J. Physiol. (1978), 283, *pp.* 523-537
With 10 *text-figures*
Printed in Great Britain

MOVEMENT-SENSITIVE AND DIRECTION AND ORIENTATION-SELECTIVE CUTANEOUS RECEPTIVE FIELDS IN THE HAND AREA OF THE POST-CENTRAL GYRUS IN MONKEYS

BY JUHANI HYVÄRINEN* AND ANTTI PORANEN†
From the Institute of Physiology, University of Helsinki, 00170 Helsinki 17, Finland

(*Received 5 December 1977*)

SUMMARY

1. In the hand area of the post-central gyrus of three alert *Macaca speciosa* monkeys neurones related to cutaneous receptors but not activated by simple touch on the receptive field were recorded using the transdural micro-electrode recording technique. Thirty-six cells were found to have complex cutaneous receptive field properties. These neurones were subdivided into the following three groups.

2. Nine neurones were not activated by punctate stimuli on the receptive fields but responded well to movement along the skin. The activity of these neurones was not affected by the direction of movement; nor was it sensitive to different textures of the moving surface.

3. Eighteen neurones responded to cutaneous movement along the skin surface in a particular direction giving no response to stimulation in the opposite direction and intermediate responses to intermediate directions. Similar responses were evoked from different subparts of the receptive field.

4. Nine neurones responded well to an edge placed on the skin in an optimal orientation or moved along the skin in a direction perpendicular to the edge. A maximal response was produced by stimuli of the same optimal orientation in different parts of the receptive field. The significance of the stimuli to the monkey had only a minor influence on the magnitude of the responses of these neurones and no influence on the receptive field properties.

5. The occurrence of the complex cutaneous cells increased from anterior to posterior within the post-central gyrus and most of them were found in Brodmann's area 2. Thus we postulate that the complex receptive field properties arise as a consequence of cortical processing in a network in which postsynaptic one-way lateral inhibition generates the directional properties of the neurones.

6. The complex cutaneous neurones constituted only 6 % of the neurones studied in the hand area of the post-central gyrus. Thus the prevalence of neurones with elongated and direction-selective receptive fields is low in the primary somatosensory cortex in comparison with the visual cortex. These neurones may, however, serve the stereognostic capacity of the hand by contributing information about stimulus motion, orientation and direction of movement on the skin.

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* Present address: Siltavuorenpenger 20 J, 00170 Helsinki 17, Finland.

† Present address: Department of Neurosurgery, University of Helsinki 17, Finland.

INTRODUCTION

The visual cortices of the cat and monkey contain a large number of neurones sensitive to orientation and movement of lines over the receptive fields (Hubel & Wiesel, 1962, 1968). In a previous study (Mountcastle, Talbot, Sakata & Hyvärinen, 1969) we described in the primary somatosensory cortex (S I) of the monkey a few neurones sensitive to movement along the skin, and more such neurones have been described by Schwartz & Fredrickson (1971) and Whitsel, Roppolo & Werner (1972). Although such neurones are not very numerous in the primary somatosensory cortex they might contribute to the capacity to extract information about shape and size of objects during active exploration using the somaesthetic sense. This capacity is severely impaired after lesions in the primary somatosensory cortex (Randolph & Semmes, 1974). We therefore decided to study cutaneous neurones encountered in the primary somatosensory cortex with a variety of stimuli that could reveal complex field properties. The hand area of the post-central gyrus of the monkey was chosen as a recording site since the hand has a great stereognostic capacity and acts as a 'fovea' of the cutaneous sense. Preliminary reports on these findings have been presented in several meetings (Hyvärinen, 1973, 1976; Hyvärinen, Poranen & Jokinen, 1974; Hyvärinen, Poranen, Jokinen, Näätänen & Linnankoski, 1975).

METHODS

Recordings were performed in the six hemispheres of three female stump-tailed monkeys (*Macaca speciosa*) in whom the activity in the parietal association cortex was also studied. The methods have been previously described in detail (Hyvärinen & Poranen, 1974). In short, transdural recordings with movable metal micro-electrodes were performed using an Evart's type hydraulic microdrive apparatus (Evarts, 1966, 1968). The recordings were made with glass-coated platinum–iridium (Wolbahrst, McNichol & Wagner, 1960) or tungsten micro-electrodes prepared with a local modification of the method described by Levick (1972). The impedances of the electrodes ranged from 1 to 5 MΩ. During the recordings the monkey was sitting in a specially constructed primate chair with the head fixed using the halo fixation method (Friendlich, 1973). The monkey was free to move its limbs except when the arms were fixed with straps in a Plasticene mould for the study of somatic receptive fields. A great deal of time was spent in training each monkey before the recording sessions. During these sessions the monkeys received food and drink of which they were deprived at other times. They were also trained in a cutaneous vibration detection task in which the correct performance was rewarded with juice. These rewards kept the monkeys docile and co-operative during the experiments for 4–5 hr daily. The action potentials recorded were stored on tape together with timing indicators of stimuli and analysed later either by photography or by a μ-Linc computer that was used for the construction of histograms.

In order to study different types of cutaneous receptive fields we used our own hands and hand-held metal, glass or polymethacrylate probes of different diameters as stimuli. In addition metal edges as well as objects of various sizes and materials such as wood, cotton, textile, metal etc. were placed on the skin or moved along it manually. We often let the monkeys manipulate food, tools and other objects and groom themselves. An electromagnetic vibrator was also used to activate the skin. It could be driven with various wave forms including DC pulses that produced steady indentation of the skin. Stimulus probes of various shapes and sizes could be attached to the tip of the vibrator.

When the receptive field of the neurone was found the hand of the monkey was fixed with straps, not covering the receptive field, into Plasticene moulded suitably for access to the field. Thus during the detailed study of the receptive fields the hands were immobile. For study of receptive fields on the hairy skin the hairs were cut and depilated.

