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# Rostrocaudal gradients in the neuronal receptive field complexity in the finger region of the alert monkey's postcentral gyrus

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**Summary.** In the primate postcentral gyrus, the cytoarchitectonic characteristics gradually shift from those of koniocortex to more homotypical parakoniocortex along its rostrocaudal axis. To find the physiological correlates of these changes we examined a large body of data accumulated during a series of our experiments with alert monkeys. Along the rostrocaudal axis of the postcentral gyrus, we found a gradual and continuous increase in the number of neurons with converging receptive fields and those in which receptive field positions or submodalities were not determined. Deep or skin submodality neurons were dominant in area 3a or 3b respectively. The proportion of skin submodality neurons decreased gradually from area 3b to the more caudal part of the gyrus. The proportion of deep submodality neurons was almost constant from area 3b to area 2 inclusive; they were not the majority in area 2. The data are consistent with the hierarchical scheme, i.e., within the postcentral gyrus sensory information is processed from the primary sensory receiving stage to the more associative, integrative stages.

## Introduction

Anatomical organization of the primate postcentral gyrus has been described in terms of several different cytoarchitectonic nomenclatures (Campbell 1905; Brodmann 1909; Vogt and Vogt 1919; Economo and Koskinas 1925; von Bonin and Bailey 1947), and there has been a common understanding that cytoarchitectonic characteristics change rostrocaudally. Powell and Mountcastle

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(1959a) described differences among the subdivisions in detail, stating that area 3 is a typical koniocortex with granular cells, while in areas 1 and 2 the morphological characteristics change gradually to the homotypical parietal association cortex showing increase in number of large pyramidal cells in layers III and V. They emphasized that the divisions between the three cytoarchitectonic areas are regions of gradients of morphological change, rather than sharp lines.

Powell and Mountcastle (1959b) studied receptive field properties of single neurons in lightly anesthetized monkeys and found that in the rostrocaudal dimension of the postcentral gyrus there is a gradient change in the representation of submodalities, which they thought to be paralleled with the gradual morphological changes in the same region described above.

Hyvärinen and Poranen (1978) reported that in the postcentral finger region of alert monkeys neurons in areas 1 and 2 tend to have larger and more complex receptive fields covering multiple fingers, while neurons in area 3b have small ones. We have been examining neuronal receptive field properties in the postcentral gyrus of alert monkeys also and reached the same conclusion (Iwamura and Tanaka 1978a, 1991; Iwamura et al. 1983a, b, 1985a–d). We concluded that the representation of different fingers overlap considerably and, as a result, the somatotopic representation of fingers was less clear there in the caudal part of the gyrus than in the rostral part (Iwamura et al. 1980). Rostrocaudal difference in the receptive field size was found in the cat somatosensory cortex also (Iwamura and Tanaka 1978b, c). The increases in the size of the receptive field of neurons in areas 1 and 2 of monkeys have been confirmed repeatedly by others since then (McKenna et al. 1982; Darian-Smith et al. 1984; Pons et al. 1985; Gardner 1988; Wannier et al. 1991).

The primary purpose of the present experiments was to determine the presence of rostrocaudal gradients in the complexity of neuronal receptive field properties in the postcentral gyrus of alert monkeys in a more quantitative manner, based on the large body of data which has been

accumulated in a series of our experiments (Iwamura and Tanaka 1978a; Iwamura et al. 1980, 1983a, b, 1985a–d).

## Material and methods

The work reported here is based on experiments performed in four Japanese monkeys *(Macaca fuscata)*, both males and females. Their weights were between 4.0 and 5.6 kg. Prior to surgery, the monkeys were familiarized with the laboratory, the monkey chair, and the experimenters. The monkeys were also trained to accept natural stimulation of their hand and fingers without struggling. The reward was pieces of diced apple.

Surgery was done aseptically in two steps under deep anesthesia with pentobarbital sodium. The initial step was to implant four metal bolts to the skull, to fix the monkey's head to the chair. About 10 days later, an opening of about 2 cm diameter was made with a trephine in the skull over the postcentral gyrus. A cylindrical chamber (20 mm diameter) was placed over the defect and fixed to the bone with dental acrylic (Evarts 1968). The chamber was filled with saline and was closed with a plastic cap. At the beginning of every recording session, it was filled with mineral oil and the base-plate for a microdrive which had $x$–$y$ scales of 100-μm steps (Narishige MO-95) was attached to it. After recording was completed in one hemisphere, a second opening was made on the other side and the experiments were repeated.

