Andrew and Dodt (5), while both Gardner (11, 12) and Skoglund (24) have traced their central projection pathways to the cerebral cortex. A striking similarity exists between the discharge properties of the joint receptors (see especially 9) and those of the group of cortical neurons described here. Furthermore, groups of neurons of similar modality and discharge properties have been observed in the thalamic relay nuclei (21) and in the dorsal column nuclei (7). The interpretation indicated is that the functional properties of the system are determined by those of the peripheral receptors. All of these facts suggest that such a system of afferent fibers, relay neurons, and cortical neurons is likely to serve as the neural basis for the sense of position of the body parts, and that the dorsal column-medial lemniscal system is prepotently involved in transmitting this sensibility.

The records and charts of Figs. 5 and 6 illustrate the fact that some pairs of cortical cells which are spatially adjacent to one another and related topographically to the same joint are excited by movements of that joint in opposite directions. The maxima and the minima of the discharge frequencies for each of such a pair are almost exactly reciprocal. The most ready explanation of such a reciprocity is that movement of the joint, *e.g.*, into flexion, excites joint receptors driving the "flexion" unit observed while completely unloading those receptors differently located in the joint which drive the "extension" neuron of the pair, and *vice versa* when the direction of movement is reversed. However, an engaging possibility is that excitation of one neuron of such a pair produces, by its own discharge, the inhibition of its fellow directly, *i.e.*, that the reciprocal inhibition is a central phenomenon and not wholly dependent upon alternation of afferent inputs. While no direct evidence is available to establish one or the other of these possibilities as the correct one, there is one aspect of the response patterns favoring the latter—that is, that when one neuron reaches its highest firing rate the other is almost always completely silent. This is true in spite of the fact that with the limb in neutral position these neurons usually discharge at a low "spontaneous" rate, which then disappears as the limb moves away from the exciting direction for the unit considered. This matter could be settled only by determining whether the disappearance of the spontaneous discharge is or is not, in this case also, itself due to unloading of receptors. Whatever the mechanism involved, the observations do show that there exists within a very small cortical region a reciprocal afferent representation capable of signalling the steady and phasic position of the joints, a sensory counterpart, as it were, of the efferent reciprocal motor innervation at the spinal level, and of its central representation in the motor cortex.

In an earlier study in which the projection pattern of this form of sensibility was determined at thalamic and cortical levels by recording from populations of neurons with gross electrodes (18) the question was raised whether the cutaneous and deep afferents from a particular peripheral part, shown in those studies to project in superimposed spatial patterns, might converge upon single neural elements common to both. The results of the present experiments, as well as those of single neurons at the thalamic level (21), show that this is not so, and that at least through the initial cortical input stage the constituent neurons are modality specific.

IV. AN HYPOTHESIS OF FUNCTIONAL ORGANIZATION OF CORTEX

The data reported in these papers support the view that there is an elementary unit of organization in the somatic cortex made up of a vertical group of cells extending through all the cellular layers. The neurons of such a group are related to the same, or nearly the same, peripheral receptive field upon the body surface. They are activated by the same type of peripheral stimulus, *i.e.*, they belong to the same modality subgroup. It follows from this last observation that they should show the same discharge properties, which they do, especially as regards adaptation to steady stimuli. Finally,

all the cells of such a vertical column discharge at more or less the same latency to a brief peripheral stimulus. They are thus grouped into an initial firing pattern. It is emphasized that this analysis is based strictly upon the first response of cortical cells to a peripheral stimulus, the early repetitive response, which our experiments as well as those of others (3) have shown to be extraordinarily sensitive to the parameters of the stimulus. It seems likely that even the light state of anesthesia in our preparations has severely suppressed the later and more complex discharge patterns, which we have seen only very rarely (19, Fig. 9-f). It suggests, however, that the cortical cells will be arranged sequentially in time into a variety of firing patterns, and a principal experimental objective at present is a detailed analysis of this later activity.

Our data should not be interpreted to indicate that all the cells of this vertical column are necessarily activated monosynaptically by the specific thalamocortical afferents, although the anatomical studies of Lorente de Nó (15), including among other regions the somatic cortex of the mouse, and of Sholl (22) on the visual cortex of the cat, have indicated that this is possible for neurons of all the cellular layers, except perhaps the second. But the powerful synaptic connections of the cells with short and ascending axons, which make up such a large percentage of the cells of the cortices of higher mammals, indicate that elements of all the cellular layers will receive spatially multiplied synaptic impingements after one or more additional synaptic transfers. Our data are compatible with these anatomical observations.