The vibrator was used to study the responses of the rapidly adapting skin neurones encountered. In addition the influence of the attentive state of the animal could be studied during the performance of a vibration detection task taught to the monkeys prior to the experiments. During the training and the experiments the monkeys were deprived of drink. The task of the monkey was to detect correctly within 0·6 sec the end of a cutaneous vibratory stimulus lasting 4 sec to obtain fruit juice. Prior to the stimuli two signal lights were lit alternately. When a yellow light was on, the monkey was always rewarded for correct performance (*relevant condition*) but when a red light was on it was never rewarded (*irrelevant condition*). The monkeys soon learned to respond correctly to the end of the vibration during the relevant condition and to refrain totally from responding during the irrelevant condition. Their behaviour indicated attention toward the cutaneous stimulus in the relevant condition and inattention toward it during the irrelevant condition. The responses of the cells to vibration were analysed with a computer programmed to construct peri-stimulus-time (pst) histograms and cycle histograms of the responses (Talbot, Darian-Smith, Kornhuber & Mountcastle, 1968). The pst histograms show the average level of firing during the responses, whereas the cycle histograms indicate the degree of synchrony with the sinusoidal skin indentation (see Fig. 9).

At the end of the recording period from each monkey a histological analysis was performed of the recording sites in the postcentral gyrus as will be described in the next paper (Hyvärinen & Poranen, 1978). On the basis of this analysis the location of the cells recorded from in Brodmann's cytoarchitectural areas 3, 1 or 2 was determined.

RESULTS

Movement-sensitive neurones

When cells that appeared to be related to the skin could not be driven with simple touch on their receptive fields, stimuli moving on the skin were tried. For many of these cells movement along the skin was an effective stimulus. The simplest kind of cells responding to movement along the skin were those that did not differentiate between the different directions of movement nor between different shapes of the moving stimuli. An example of such a cell is shown in Fig. 1. This neurone gave negligible responses to skin indentation (Fig. 1*B*) but it responded briskly to movement of the examiner's finger along the skin in any direction (Fig. 1*A*). It did not differentiate between different textures of the moving stimuli (Fig. 1*C*). Nine neurones of this type were found.

Direction-selective neurones

This type of neurone was the most common of the ones not activated with simple skin indentation. Eighteen such cells were observed. Fig. 2 shows an example of such a cell. Like the neurone illustrated in Fig. 1, this neurone responded poorly to punctate stimuli on the skin (*B*), but it produced a good response to surface movement. However, in this case the direction of movement was critical; the cell responded only to stimuli moving distally. The Figure shows the responses to movement of a small probe tip in various directions (*A*). A cycle of moving stimuli was repeated three times and the number of impulses for different directions were recorded (*C*).

Several direction-selective neurones related to the finger tips or pads were observed. Fig. 3 shows responses to movements of a small probe tip in two opposite directions over the distal pad of the index finger. The movement towards the ulnar side was effective. Fig. 4 illustrates another cell, whose receptive field covered the palmar surface of the index finger and the first palmar whorl. In all parts of this receptive field stimuli moving towards the ulnar side were most effective.

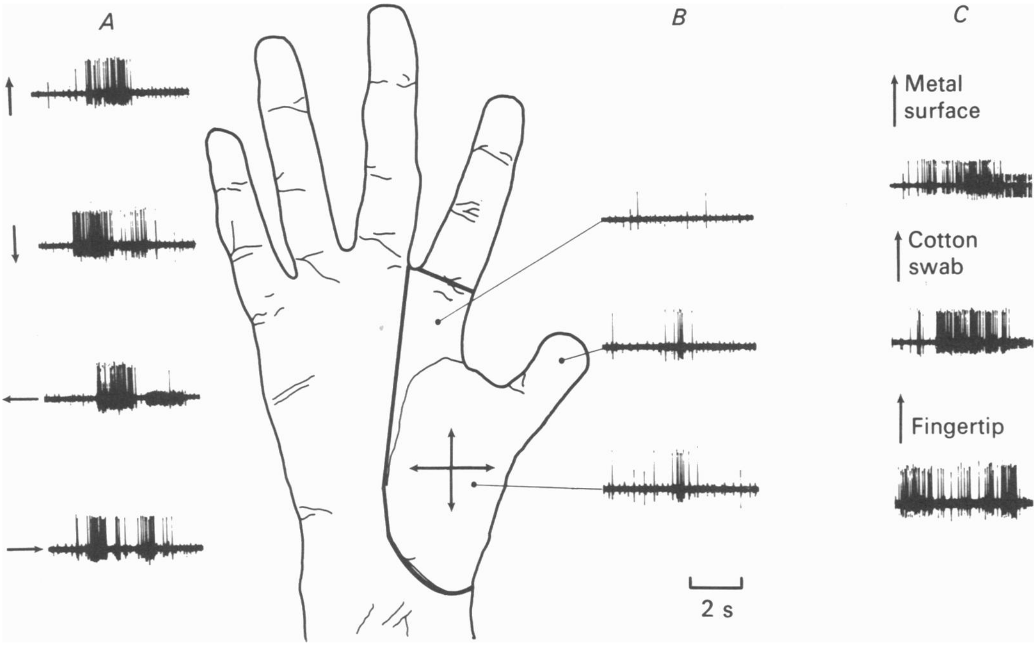

Fig. 1. The receptive field and the responses of a cell sensitive to movement of any type of surface along the skin in any direction. The cell was located in area 1. Its receptive field covered the thenar eminence, the first palmar whorl and the glabrous skin of the thumb. *B* shows that there were negligible responses to punctate stimuli delivered with a probe tip at the loci indicated on the receptive field. *A* shows responses to moving stimuli in four different directions. In *C* the distally moving stimulus was either a metal surface, cotton swab or the examiner's finger-tip all resulting in similar responses.