During daily recording sessions, the monkey's head was fixed to the monkey chair by two metal bars screwed on the head-bolts. The electrodes were glass-coated platinum–iridium with a resistance of 4–6 MΩ. Only well-isolated, initially negative spikes were studied. Over a period of 4 weeks, 30–40 penetrations were made in each hemisphere. We attempted to study as many neurons as possible along a single microelectrode penetration, so that a direct comparison could be made of the properties of neurons located closely to each other. At the end of each penetration, one to three electrolytic lesions were made, by passing a constant current of 10 μA for 5–8 s, for later identification and reconstruction of these penetrations histologically.

After the two hemispheres were explored, the animal was killed with an overdose of pentobarbital sodium and perfused transcardi-ally with 0.9% saline followed by a solution of 10% formalin. The brain was sectioned at 40 μm. Every section was saved and stained by the Klüver-Barrera method for cell bodies and fibers. Gliosis around electrode tracks and electrolytic lesions were looked for carefully in each section. Most tracks (95%) could be identified by their patterned lesions and, in most cases, the whole trajectory of electrode penetration from the surface to the site of the lesions could be reconstructed. Since most electrode trajectories traversed many sections, they were traced by superimposing serial sections. The ratio of shrinkage of the brain through the histological procedures (20–30%) was estimated by overall shrinkage of the brain block and the decrease in intervals between lesions and was used for the recalculation of recording sites. The boundaries between the cy-toarchitectonic subareas were determined in each section using the criteria described by Powell and Mountcastle (1959a).

Figure 1 is a sketch of a histological section in a nearly sagittal plane with a right angle to the central sulcus, as shown on the dorsal view of the cortical surface. It illustrates the trajectory of an elec-trode penetration and the estimated depth of two units recorded along the penetration, based on the distance reading of the electrode manipulator during the experiment. The recording sites were pro-jected onto a line drawn through the middle of layer IV on the sagittal plane along histologically recognizable neuronal arrays, which were roughly perpendicular to the cortical surface. The rela-tive positions of recording sites were estimated along this line. A similar estimate was made in each of the serial sections and the recording sites of all neurons in one hemisphere were determined and plotted. In combining data from different hemispheres, the zero point of the coordinate was referred to, and thus small individual
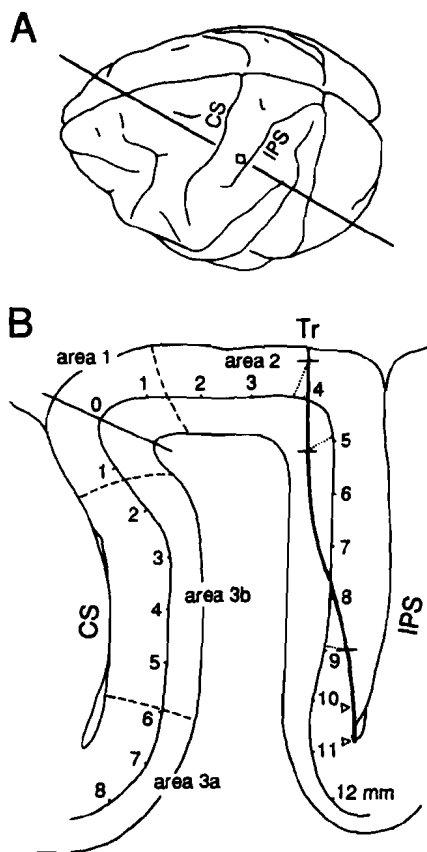


**Fig. 1A, B.** Histological section explaining how to unfold the gyrus. **A** A dorsal view of the cortical surface showing the direction of nearly sagittal histological sectioning, which is intended to be per-pendicular to the central sulcus. **B** A nearly sagittal section through the postcentral gyrus illustrating how the recording sites were deter-mined for plotting on the unfolded map of the cortex shown in Figs. 3 and 4. The recording sites *(short bars)* along an electrode track *(Tr)* were estimated based on the depths measured during recording and their relationships to the histologically identified electrolytic marks *(triangles)*. The corner of the central sulcus was taken arbitrarily as the zero point and the distance from it along layer IV *(line)* was measured either anteriorly or posteriorly and scaled in millimeters. The recording site of each unit was projected to this line along the histologically defined perpendicular arrange-ment of neurons *(dotted lines)* and then represented as the distance along this line in millimeters. *Broken lines* indicate the borders between areas 3a and 3b, 3b and 1, and 1 and 2. *CS*, central sulcus; *IPS*, intraparietal sulcus

variations in the width of the postcentral gyrus were disregarded. The resulting unfolded scatter maps are as shown in Figs. 3 and 4.