The hypothesis that such a vertically linked group of cells is the elementary unit for cortical function is not new. Such a conclusion was reached by Lorente de Nó from his extensive studies on synaptic linkages of cortical neurons. He emphasized from the pattern of those linkages that the vertical chains of neurons were capable of input-output activity without necessarily wide horizontal spread. That such a horizontal spread is not required for even rather high order functioning of the cortex is indicated by recent experiments reported by Sperry (26). He showed that cats after widespread vertical subpial dicing of the visual cortex, the incisions extending through the grey and into the white matter, were then still capable of very fine visual pattern discriminations. This capacity survived the subsequent removal of the superior colliculi. Sperry had previously found (25) that monkeys after similar vertical dicing of the sensory and motor cortices were capable of what appeared to be normal motor activity. It follows from his experiments that rather small vertical columns of cortex are capable of integrated activity of a complex order. This conclusion fits the results of the present experiments, and the hypothesis of functional organization proposed.

SUMMARY

1. The modality and topographical attributes of the neurons of the somatic sensory cortex have been studied by the method of single unit analysis.

All the neurons observed were activated by mechanical deformation of some peripheral tissue.

2. Within this broad modality class, three distinct subgroups were observed, made up of cells activated by movement of hairs, by pressure upon the skin, and by mechanical deformation of deep tissues. No neuron was ever observed which could be classified in more than one of these subgroups. All were activated by stimulation of the contralateral side of the body only.

3. The two groups of neurons related to the skin showed different discharge properties, those responsive to hair movement adapting quickly, those driven by pressure upon the skin continuing to discharge steadily to a steady stimulus.

4. Cells belonging to each subgroup were found in all of the cellular layers. In 84 per cent of penetrations across the cellular layers which were directed perpendicularly, all the neurons encountered belonged to either cutaneous or deep subgroups. These modality-specific vertical columns of cells are intermingled for any given topographical region.

5. Cells related to deep structures were activated from deep fascia and connective tissue and the regions of the joints and joint capsules, but never from muscle. Those driven by joint movement signal the steady position and phasic changes in positions of joints, and are suitably arranged to subserve position sense. Pairs of closely adjacent cells were seen to respond reciprocally to alternating joint movements, a form of reciprocal afferent innervation.

6. Direct measurements of the size of the peripheral receptive fields playing upon cortical neurons were made. They are comparable in size to those related to dorsal root fibers, cells of the dorsal column nuclei, or the thalamic neurons. A form of afferent inhibition of cortical neurons is described, the peripheral inhibitory field surrounding the peripheral excitatory field of cortical neurons. These data, together with those on the discharge properties of the cortical cells (19), are used in a discussion of the neural correlates of sensory localization, two-point discrimination and pattern and contour recognition, on the basis of partially shifted reciprocal overlap rather than on the basis of a patterned sensory mosaic, with insulated central projections.

7. The neurons encountered in a perpendicular traverse of the cortex are activated from almost identical peripheral receptive fields at latencies which on the average are not a function of the position of the cell in depth within the cortex.

8. These facts support an hypothesis: that the elementary pattern of organization in the cerebral cortex is a vertically oriented column or cylinder of cells capable of input-output functions of considerable complexity, independent of horizontal intragrain spread of activity.

ACKNOWLEDGMENT

I wish to express my appreciation to Mr. Edward H. Ramey, who designed and constructed most of the electronic circuits used in these experiments.