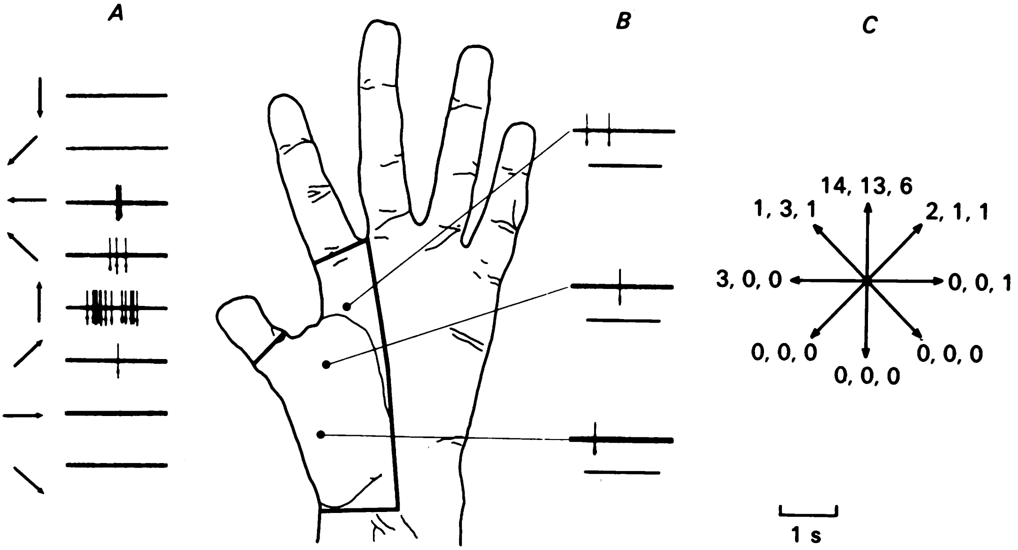

Fig. 2. The receptive field and responses of a cell recorded in area 1 and sensitive to distally moving skin stimuli. The receptive field covered the thenar eminence, the first palmar whorl and the base of the thumb. *A* shows responses to punctate stimuli moving in different directions across the receptive field. These stimuli were produced with the hand-held probe tip. *B* shows negligible response to punctate stimuli delivered with the same probe tip at the loci indicated on the receptive field. *C* gives the numbers of impulses evoked on three consecutive cycles of stimuli delivered in different directions across the receptive field. Only the distal ward direction produced good responses.

Direction-selective neurones with receptive fields on the dorsum of the hand were also found. All of them produced optimal responses to stimuli moving distally (Fig. 5). For the investigation of these neurones the hairs on the receptive fields were cut and the skin was treated with a depilating agent. Thus it seems that the role of the hairs was not crucial for the direction selectivity of these neurones, although the best responses were produced by 'windward' moving stimuli (i.e. in the direction of the growth of the hairs). In some direction-selective neurones movements in the two opposite directions were equally effective whereas movements perpendicular to the optimal direction were ineffective.

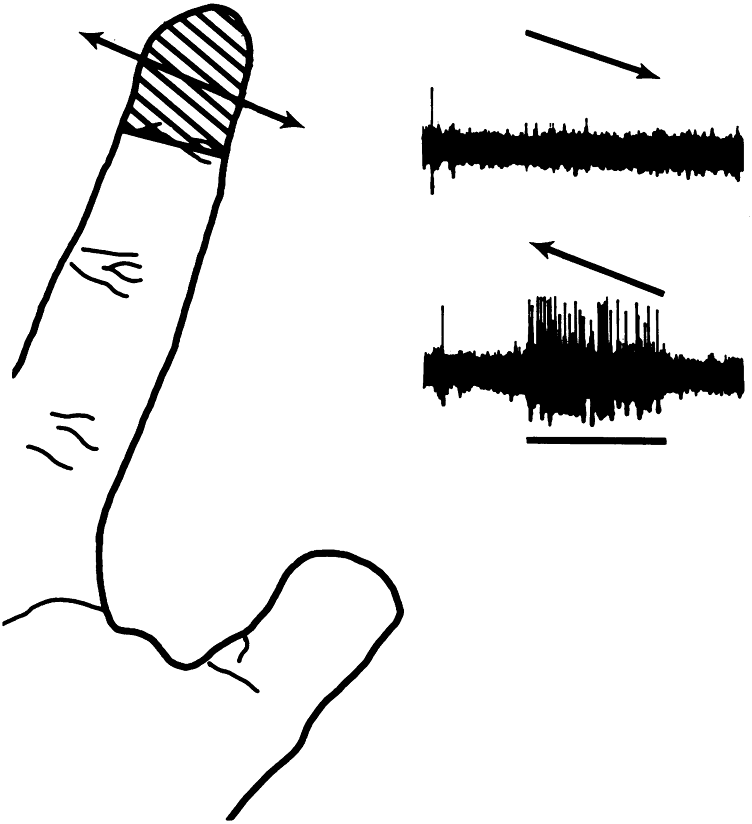

Fig. 3. The receptive field (hatched) and responses to surface movement performed with a small, circular probe tip in the two opposing directions. The neurone was recorded in area 2. Duration of the record 1 sec.

For a few neurones the effect of varying the speed of movement along the skin was tested. In these neurones a response to movement in the optimal direction was produced when the speed of movement was between 0·01 and 0·5 m/sec. Variation of velocity within these limits had little influence on the response.

Orientation-selective neurones.

In the posterior part of the gyrus nine neurones were studied that were not excited by the stimuli described above. These cells responded to stationary or moving edges on the skin, the degree of their activity depending on the orientation of the edge. An example of such a cell is given in Fig. 6. Its receptive field covered the glabrous skin on the distal pad of the thumb. It did not respond to stationary punctate stimuli in any part of the receptive field but distally moving punctate stimuli caused a small response. A strong response was evoked with a stationary edge placed across the distal phalanx of the thumb, and distal movement of an edge of this orientation was also effective. Another example of this class is shown in Fig. 7. The receptive field of this cell covered the first and part of the middle palmar whorl.

