Converging Patterns of Finger Representation and Complex Response Properties of Neurons in Area 1 of the First Somatosensory Cortex of the Conscious Monkey*

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Summary. The representation of the hand and fingers in area 1 of the first somatosensory cortex was studied in conscious monkeys by recording single neuronal activity. The results are as follows.

(1) We found multi-finger type receptive fields which cover more than one finger discontinuously or wide-field type ones which cover both finger and palmar skin or two halves of the palmar skin together. Multi-finger type receptive fields were also found in some joint manipulation neurons. Multi-finger or wide-field type receptive fields were found in nearly 40% of area 1 neurons. The rate was even higher, up to 70%, in the medial part of the cortical finger region. However, the finger representation in area 1 was less discretely somatotopic than that in area 3b.

(2) The somatotopy of area 1 was somewhat similar to that of area 3b: 74.5% and 20.9% of area 1 neurons were, respectively, cutaneous and deep. The distribution of neurons with different somatotopies overlapped in area 1.

(3) Among area 1 neurons with multi-finger type receptive fields, response characteristics of those with inhibitory receptive fields, those with directional selectivity to moving stimuli, and those with converging affector inputs, were studied in detail. Evidence is presented to suggest that information from different parts of the body, or from the same body parts but different affector sources, is integrated in area 1.

Introduction

Area 1 in cynomolgus monkeys is characterized by a decrease in granular cells and an increase in pyramidal cells, as well as a pronounced columnar arrangement of cells (Powers and Mountcastle 1959a). The thalamic afferent projection is less dense to area 1 than to area 3b (Jones and Powell 1970; Jones 1975; Jones and Brown 1976; Jones et al. 1979; Nelson and Kaas 1981). Area 1 receives one-way cortico-cortical projections from area 3b (Vogt and Pandya 1977; Künzle 1978; Jones et al. 1978). The physiological correlates of these morphological differences between two areas remain to be described.

In the preceding paper (Iwamura et al. 1983) we described the functional representation of hand and fingers in areas 3a and 3b. We demonstrated that the finger representation in area 3b is composed of three different subdivisions. Each of them uniquely represented a functional region of fingers. The receptive field of each neuron was small and thus a topographic arrangement of fingers was noticeable in each subdivision. We confirmed that area 3a receives predominantly deep inputs and we regarded it as another functional subdivision in the rostral first somatosensory area (SI).

The data in the preceding paper indicated that area 1 is characterized by the presence of many more neurons with multi-finger or wide-field type receptive fields which were only rarely found in area 3b. A multi-finger type receptive field is defined as one which covers more than one finger discontinuously, and a wide-field type is defined as one which covers both finger and palmar skin mostly continuously, or both the radial and ulnar half of the palmar skin which are separately represented in area 3b.

In the present paper we demonstrate that multi-finger type receptive fields are common in area 1.

Key words: Postcentral gyrus – Area 1 – Finger representation – Neural integration – Monkeys

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describe the pattern of finger representation in area 1 and compare it with that in area 3b. The principles of
finger representation, found in areas 3a and 3b, i.e., the
topographical arrangement of fingers in the
multiple functional subdivision are not applicable
to area 1. From the comparison of receptive fields within areas 3a, 3b and 1, and from the study of
response characteristics of some area 1 neurons, we
propose that the integration process found in area 1 is
primarily based on the information drawn together in
areas 3a and 3b and transferred to area 1 via cortico-
cortical pathways and also via additional thalamic
inputs. A preliminary report has been published
(Iwamura et al. 1982).

Methods
The preparation of the animal and the experimental methods were
the same as those described in the preceding paper (Iwamura et al.
1983).