The receptive fields and submodality preferences of neurons were examined with hand-held probes, paintbrushes, and other tools. To activate certain types of neurons, we employed a variety of "natural" tactile stimuli such as rubbing, scraping, twisting, or pulling of the skin surface. They were often more effective and selective than topical application of probes to the skin. Various common materials or objects with different roughness or hardness were also applied to the skin. Joints of fingers, wrist, elbow, and shoulder were manipulated when the monkeys were passive and relaxed. In addition, neuronal responses were recorded during the monkey's active hand movements. The entire stimulation and re-cording procedure was video-taped using two cameras and com-bined on one TV screen. This record was very useful in examining the correlation between the unit activity and the stimulation procedures.

## Results

A total of 2656 neurons were recorded, from six hemispheres of four monkeys, in various portions of the post-central gyrus, including the deep rostral bank of the intraparietal sulcus (dIPS). Among them, 1979 neurons were responsive to somatosensory stimulation, and their submodality types were identified.

### Distribution of skin neurons

As described in our earlier papers (Iwamura et al. 1980, 1983a, b), the smallest receptive fields of the neurons of the primary somatosensory cortex (SI) are those confined to one segment or single joint of a finger. In the present paper we define the unitary receptive fields as those summarized in Fig. 2: the distal skin area covering either one of the digits (I–V), the hand dorsum (D), and the radial (R) or ulnar (U) half of the palmar skin. The middle zone of the palmar skin belongs to either one of the two halves. The forearm skin (F) is the only proximal skin area encountered in the present study. Deep submodality neurons were classified into the digit type (I–V), the wrist (W), the forearm muscles (F), the elbow (E) and the shoulder joint (S) manipulation types (Fig. 2B).

Large receptive fields of neurons were found more often in areas 1 and 2. They cover multiple fingers, both
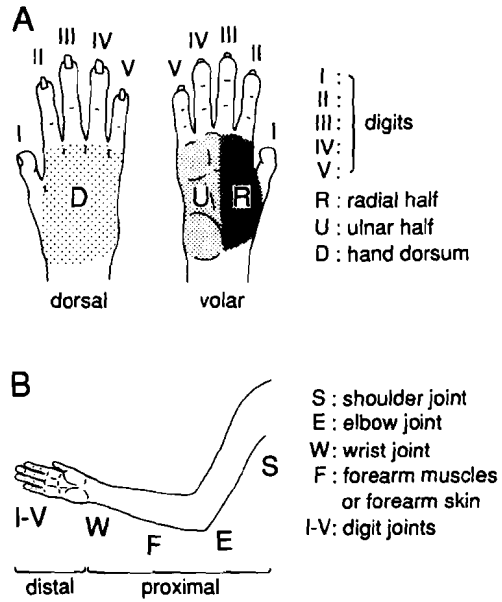


I : ⎫
II : ⎪
III : ⎬ digits
IV : ⎪
V : ⎭

R : radial half
U : ulnar half
D : hand dorsum

S : shoulder joint
E : elbow joint
W : wrist joint
F : forearm muscles
   or forearm skin
I–V : digit joints