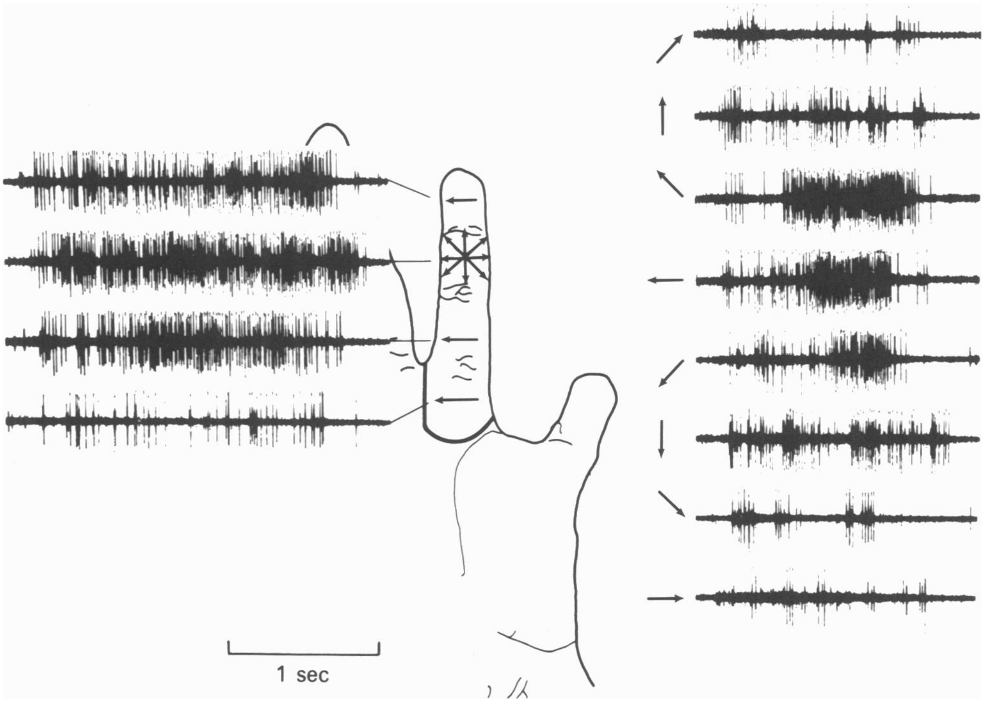

Fig. 4. The receptive field and responses of a cell recorded in area 2. This neurone was sensitive to the direction of surface movement along the skin. The receptive field covered the forefinger and the first palmar whorl. The cell was optimally activated by stimuli moving across the receptive field from the radial to the ulnar side. Responses to movements of the hand-held probe in different directions over the glabrous skin of the phalanx are shown on the right. On the left are the responses to the optimal direction of stimulus movement on the distal, middle and proximal phalanges and the first palmar whorl.

It responded poorly to stationary or moving punctate stimuli but well to a metal edge placed transversely on the receptive field. In this orientation the response was maximal and it decreased when the orientation was changed (Fig. 7). In different parts of the receptive field the same stimulus orientation produced the maximal response (Fig. 8).

Influence of behavioural significance on the responses

The influence of the level of alertness of the monkey on the responses of this cell was tested using the vibration detection task described in methods. For this purpose the response of this cell was first studied using a small round vibrator tip. The top histograms in Fig. 9 show the responses to vibratory stimuli of 4 sec duration. The pst histograms indicate the level of activity during the stimulus and the cycle histograms show the degree of phase-locking of the responses to the stimulus sine wave. The responses were minor when a small, round probe tip was used. A difference in the average strength of the responses was observable however, between the relevant and irrelevant conditions. The responses were stronger during the relevant condition, i.e. when the monkey's attention toward the stimulus presumably was higher. The second row in Fig. 9 shows that the responses were much augmented when the vibration was delivered with a metal edge in the optimal orientation. Again a slight difference in the relevant and irrelevant responses is seen in favour of the relevant condition. When the orientation of the edge was changed so that it was perpendicular to the optimal the response decreased considerably, but again it was stronger during the relevant condition. The conclusion from this experiment was that the orientation

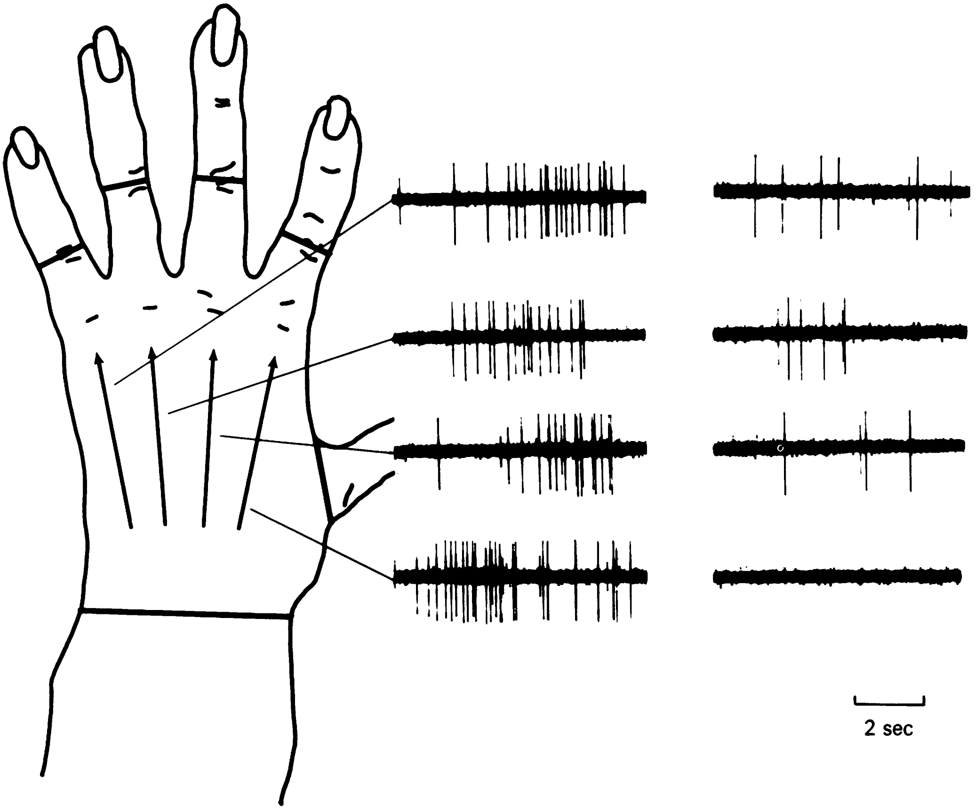

Fig. 5. Responses of a cell recorded in area 2 to cutaneous stimuli moving along the receptive field in the optimal (arrows) and in the opposite direction. In four places over the dorsum of the hand a response was obtained to stimuli moving distally (left recordings), but at the same locations stimuli moving towards the proximal were ineffective (right recordings).

of the edge was more important for the response of this cell than was the behavioural significance of the stimulus to the animal. However, the behavioural significance did have a minor effect on the responses.