Results
Multi-finger Type Receptive Fields of Neurons in Area 1
A total of 61 penetrations were made in area 1 of the
hand and finger regions in four hemispheres. The
receptive field positions and subsidualities were
examined in each neuron similarly to the study in
area 3b described in the preceding paper (Iwamura et al.
1983). As mentioned there, nearly 40% of area 1
neurons had a multi-finger type receptive field. Figure 1A shows examples of such receptive fields.
The initial four neurons had a receptive field on
the nail bed, the next three on the ventral glabrous skin
and the last two on the dorsal hairy skin. Most of
them were of the multi-finger type. By contrast, in
area 3b the receptive fields of neurons were almost
exclusively of the single finger type. In this track all
neurons recorded in area 3b had their receptive field
on the fourth finger as exemplified in Fig. 1B.
Figure 2A shows another example of the receptive
field of neurons recorded in area 1. In this track, a
relatively large cluster of joint manipulation
neurons were recorded in close proximity to the preceding cluster of cutaneous neurons. These joint manipulation neurons also had multi-finger receptive fields and some of them had inhibitory fields. As shown in Figs. 1 and 2, neurons with similar receptive fields were found in succession as a small cluster, and various clusters with different receptive field or submodality categories were recorded one after another within a relatively short distance along the diagonally oriented electrode track. This contrasted with the organization of area 3b where the receptive fields of one category were found in a much longer span along an electrode track. These examples thus suggest that different receptive regions with the same or different submodalities are considerably mixed in area 1.

Figure 3A shows receptive fields of a cluster of neurons recorded in the medio-posterior part of area 1 near the border with area 2. The initial seven neurons had a receptive field on the dorsal surface. The next five responded to finger joint manipulation. Two of them also responded to palmar skin stimulation. These and the last two neurons had a receptive field on the volar skin. These neurons were recorded along a single penetration nearly perpendicular to the cortical surface and thus they possibly belonged to a single or, at most, a few columns within a diameter of several hundred microns.

Representation Pattern of the Fingers in Area 1

Figure 4 is the map summarizing the results of systematic mapping of area 1 done in one hemisphere (233 neurons from 21 penetrations). In this map the
recording site of each neuron was projected to the unfolded surface map of the postcentral gyrus (for the method see Fig. 2 of the preceding paper). The numbers represent the fingers (1: thumb, 2: index finger, etc.) and letters represent other portions of the hand. In this case, the mapping did not cover the lateralmost part of the finger region where the thumb representation was expected. In this map, the receptive fields of the multi-finger or wide-field type are indicated by encircled double numbers, or numbers and letters. Of area 1 neurons plotted here 44% had multi-finger or wide-field receptive fields. The map demonstrates that the number of this type of neuron increased in the medial part: about 35% of neurons in the lateral half and about 70% of neurons in the medial half of the map had these types of receptive fields. In the lateral half of the map, the majority of multi-finger type receptive fields covered two fingers. In the medial half of the map, the receptive fields covering three or more fingers were in the majority. Consequently, the somatotopic arrangement of fingers along the latero-medial axis is not discrete in area 1. A shift of finger representation was recognized only when neurons of a single-finger type receptive field were taken into consideration.

Overlapping Representation of Different Submodalities and Different Surfaces of Fingers

The submodality contents in area 1 have already been described and summarized in Table 1 of the preceding paper. In brief, less light-touch neurons

Fig. 5A–E. Lack of differential distribution of area 1 neurons in terms of functional surfaces of fingers or submodalities. Graphs are based on the same data as shown in Fig. 4. A Neurons whose receptive fields were on the distal segment of the finger. B Neurons whose receptive fields were on the proximal–ventral segments of the finger. C Neurons whose receptive fields were on the dorsal surfaces of fingers. D Joint manipulation neurons. Open circles: neurons responding to light touch in the skin. Open circles with dots: neurons responding to specific skin stimulation such as tapping, rubbing, scraping or pinching. Squares: neurons responding to hair bending. Open triangles: nail or nail bed neurons. Open circles with a square: neurons responding to both skin stimulation and hair bending. Open circles with a triangle: neurons responding to both skin and nail stimulation. Filled circles: joint manipulation neurons. Filled triangles: neurons responding to stimulation of deep tissues other than joint manipulation. Filled circles: neurons responding to both skin stimulation and joint manipulation. E Summary diagram indicating the zone of overlapping in which neurons representing the ventral glabrous surface of fingers and those representing the dorsal surface of fingers as well as those activated by joint manipulation are mixed. Dots and lines and broken lines indicate the approximate limits of distributions of neurons representing the ventral or those representing the dorsal surface of fingers, respectively.
and more hair, nail and Pacinian type neurons were found in area 1, but the relative number of cutaneous neurons in area 1 (74.7%) was identical to that of area 3b (77.7%). It was also shown in the preceding paper that particular functional surfaces of different fingers tended to be represented grouped together in area 3b. In the present study, we investigated whether analogous differential representations of different finger surfaces exist also in area 1. Figure 5 demonstrates the distribution of various types of cutaneous or "deep others" modality neurons in each of three groups of neurons having receptive fields on different parts of fingers: the distal finger segments (A), the ventral-proximal finger skin (B), and the dorsal-proximal finger skin (C). In these graphs, neurons with large receptive fields covering more than one category were plotted in more than one graph. No clear segregation of one type of neurons from others was observed in each group, except that hair or nail neurons tended to be in the anatomical region. From comparison of these graphs we conclude that the representation areas of distal finger segments (A) and ventral-proximal finger skin (B) overlap with each other, and that the representation area of these surfaces (A and B) and that of the dorsal-proximal finger skin (C) partially overlap. Figure 5D shows that joint or muscle manipulation neurons were also distributed in the region of overlap as described above and summarized in Fig. 5E.