**Fig. 2A, B.** Unitary receptive fields on distal **(A)** and proximal **(B)** parts of the forelimb. **A** Receptive fields confined within a single finger, on either the dorsal or volar side, are numbered *I–V*. The receptive fields on the hand dorsum are classified as *D* and those on either the radial or ulnar side of the volar skin, *R* or *U*. **B** The receptive fields of deep submodality neurons are either on the finger joints *(I–V)* or on one of the proximal joints, the wrist *(W)*, the elbow *(E)*, or the shoulder *(S)*. Those on the forearm skin or muscles are defined as *F*
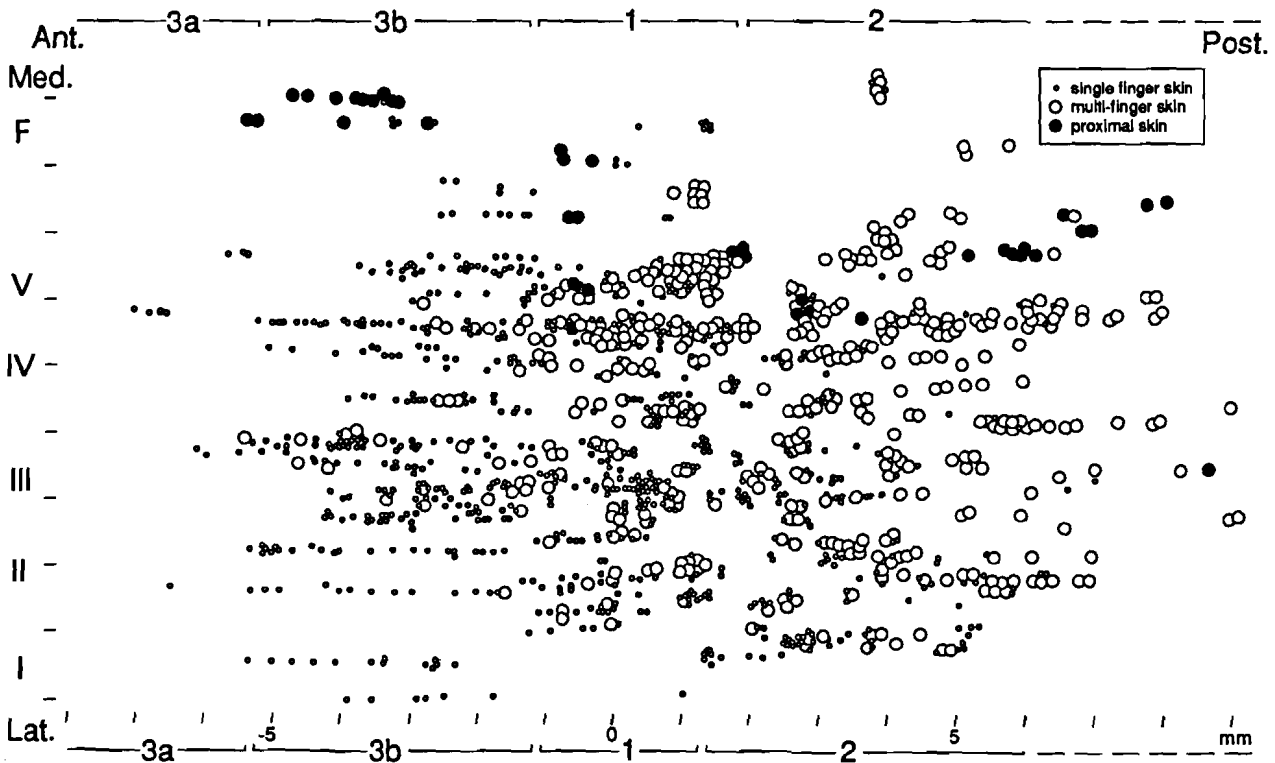


**Fig. 3.** A scatter map on the unfolded postcentral gyrus showing differential distribution of skin neurons. The *abscissa* represents the anterior–posterior *(Ant.–Post.)* distance along the gyrus, and the *ordinate* represents the medial–lateral *(Med.–Lat.)* distance. *Letters* along the ordinate indicate approximate sites of representation of fingers *(I–V)* or forearm *(F)* in area 3. *Small open circles*, neurons with single-finger-(location)-type receptive fields; *large open circles*, neurons with composite-type receptive fields; *filled circles*, neurons representing the forearm skin. All the skin submodality neurons are included that responded to light touch, specific types of skin stimulation, hair bending, and nails. Those neurons of which receptive fields were not identified were not included. Data from six hemispheres of four monkeys are superimposed

the fingers and the palmar skin, both sides of the palmar skin, etc. These large and more complex receptive fields could be considered as the composite of the unitary ones (Iwamura et al. 1985d). We classified all neurons into single-locus type and multi-loci (composite) type in terms of their receptive fields. Figure 3 is a scatter map showing the distribution of skin neurons of single-locus type (small open circles) or neurons of composite type (large open circles). Neurons with single-locus-type receptive fields make up the great majority in area 3b. The single-locus-type neurons were found in area 2 up to 7 mm caudally from the reference point, but they were mostly in the lateral part. In contrast, composite-type neurons increased rapidly in area 1 and were dominant in further caudal regions. This tendency was remarkable in the mediocaudal part, where neurons representing the forearm skin (filled circles) were intermingled. Skin neurons were rare in area 3a.

### Distribution of deep neurons

A similar tendency was found in deep submodality neurons (Fig. 4) which responded to manipulation of either single (small dots) or multiple joints (large filled circles). In general the deep submodality neurons were less numerous than the skin neurons. They were sparse, particularly in the lateral part where receptive fields of skin neurons

were on the thumb or the index finger. The composite type dominated the single-locus type in the mediocaudal part of the finger region similarly to the skin submodality neurons.

Figure 4 also shows that neurons responding to manipulation of the proximal joints or muscles (filled circles) were intermingled extensively in the finger region. It was remarkable in the caudalmost part of the finger region which lay in the dIPS.

### Rostrocaudal increase in complexity of the postcentral neurons

To evaluate the differences along the rostrocaudal axis of the finger region, we performed a quantitative analysis based on the data obtained from six hemispheres. Data from six hemispheres were combined together, regardless of small mediolateral or individual variations in the width of the postcentral gyrus. The ratios of neurons with different characteristics were calculated in each mediolateral strip of 1 mm width along the entire rostrocaudal axis of the map.