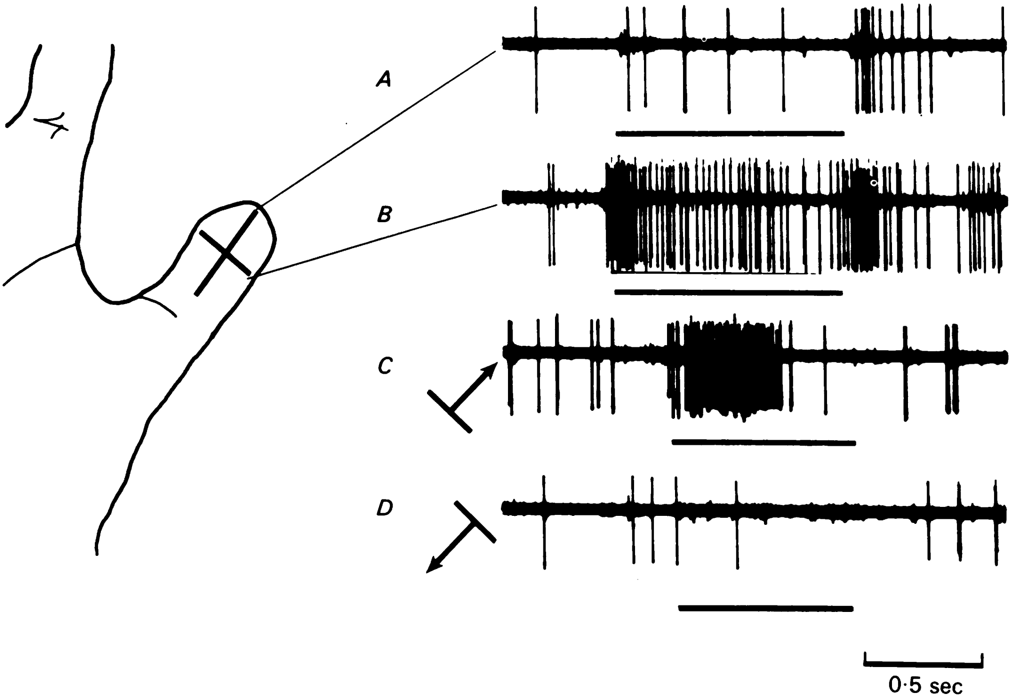

Fig. 6. Responses of an edge sensitive cell recorded in area 2. This cell responded to an edge placed on the skin across the volar surface of the thumb perpendicularly to its axis and to distal movement of such an edge. The duration of the stimulus is indicated by a black line under the record. *A*, responses to a 1 sec skin indentation of 1 mm depth performed with a metal edge placed at the tip of the vibrator along the axis of the thumb. A slight off-response. *B*, response to the same edge now perpendicularly to the axis of the thumb. *C*, response to movement of an edge extending perpendicularly to the axis of the thumb and moving distally. *D*, response to movement of a similar edge in the proximal direction.

TABLE 1. Histological localization of the complex skin neurones

Description of the neurone type	Area 3b	Area 1	Area 2	Total
Neurones that respond to surface movement in any direction	2	5	2	9
Neurones that respond to surface movement in a specific direction	0	4	14	18
Neurones that respond to the orientation of an edge	0	0	9	9
Total	2	9	25	36
Total as percentage of all cells recorded	2	4	10	6

Histological results

The distribution of the complex cutaneous cell types in the three cytoarchitectural subdivisions of the post-central gyrus are shown in Table 1. As is described in the next paper the size of the total sample of neurones was similar in areas 1 and 2 and about half of that in area 3b. From this Table it is evident that the number of the neurones with complex cutaneous receptive fields increase posteriorly within SI. The Table shows that most movement sensitive cells that do not differentiate between directions occur in area 1 but that they are seen also in the anterior part of the gyrus (which receives the major thalamocortical input to SI). The more complex cell types specifically sensitive to direction of movement or to orientation of an edge were not seen in area 3b and their number increases posteriorly. These findings suggest that the complex receptive field properties arise through cortical processing within SI.