**Response Characteristics of Multi-finger Type Neurons**

As pointed out in the preceding section, we found the receptive field of area 1 neurons to be systematically larger than those of area 3b neurons. Not only were the receptive field sizes larger, but also the response characteristics of area 1 neurons were often more complex. We now present several examples of neurons with complex receptive field characteristics in area 1.

**Inhibitory Receptive Fields**

A total of 10 neurons had inhibitory receptive fields. Spatial dispositions of some of these receptive fields are shown in Fig. 6. In 4 of them the excitatory and inhibitory receptive fields were in side-by-side positions (Fig. 6A-8). The inhibitory effect was observed either on the spontaneous activity or on the evoked activity only, or on both of them. In another two neurons only the inhibitory receptive field was found (Fig. 6E, F). In still another two, illustrated in Fig. 6G and H, and in two additional neurons, the excitatory and inhibitory receptive fields were coextensive. The response observed in one of them is shown in Fig. 7 in which light rubbing of the palmar skin evoked excitatory responses while continuous pressing of the same skin region, particularly with the broad surface, was inhibitory on both the spontaneous and evoked activity. This type of response will be described in greater detail in the following section in combination with the directional selectivity.

**Fig. 4A-H.** Inhibitory receptive fields of area 1 neurons. In A-D the excitatory (shaded) and inhibitory (dotted) fields were in side-by-side position. In E and F, only inhibitory fields were broad. In G and H, no excitatory and inhibitory fields were coextensive.

**Fig. 7A-C.** Coextensive excitatory and inhibitory receptive field of an area 1 neuron. A: Excitatory effect from repeated palmar skin stimuli. B: Inhibitory effect from the steady contact of a broad surface to the glabrous skin. C: The receptive field marked with the symbol.***
Directional Selectivity and Excitatory and Inhibitory Interactions Between Different Afferent Inputs. Directional selectivity to the moving stimulus (rubbing, sweeping, scraping, etc.) was observed in a total of 35 neurons in area 1. Among them, 18 neurons had a multi-finger receptive field. Figure 8 shows a neuron in which a moving stimulus in the ulnar-to-radial direction was excitatory while that in the opposite direction was quite ineffective. This neuron was found in the medial region where the ulnar and radial palmar skin was represented together. As with most neurons with multi-finger receptive fields, the directional selectivity was observed even upon stimulation of a part of it's receptive field, although the amount of the response was smaller. The receptive field thus determined by a moving brush covered both fingers and palm skin (Fig. 8A). We noticed that this neuron fired most briskly in a particular action of the hand which rubbed the rim of an acrylic table (Fig. 8B) at a medio-lateral direction, in a grasping posture which secured firm contact of the whole palmar and finger skin. In this case the active movement of the animal was not essential: passive stimulation of the same hand action was also effective. A movement in the opposite direction was ineffective. We also noted that the background activity of this neuron was inhibited when the fingers in contact with appropriate tactile objects were kept in contact either actively or passively with objects of relative movement between two surfaces. In such circumstances broader contact surfaces of large or flat objects with the palmar skin were more effective than narrower ones (Fig. 8C-D). The results suggest that neurons of this type in area 1 may encode either certain aspects of hand action or specific features of tactile objects. Figure 9 illustrates a case in which the directional selectivity was observed only when adjacent fingers were rubbed sequentially. The receptive field of this neuron was already introduced in Fig. 2. It was activated when each of four fingers was lightly rubbed in any direction (Fig. 9A). Rubbing was a more effective procedure in evoking a response than was simple touch. No directional selectivity was seen with this mode of stimulation. However, when the adjacent fingers were sequentially rubbed, the directional selectivity was seen in the radial-ulnar direction (Fig. 9B). When the whole receptive field was touched and rubbed at once, however, the response was much less and no directionality was seen (Fig. 9C). Furthermore, a continuous and stationary pressing of fingers produced no responses (Fig. 9D); pressing all four fingers at the same time was more effective than that applied to each finger separately (Fig. 9D). In summary, differences in temporo-spatial patterns of stimulation may yield different effects on this neuron. The results suggest that different types of receptors, such as the rapidly or slowly adapting type, which are distributed in the same peripheral field, may contribute differentially to produce either excitation or inhibition. Based on such assumptions, a putative and hypothetical circuit to induce such complex effects in neuron 5 is delineated in Fig. 9F. In this diagram, neuron 5 is situated at the
center, receiving inputs from both slowly and rapidly adapting type receptors in fingers II-V. However, these inputs do not reach neuron 5 directly, but come through modulatory stages. Slowly adapting type inputs from different fingers converge on an inhibitory interneuron which in turn connects to neuron 5. Rapidly adapting type inputs come through the stage of inhibitory interaction from the adjacent fingers so that they are organized to give the directional selectivity to neuron 5. Neurons in area 3b with inhibitory receptive fields such as shown in the preceding paper (Iwamori et al. 1983) or in Fig. 6 would be the candidates for these stages of inhibitory interactions.