*Receptive field positions.* Figure 5A shows the relative distribution of neurons based on their receptive field positions. The number of neurons in which receptive field position could not be determined increased toward the
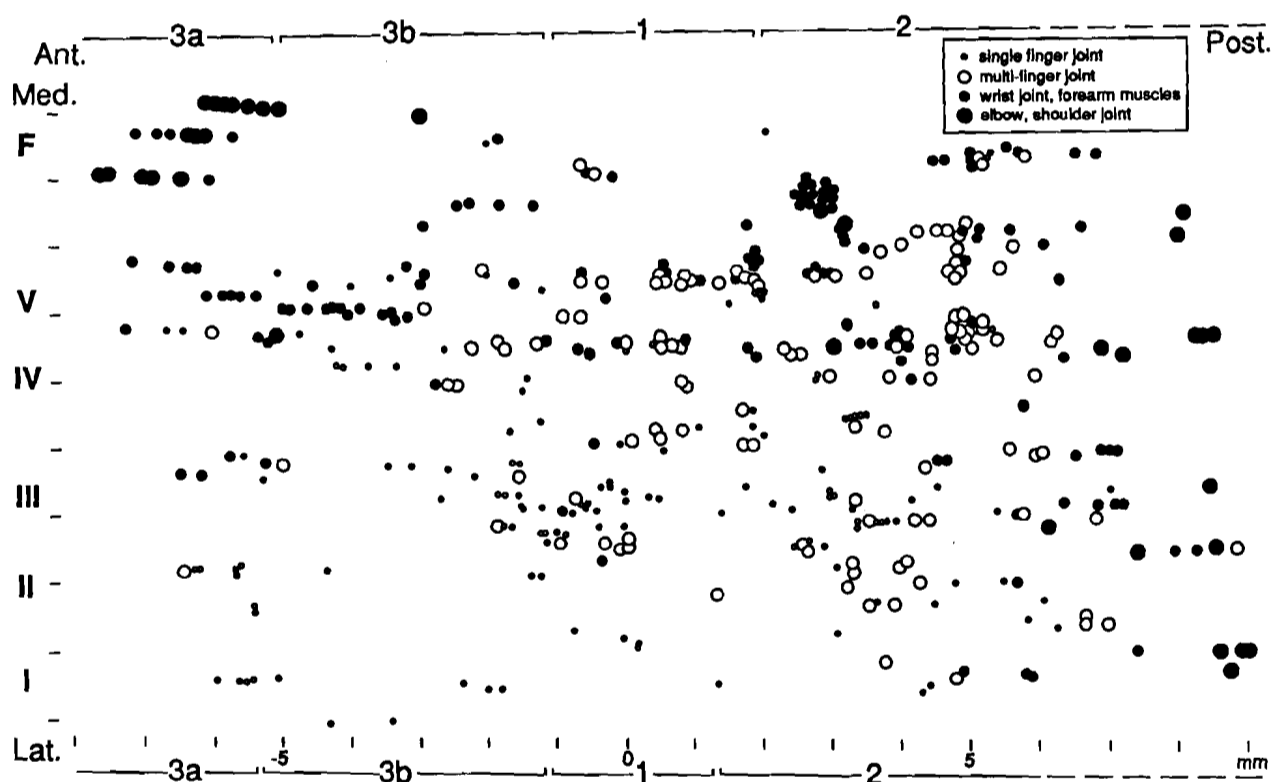


**Fig. 4.** A scatter map on the unfolded postcentral gyrus showing distribution of deep submodality neurons. The same arrangement as in Fig. 3. *Small open circles,* neurons with single-finger- (location)-type receptive fields; *large open circles,* neurons with composite-type receptive fields; *small filled circles,* neurons representing the wrist joint or forearm muscles; *large filled circles,* neurons representing