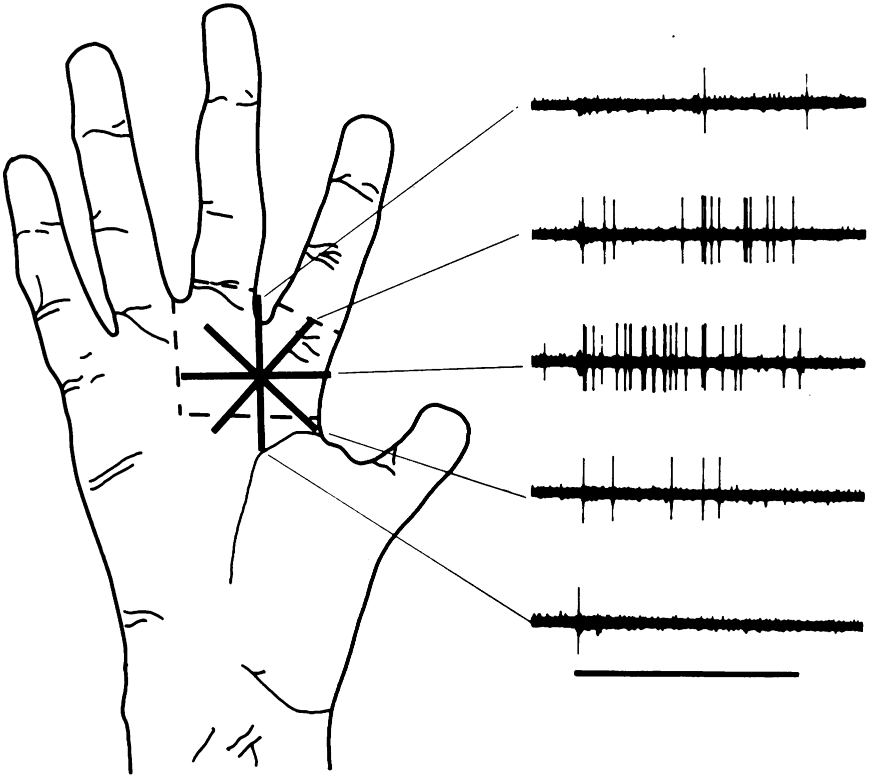

Fig. 7. The receptive field and responses of a cell recorded in area 2. The cell was sensitive to the orientation of an edge placed on the receptive field which covered the first and second palmar whorls as indicated by the dashed line. Across the most sensitive part of the receptive field between the first and second palmar whorls a 0·7 mm wide metal edge was positioned in different orientations as indicated in the figure. The metal edge was attached to the tip of the vibrator. This edge produced a 1 mm skin indentation when direct-current of 1·3 sec duration (continuous line under the record) was passed through the vibrator. A good response was obtained only when the orientation of the edge was perpendicular to the axis of the hand.

DISCUSSION

Three complex types of primary somatosensory cortical neurones with cutaneous input are described in this paper. All the three types have more complex properties than the most common cutaneous cell types in SI. The first group consists of cells sensitive to movement along the skin, but independent of the direction of movement The second and largest group consists of direction-selective neurones that respond to surface movement, whereas the third group is selective for orientation of stationary or moving edges on the skin. Cells resembling the latter group have recently been described in S I of the raccoon by Pubols & Leroy (1977). Such neurones were not very common in S I of the monkey constituting only 6% of the neurones.

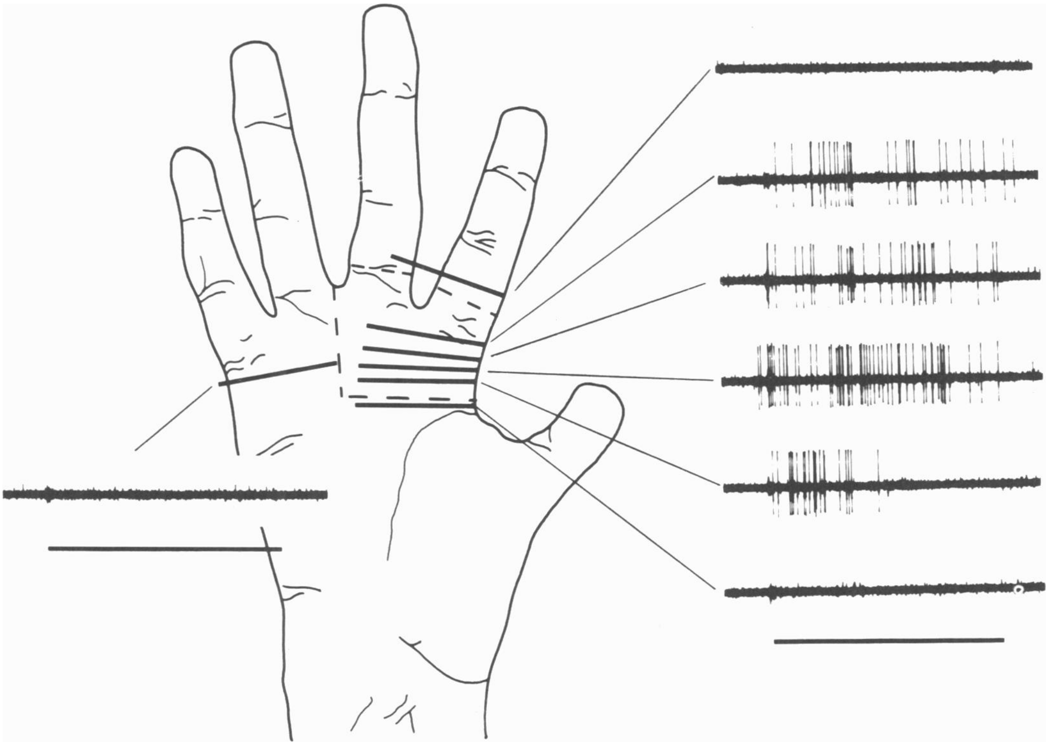

Fig. 8. Responses of the same cell as described in Fig. 7 to an optimally oriented edge in different parts of the receptive field and outside it. A good response was obtained for an optimally oriented edge in all parts of the respective fields.

This percentage is small enough to warrant the question whether such properties are essential in the function of SI or whether they are explained by a random fluctuation in the receptive field properties. They could either be formed in the post-central gyrus during the early ontogenesis by a genetic programme or develop gradually through tactile experience which would modify selectively synaptic structures in a similar fashion to that described in the visual cortex (Wiesel & Hubel, 1963, 1965*a*, *b*; Hirsch & Spinelli, 1971; Blakemore & Mitchell, 1973). However, since our monkeys have not experienced any selective stimulation this assumption would mean that the inputs to individual neurones in SI vary spontaneously. A random distribution of synaptic contacts could perhaps generate these features in S I, since the occurrence of these neurones is so low. In the association cortex, however, a large proportion of neurones with cutaneous receptive fields are direction-selective (Sakata, Takaoka, Kawarasaki & Shibutani, 1973; Hyvärinen & Poranen, 1974; Mountcastle, Lynch, Georgopoulos, Sakata & Acuna, 1975) and one could not readily assume here that such receptive fields arise purely as a result of chance. In the association cortex either the genetic programme or experience must have a stronger influence than in SI in shaping the synaptic contacts so that the cells become direction-selective. One should also keep in mind the possibility that the association areas (Brodmann's areas 5 and 7) may get their cutaneous input primarily from direction-selective cells in SI.