From the results described above one can surmise that the functional significance of this type of neurons is to detect the movement of the fingers in a certain direction relative to an object.

**Multi-finger Type Receptive Field in Joint Manipulation Neurons.** Among 42 joint manipulation neurons in area 1, 3 neurons were concerned with multiple joints on single finger and 25 with multiple joints on several fingers. The rest were activated by the movement of a single joint. Two multi-finger neurons were also activated by the manipulation of the wrist joint. In 3 multi-joint neurons the manipulation of some joints was excitatory but that of others was inhibitory. Examples of such neurons which were recorded in a cluster in the deeper layers of area 1 have been shown in Fig. 2. In these three neurons, simultaneous manipulation of multiple joints resulted in either facilitatory or inhibitory interactions. For example in neuron 10 (Fig. 10A), flexion of the second finger was excitatory, but flexion of the third, fourth or fifth finger was inhibitory, because simultaneous flexion of these fingers with the second finger did not evoke the response (Fig. 10B). Another type of finger-to-finger interaction was found in neuron 8 in the same track (Fig. 2A). It was activated by flexion of the fourth or fifth finger's metacarpophalangeal joint, but pressing of the second or third finger tip was inhibitory. This finding suggests a possibility that inputs from different types of receptors converge on this area 1 neuron in
Fig. 10A-C. Inhibitory interaction between homologous joints of different fingers. Response histograms of neurons 19 in Fig. 2. A: Responses of the neuron to flexion of the second finger (impressed four times). B: Responses of the same neuron to flexion of the second and the third finger together. A similar cancelling effect was observed when the fourth or fifth finger was flexed together with the second finger. C: Receptive field of the neuron.

Fig. 11A–C. Convergence of effects from skin stimulation and joint manipulation. A: Responses to repeated gentle touch to four fingers simultaneously. The bar in A indicates the touch period. B: Responses to extension of four fingers together. At the arrow the fingers were held by the experimenter. Bars indicate the period of joint extension. C: The skin or joint receptive field (shaded or encircled area, respectively)

different ways. Area 1 neurons with inhibitory receptive fields tended to be located in deep layers (layers V and VI), as was the case in area 3b (Fig. 2D).