the elbow or shoulder joint. All deep submodality neurons are included which responded to joint manipulation, tapping, or pressing of joints or muscles. Those neurons of which receptive fields were not identified were not included. Data from six hemispheres of the same four monkeys as in Fig. 3
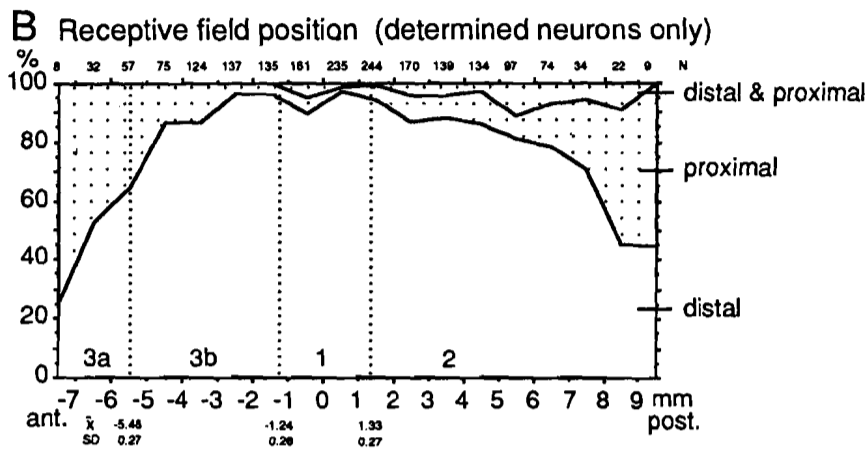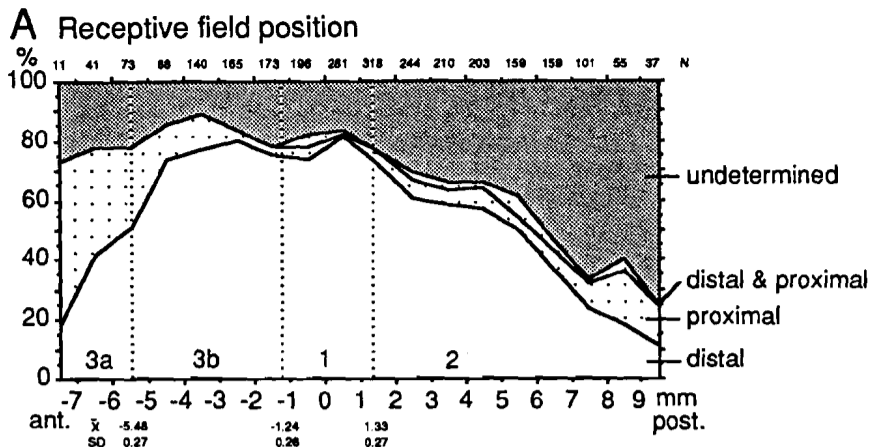
**A Receptive field position**

**B Receptive field position (determined neurons only)**

Fig. 5A, B. Relative distribution of receptive field positions along the anterior–posterior axis of the postcentral finger region. A The whole population. B The same data, but excluding unidentified neurons. In these graphs *dotted lines* indicate borders between two successive cytoarchitectonic subareas. They were the mean of those which were determined in each histological section. Data from six hemispheres of four monkeys

**A Submodality**

**B Submodality (specified neurons only)**

Fig. 6A, B. Relative distribution of submodalities. A The whole population. B The same data, but excluding unidentified neurons. *Dotted lines* indicate borders between two successive cytoarchitectonic subareas. They were the mean of those which were determined in each histological section. Data from six hemispheres of four monkeys
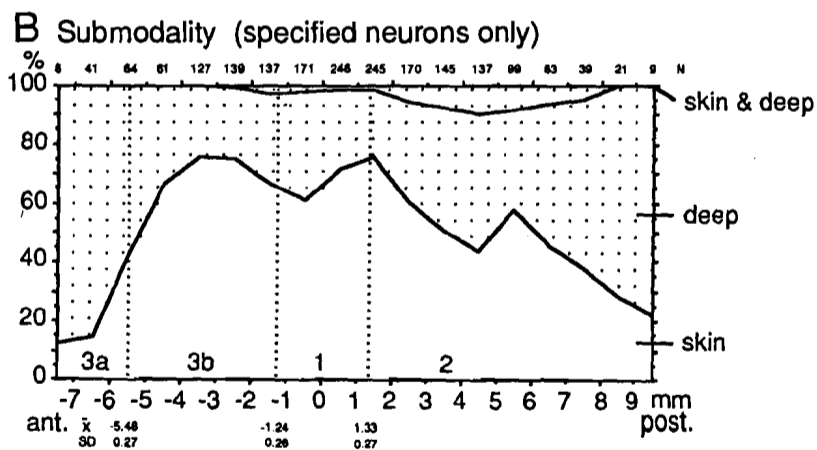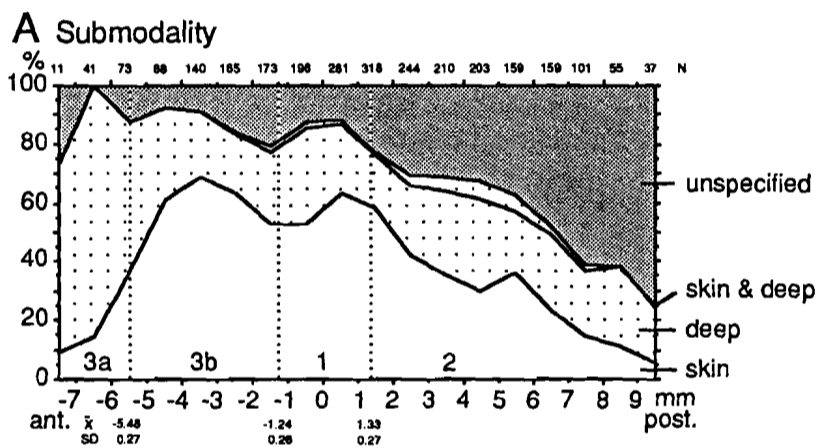
caudal part of the gyrus. Figure 5B replicates the relative distribution, but excludes the undetermined neurons. Distal neurons prevailed in area 3b, area 1, and the rostral part of area 2. Neurons with proximal receptive fields were found mainly in area 3a and the caudal part of area 2. Neurons with receptive fields covering both the distal and proximal part of the forelimb were fewer; they were found in the region caudal to the border between area 3b and 1.