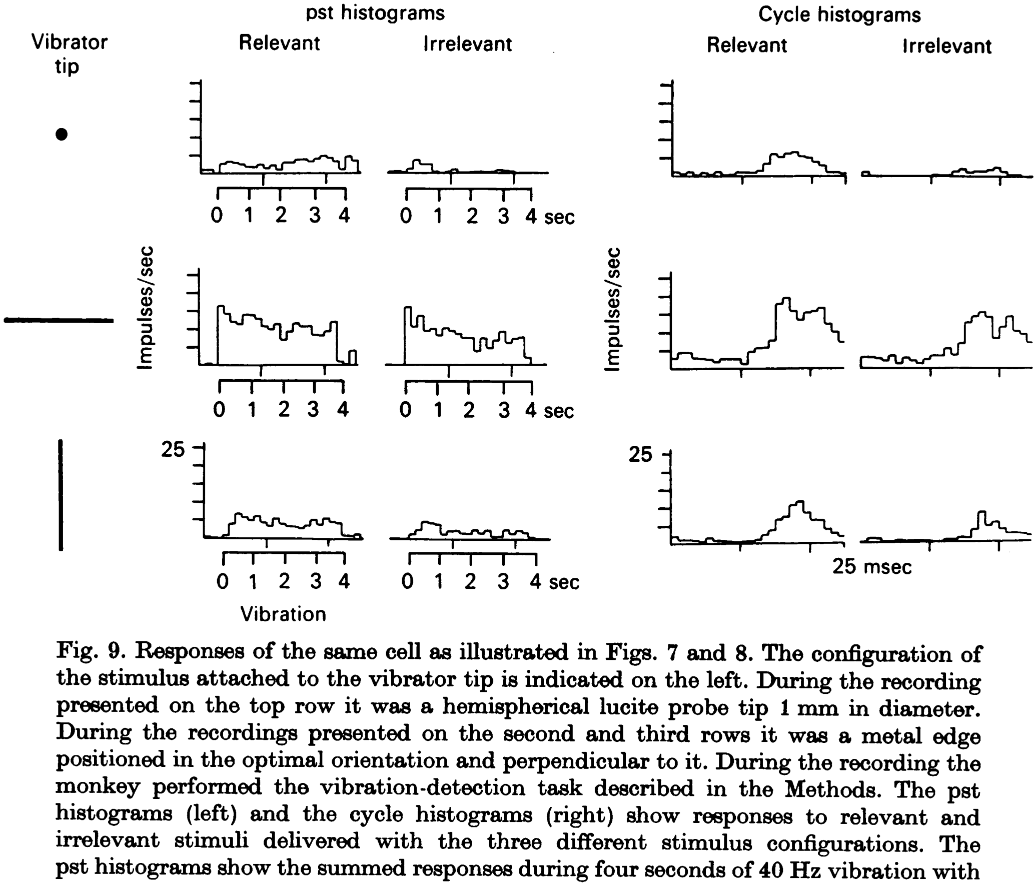

Fig. 9. Responses of the same cell as illustrated in Figs. 7 and 8. The configuration of the stimulus attached to the vibrator tip is indicated on the left. During the recording presented on the top row it was a hemispherical lucite probe tip 1 mm in diameter. During the recordings presented on the second and third rows it was a metal edge positioned in the optimal orientation and perpendicular to it. During the recording the monkey performed the vibration-detection task described in the Methods. The pst histograms (left) and the cycle histograms (right) show responses to relevant and irrelevant stimuli delivered with the three different stimulus configurations. The pst histograms show the summed responses during four seconds of 40 Hz vibration with peak-to-peak amplitude of 1 mm. The cycle histograms indicate the degree of phase-locking of the action potentials to the sinusoidal stimulus. The optimally oriented edge produced the best responses, and the responses were more affected by the orientation of the edge than by the relevance of the task.

Since the numbers of different types of complicated cutaneous receptive fields observed were rather low, the reliability of these data should be considered. Direction-selective peripheral afferent nerves have not been described in the monkey.

They were explicitly searched for by Whitsel *et al.* (1972) who found them in the cortex but not in the peripheral afferents. In humans, however, a few direction-selective neurones have been described (Knibestöl & Vallbo, 1970; Järvilehto, Hämäläinen & Laurinen, 1976). These peripheral afferents were differently activated by stretching of the skin in two perpendicular directions. Our directional neurones were not activated by skin stretch in different directions but by real movement along the skin. Sensitivity only to real movement along the skin is not known to be a property of any peripheral receptors; it is most likely to a be a consequence of processing within the C.N.S. Since we observed few such neurones in the anterior part of the post-central gyrus (area 3) and an increasing amount in central and posterior parts we presume that they arise through intracortical processing. Nevertheless, it could be argued that the selective properties of the neurones observed could be an artefact resulting from the mechanically uneven stimulation of the peripheral receptors. On many receptive fields there is a best spot from which the strongest response can be evoked. Thus if one stimulus excites receptors at this spot better than others, there is a difference in the cellular response. Could this fact explain the complicated receptive field properties that we observed? For the direction-selective neurones we do not think that this is the case since they were differently activated by stimuli moving in opposite directions in various subparts of the receptive fields. Thus the selectivity of the response to the direction of movement was a feature present in all parts of the receptive fields and consequently it could not result from effective coupling to the receptors at the best spot of the receptive field.

Likewise differences in mechanical coupling to the peripheral receptors do not readily explain the sensitivity to surface movement in any direction and simultaneous lack of response to skin indentation on the receptive fields.

The only finding that could be explained on the basis of the differences in mechanical coupling to the receptors relates to the cells sensitive to edges. The edges could pass over the best spot on the receptive fields or bypass them depending on their placement. The stretch produced within the skin by different orientations of the edge could be coupled differently to the receptors. This could be the case in the finding presented in Fig. 7 but it could not explain the fact that the optimal orientation of the edge was the same in different parts of the receptive field as illustrated for the same cell in Fig. 8. Thus, for such neurones this explanation is not likely, either.