Neurons with Converging Inputs from Skin and Deep Tissue. The possibility that skin and deep afferents may converge onto single neurons was suggested in a total of 6 neurons. Among them, three neurons responded to hair stimulation and joint manipulation. They were found in the anterior region of area 1 near the border to area 3b. The other three neurons responded to glabrous skin stimulation and joint manipulation and were found in the posterior region near the border to area 2. Figure 11 shows responses of such a neuron. Repeated light touching to the skin evoked responses (Fig. 11A). The response to the joint manipulation was more vigorous than those to the skin stimulation in this case (Fig. 11B). In addition to responses to passive skin stimulation or joint manipulation, this neuron was briskly activated at the moment of active hand movements to reach a piece of food with extended fingers.

Discussion

The Multi-finger Type Receptive Fields and Overlapping Representation of Fingers

We found that nearly 40% of area 1 neurons were of the multi-finger or wide-field type. These types of receptive field were found not only in cutaneous neurons but also in joint manipulation neurons. The percentage was even higher (70%) in the medial half of the finger region. The medial part receives the main inputs from the ulnar fingers, and the lateral part from the radial ones. The difference may reflect the functional difference between these fingers. In the medial part of area 1, the representation of fingers largely loses its somatotopy since the representation of a particular finger is scattered over a wider cortical region, overlapping with those of others. The overlapping representation was much more extensive in area 2 where multiple functions, not just body parts, are represented (Iwamura et al. 1978, 1980).

It has been reported that the cortical representation of the body is multiple in the SI (Kaas et al. 1979). The multiple representations were described in relation to the cytoarchitectonic subdivisions of the SI, and it was claimed that the somatotopic represent-
tation was repeated in each subdivision in an almost identical fashion, and that the representation in area 1 was an mirror image of that in area 3b. However, the present results show that such a simple scheme of the SI organization does not hold in unanesthetized animals. Their experiments were performed in Ketamine-anesthetized monkeys. Duncan et al. (1992) reported that Ketamine considerably alters the receptive field properties of SI neurons in the monkey.

In area 1, the representation of different finger regions such as distal, ventro-proximal, and dorsal surfaces of fingers were considerably mixed. This was different from their pattern of representation in area 3b. A possible principle which underlies the organization of area 1 will be discussed later.

Comparison of Neuronal Submodalities Between Area 1 and Area 3b

In the preceding paper (Iwamura et al. 1983) the classification of area 1 neurons by submodality was described together with that of area 3b neurons (Table 1 of the preceding paper). Of area 3b neurons 68% and of area 1 neurons 51% responded to glabrous skin stimulation. The difference was accounted for by slightly larger numbers of hair, nail, and Pacinian-type neurons. Thus, the whole population of cutaneous neurons occupied 77.7% and 74.7% in area 3b and 1 respectively. On the other hand, 20.5% in area 3b and 20.2% in area 1 were deep submodality neurons. These results indicate that there is no big difference in the submodality content between area 1 and area 3b. The conclusion is consistent with the results of Hyvärinen and Poranen (1970b) and McKenna et al. (1982) but at variance with those in an earlier study (Powell and Mountcastle 1959b) in which more than 80% of neurons in area 1 were deep. The discrepancy may be attributed to the regional difference within area 3b and 1; in this earlier study more of the proximal forelimb region was explored. Or it may be due to the use of anesthetics in the earlier study which could have caused a sampling bias. Whatever the explanation may be, however, it is important to point out that the present results are more consistent with the recent anatomical findings that area 1 and area 3b receive thalamic projections from the same nuclear portion of the ventrobasal complex (Jones et al. 1979; Lin et al. 1979; Nishi and Kaas 1981) and that area 1 receives rich cortico-cortical projections from area 3b as well (Vogt and Pandya 1977; Jones et al. 1979).

The segregated representation of different submodalities such as observed in areas 3a and 3b was
not recognized in area 1. The different submodalities were mixed in area 1 although they did not frequently converge onto single neurons. These observations are consistent with the hypothesis that the information originating from the same sources reach area 1 but that they are organized according to a different principle from that in area 3b.

**Inhibitory Phenomena as Evidence for Neuronal Integration**

Several examples of neuronal responses with complex spatio-temporal characteristics have been demonstrated in the present study. Inhibitory receptive fields were found in cutaneous neurons and in joint mechanoreceptors neurons. In some neurons the inhibitory effects were seen only as the cancellation of the excitatory effect, and not on the spontaneous activity. This indicates that the inhibitory action is indirect for the particular neurons recorded. In all of these neurons, the receptive field arrangements were of a side-by-side type. The excitatory and inhibitory receptive fields are separated but frequently located in homologous parts of different fingers. This type of receptive field arrangement may be essential for the monkey to identify one locus and discriminate it from another. These neurons may also provide the preprocessed signals for higher integrative processing, as shown in Fig. 5.