REFERENCES

- ADRIAN, E. D. Afferent discharge to the cerebral cortex from peripheral sense organs. *J. Physiol.*, 1941, 100: 159-191.
- AMASSIAN, V. E. Interaction in the somatovisceral projection system. *Res. Publ. Ass. nerv. ment. Dis.*, 1952, 30: 371-402.
- AMASSIAN, V. E. Evoked single cortical unit activity in the somatic sensory area. *EEG clin. Neurophysiol.*, 1953, 5: 415-538.
- ANDREW, B. L. The sensory innervation of the medial ligament of the knee joint. *J. Physiol.*, 1954, 123: 241-250.
- ANDREW, B. L. AND DORT, E. The deployment of sensory nerve endings at the knee joint of the cat. *Acta physiol. scand.*, 1953, 28: 287-296.
- BAIRD, P. Studies on the cortical representation of somatic sensibility. *Harvey Lect.*, 1937-38, 33: 143-169.
- BERMAN, A. L. Unpublished results of single unit analysis studies of cells of the dorsal column nuclei. (Personal communication.)
- BOYD, J. A. The histological structure of the receptors in the knee-joint of the cat correlated with their physiological response. *J. Physiol.*, 1954, 124: 476-488.
- BOYD, J. A. AND ROBERTS, T. D. M. Proprioceptive discharges from stretch-receptors in the knee joint of the cat. *J. Physiol.*, 1953, 122: 38-58.
- DAVIES, P. W., BERMAN, A. L., AND MOUNTCASTLE, V. B. Functional analysis of the first somatic area of the cat's cerebral cortex in terms of activity of single neurons. *Amer. J. Physiol.*, 1955, 183: 607.
- GARDNER, E. Conduction rates and dorsal root inflow of sensory fibers from the knee joint of the cat. *Amer. J. Physiol.*, 1948, 152: 436-445.
- GARDNER, E. AND HADDAD, B. Pathways to the cerebral cortex for afferent fibers from the hindleg of the cat. *Amer. J. Physiol.*, 1953, 172: 475-482.
- HAGEN, E., KNOCH, H., SINCLAIR, D. C., AND WEDDELL, G. The roles of specialized nerve terminals in cutaneous sensibility. *Proc. Roy. Soc.*, 1953, B141: 279-287.
- LI, C.-L., CULLEN, C., AND JASPER, H. H. Laminar microelectrode studies of specific somatosensory cortical potentials. *J. Neurophysiol.*, 1956, 19: 111-130.
- LORENTE DE NÓ, R. Cerebral cortex: architecture, intracortical connections, motor projections. Chap. 15 in: FULTON, J. F., *Physiology of the nervous system*, 3rd ed. New York and London, Oxford University Press, 1949.
- MARSHALL, W. H. AND TALBOT, S. A. Recent evidence for neural mechanisms in vision leading to a general theory of sensory acuity. *Biol. Symp.*, 1942, 7: 117-164.
- MOUNTCASTLE, V. B., BERMAN, A. L., AND DAVIES, P. W. Topographic organization and modality representation in first somatic area of cat's cerebral cortex by method of single unit analysis. *Amer. J. Physiol.*, 1955, 183: 646.
- MOUNTCASTLE, V. B., COVIAN, M. R., AND HARRISON, C. R. The central representation of some forms of deep sensibility. *Res. Publ. Ass. nerv. ment. Dis.*, 1952, 30: 339-370.
- MOUNTCASTLE, V. B., DAVIES, P. W., AND BERMAN, A. L. Response properties of neurons of cat's somatic sensory cortex to peripheral stimuli. *J. Neurophysiol.*, 1957, 20: 405-434.
- MOUNTCASTLE, V. B. AND HENNEMAN, E. Pattern of tactile representation in thalamus of cat. *J. Neurophysiol.*, 1949, 12: 85-100.
- MOUNTCASTLE, V. B. AND ROSE, J. E. (Unpublished data from single unit analysis studies of the activity of thalamic neurons.)
- SHOLL, D. A. The organization of the visual cortex in the cat. *J. Anat., Lond.*, 1955, 89: 33-46.
- SINCLAIR, D. C., WEDDELL, G., AND ZANDER, E. The relationship of cutaneous sensibility to neurohistology in the human pinna. *J. Anat., Lond.*, 1952, 86: 402-411.
- SKOGLUND, S. Anatomical and physiological studies of knee joint innervation in the cat. *Acta physiol. scand.*, 1956, 36: Suppl. 124.
- SPERRY, R. W. Cerebral regulation of motor coordination following multiple transection of sensorimotor cortex. *J. Neurophysiol.*, 1947, 10: 275-294.
- SPERRY, R. W., MINOR, N., AND MYERS, R. E. Visual pattern perception following

- subpial slicing and tantalum wire implantations in the visual cortex. *J. comp. physiol. Psychol.*, 1955, 48: 50-58.
27. Tower, S. S. Pain: definition and properties of the unit for sensory reception. *Res. Publ. Ass. nerv. ment. Dis.*, 1943, 23: 16-43.
 28. Woolsey, C. N. Patterns of localization in sensory and motor areas of the cerebral cortex. Chap. 14 in: MILBANK MEMORIAL FUND. *The biology of mental health and disease*. New York, Hoeber, 1952.
 29. Woolsey, C. N. and FAIRMAN, D. Contralateral, ipsilateral and bilateral representation of cutaneous receptors in somatic areas I and II of the cerebral cortex of pig, sheep, and other mammals. *Surgery*, 1946, 19: 684-702.
 30. Woolsey, C. N., MARSHALL, W. H., and BARD, P. Representation of cutaneous tactile sensibility in the cerebral cortex of the monkey as indicated by evoked potentials. *Johns Hopk. Hosp. Bull.*, 1942, 70: 399-441.
 31. YAMAMOTO, S., SUGIHARA, S., and KURU, M. Microelectrode studies on sensory afferents in the posterior funiculus of the cat. *Jap. J. Physiol.*, 1956, 6: 68-85.