Many different anatomical schemes could be proposed to explain the complicated receptive fields. Within the visual and the auditory systems models that explain direction selectivity have been proposed (Barlow & Levick, 1965; Michael, 1968; Fernald, 1971; Fernald & Gerstein, 1972). As Fernald has shown, it is possible to explain direction-selectivity within the auditory system by assuming uneven distribution of synaptic contacts on the dendrites and soma of the receiving cells. Barlow & Levick (1965) and Michael (1968) suggested that post-synaptic inhibitory mechanisms within the retina are responsible for the formation of direction-selective properties of retinal ganglion cells. The same mechanism may be involved in the formation of directional cells within the somatosensory cortex. In the cat direction-selective somatosensory neurones have been observed even at the level of the thalamus (Gordon & Manson, 1967), but in the monkey we did not find them in the anterior part of S I. Therefore we assume that they arise as a consequence of intracortical processing.

Iwamura & Tanaka (1978) have recently described direction-selective cells in the somatosensory cortex of the cat responsive to movement along the skin. They found that in some such cells movement in the direction opposite to the one producing the optimal response was inhibitory to the spontaneous activity of the cell. For a few neurones in our material we also got the impression that movement counter to the optimal direction produced a slight inhibition of the ongoing activity. However, since the level of spontaneous activity was rather low in these neurones, a firm conclusion can only be made with help of quantitative analysis of several summed responses.

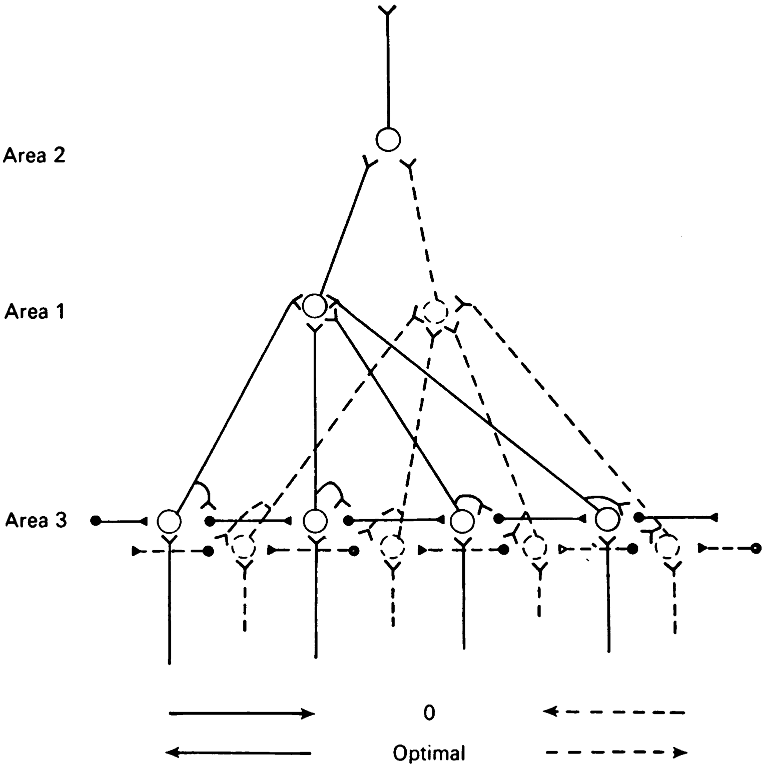

Fig. 10. A hypothetical scheme to explain the direction-selectivity of the neurones observed in the primary somaesthetic cortex. Two direction selective neurones are drawn in area 1; they respond maximally to stimuli moving in opposite directions. The small black circles are inhibitory interneurones. The network shown with continuous lines produces optimal responses to stimuli moving to the left and prevents responses to stimuli moving to the right, whereas the opposite is true for the network indicated with interrupted lines. The neurone in area 2 would respond to stimuli moving in the two opposite directions, as was observed in a few neurones. The lateral inhibitory connexions are not necessarily located in the same cytoarchitectural area but are so presented here for the sake of simplicity.

Fig. 10 shows one hypothetical scheme modified from Barlow & Levick (1965) for explaining the direction-selectivity that we observed. Obviously many other schemes could be devised to explain how the excitation produced by movement in one direction reaches the neuron whereas excitation caused by movement in the opposite direction is inhibited. Within the visual system the retinal level already contains complicated synaptic connexions, and the ganglion cells are two synapses centrally from the receptors. The corresponding synaptic level in the mechanosensitive somaesthetic system lies in the thalamus or cortex since the first neurones extend all the way to the dorsal column nuclei, the second to the ventrobasal complex of the thalamus and the third to the cortex. Thus it is natural that the receptive field properties of the neurones are in general more complex in the visual than in the somatosensory cortex. A complexity comparable to the visual cortex may be achieved within the somatosensory system only in higher order cortical neurones in the post-central gyrus and in the association areas (Sakata *et al.* 1973; Hyvärinen & Poranen, 1974).

What purpose could the cortical neurones with complex cutaneous receptive field properties serve? Exploratory movements of the hand are used for sensing many different types of objects. From the edges of these objects a synthetic picture of the three-dimensional structure is constructed, the capacity known as stereognosis. During such activity sensory feed-back of the direction of the movement occurring on the sensory surface is also useful. Thus neurones demonstrating movement and edge sensitivity as well as orientation and direction selectivity could aid the stereognostic function of the somatosensory cortex and probably operate in connexion with neurones whose activity signals joint position and muscle stretch.

This work was supported by the Foundations' Fund for Research in Psychiatry, U.S.A. and the National Research Council for Medical Sciences, Finland. We wish to express our thanks to Dr Yrjö Jokinen for the computer programs of the μ-Linc and Mr Ilkka Linnankoski and Mrs Katriina Laurén for technical assistance. We also wish to thank Drs Hideo Sakata, Timo Järvilehto, Herbert Silfvenius and George Gordon for constructive criticism of the manuscript.

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