Another interesting finding was that the excitatory and inhibitory receptive fields were coextensive in some cutaneous neurons and the different mode of stimulation evoked either excitation or inhibition. This suggests that different types of receptors converge on single cells. Similar observations were made in the cat SI (Iwamura and Tanaka 1978b). The most complete inhibitory interaction in area 1 was observed in a neuron illustrated in Fig. 9. The observation of inhibitory interaction in this area 1 neuron provides strong evidence that the systematic integration of neural messages takes place in area 1, since the inhibitory interaction necessarily involves many neurons working together as proposed in Fig. 9F. This case also indicates that directional selectivity may be brought about as the result of an interdigitational integration, possibly by the mechnism of lateral inhibition as already suggested by others (Barlow and Levick 1985; Hyvärinen and Poranen 1978a; Gardner and Costanzo 1980).

**A Hierarchical Model of SI Organization and Functional Linkages Between Area 1 and Area 3**

Recent anatomical studies have demonstrated the presence of rich cortico-cortical connections among different clusters of neurons in the same or different extrastriate subsets of the SI (Vogt and Pandya 1977; Künzle 1978; Jones et al. 1978). Areas 3a and 3b receive the main thalamic inputs and in turn send cortico association fibers to areas 1 and 2 to which a large amount of specific thalamic input is directed (Jones and Powell 1970; Jones 1975; Jones and Burton 1976). Thus, from these anatomical results, a hierarchical scheme emerges: areas 3a and 3b are a pivotal position (Vogt and Pandya 1977) receiving primary sensory afferents from the thalamus. More caudal parts of the SI (areas 1 and 2) are more associative because they are influenced more and more by the intracortically processed somatic information sent from areas 3a and 3b via corticocortical connections. This scheme fits with a simple hierarchical model of information processing in the sensory cortex proposed originally in a more general sense by Künzle (1978).

As discussed in the preceding paper (Iwamura et al. 1983), one of the important steps in cortical information processing is the parcellation of information among multiple groups of cells. This might facilitate the integration of information in the next step. Areas 3b and 3a may be the site of such parcellation of information concerning the submodality and stimulation position. Homologous parts of different fingers are represented in single area 1 neurons, for example, their ventral or dorsal skin. These types of receptive field organization may be based on the parcellation in area 3b. On the other hand, they seem to be suitable for processing of somatosensory information during distinct types of monkey behavior because different fingers frequently act together and information from homologous parts of the fingers needs to be integrated.

We found no definite signs of parcellation of cells in area 1 in terms of submodality or receptive field positions. We imagine that the parcellation in area 1 would be formed in a broader area. Figure 12 illustrates how the functional cluster in area 1 might be formed as the result of systematic convergence of information from area 1, suggesting that the functional implication of a cluster in area 1 should be interpreted in reference to the characteristics of neurons in the next area, i.e., area 2, where it is proposed that the types of information sorted in area 1 are integrated (Iwamura et al. 1981). The different submodalities may converge into single columns in this stage. In fact, we presented an example of such a case in Fig. 3, which was recorded near the border between area 1 and area 2.

It has been reported that ablation of area 1 in the monkey impaired the performance of roughness discrimination by palpation of test objects (Randolph...
and Smennes 1974). Our present results are consistent with this previous finding by showing examples of neurons with complex receptive fields and response properties which might be related to the palpatory apparatus. Area 1 sends information to area 2 where each neuron now bears information concerning the hand manipulation, reaching or more complex mode of action (Mountcastle et al. 1975; Iwamura and Tanaka 1978a; Iwamura et al. 1981). Area 2 has rich cortico-cortical connections with areas 4 and 6. Even area 1 has some connections with area 4 (Vogt and Pandya 1977; Künzle 1978; Jones et al. 1978). Thus, it is quite likely that area 1 is a source of organized information to the motor cortex directly or indirectly through its connection with area 2 for the monkey to use a directing skilled finger action which require elaborate tempo-spatial patterns of sensory responses.

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