*Submodality types.* Figure 6A illustrates the relative distribution of submodality types. Again, the unspecified neurons increased in more caudal regions. Figure 6B replicates the relative distribution, but excludes the unspecified neurons. Deep submodality neurons were the majority in both the rostralmost and caudalmost parts of the gyrus; skin neurons were dominant in the region in between. Neurons with both skin and deep submodalities were found mainly in area 2.

*Receptive field convergence.* Figure 7 shows how the composite-type receptive fields increase toward the caudal part of the gyrus. Only those neurons of which receptive fields involve the digits were taken into account. Neurons with receptive fields of a single-locus type comprised the overwhelming majority in the rostral part (areas 3a and 3b), but its ratio started to decrease at the border between areas 3b and 1. Neurons with two-loci-type receptive fields started to increase within area 3b near its border to area 1; neurons with three-or-more-loci-type receptive

fields started to increase more caudally in area 1 and further in area 2.

*Comparison between cytoarchitectonic subdivisions of the postcentral gyrus*

We now compare receptive field properties of neurons collected in the entire postcentral gyrus among different cytoarchitectonic subdivisions. The cytoarchitectonic borders were determined in each histological section according to the criteria described by Powell and Mountcastle (1959a), and the recording site of the individual neuron was assigned to one of the subdivisions.

The caudal border of area 2 is unclear cytoarchitectonically. Physiologically, however, we found changes of neural activity in several features at around 6 mm caudal from the reference point. The changes included an increase in the number of neurons responding to proximal forelimb manipulation (Fig. 4) and an increase in the number of neurons whose receptive field positions (Fig. 5) or submodalities (Fig. 6) were undetermined. We take these observations to indicate the presence of a functional subdivision in the caudalmost part of the postcentral gyrus. We tentatively labeled this region as dIPS. Within dIPS, we encountered neurons responding to stimulation of the body parts other than the contralateral forelimb: the trunk, face, or ipsilateral hand. We also found neurons influenced by visual stimulation, such as movement of common objects. Some of them had a re-
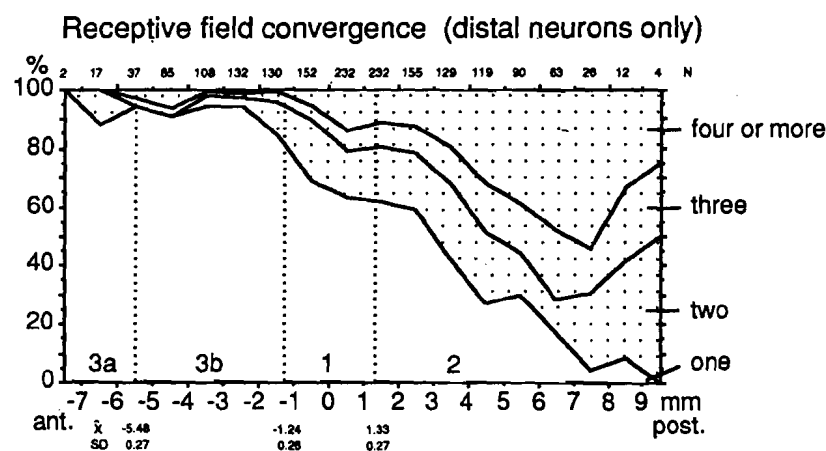
## Receptive field convergence (distal neurons only)



Fig. 7. The increase in the receptive field convergence toward the caudal part of the gyrus. *Dotted lines* indicate borders between two successive cytoarchitectonic subareas. They were the mean of those which were determined in each histological section. Only neurons representing the distal part were included. Data from six hemispheres of four monkeys

Table 1. The classification of neurons which responded or were influenced by unusual types of stimulation in different cytoarchitectonic subareas, areas 3a, 3b, 1, 2, and the deeper part of the intraparietal sulcus

| | Area 3a | Area 3b | Area 1 | Area 2 | | | dIPS | | | Total | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | % | n | Contra | % | n | Contra | % | n |
| Face; trunk | 0 | 0 | 0 | 0.1 | 1 | 1 | 1.4 | 5 | 2 | 0.2 | 6 |
| Ipsilateral influences | 0 | 0 | 0 | 0.3 | 3 | 1 | 3.6 | 13 | 5 | 0.6 | 16 |
| Visual influences | 0 | 0 | 0 | 0.1 | 1 | 0 | 5.2 | 19 | 7 | 0.8 | 20 |
| Total | 0 | 0 | 0 | 0.5 | 5 | 2 | 10.2 | 37 | 14 | 1.6 | 42 |

Data from six hemispheres of four monkeys. Several neurons were listed more than once. Percentages are of the total population dIPS, deep part of intraparietal sulcus; Contra, with receptive field on the contralateral forelimb
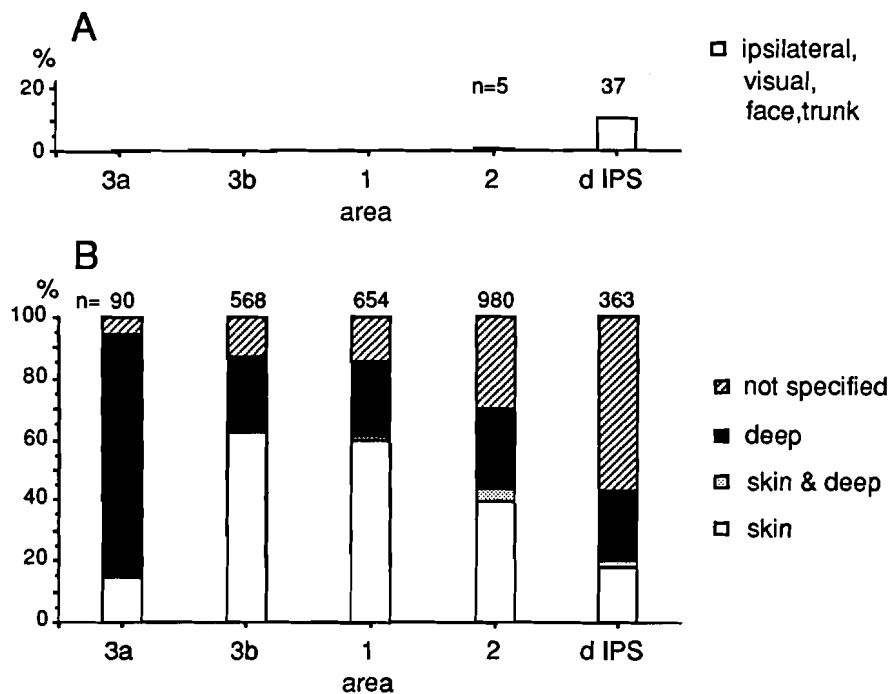
**Fig. 8. A** The ratio of neurons influenced by unusual types of stimuli among different cytoarchitectonic subareas. The stimuli include those to the contralateral trunk, face, the ipsilateral body, and visual stimulation, as shown in Table 1. **B** Comparison of the ratio of submodality populations. Data from six hemispheres of four monkeys.
*dIPS*, deep part of intraparietal sulcus

**Table 2.** Classification of neurons in different cytoarchitectonic areas by their submodality

|  | Area 3a | | Area 3b | | Area1 | | Area2 | | dIPS | | Total | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | % | n | % | n | % | n | % | n | % | n | % | n |
| Skin | 14.4 | 13 | 62.7 | 356 | 59.5 | 389 | 39.6 | 388 | 18.2 | 66 | 45.6 | 1212 |
| Light touch skin | 8.9 | 8 | 37.7 | 214 | 24.8 | 162 | 19.9 | 195 | 8.8 | 32 | 23.0 | 611 |
| Specific skin | 2.2 | 2 | 14.1 | 80 | 16.2 | 106 | 13.0 | 127 | 5.2 | 19 | 12.6 | 334 |
| High-threshold skin |  | 0 | 2.1 | 12 | 1.2 | 8 | 0.5 | 5 |  | 0 | 0.9 | 25 |
| Hair; hair and skin | 3.3 | 3 | 6.5 | 37 | 10.2 | 67 | 2.9 | 28 | 3.6 | 13 | 5.6 | 148 |
| Nail; nail and skin |  | 0 | 2.3 | 13 | 7.0 | 46 | 3.4 | 33 | 0.6 | 2 | 3.5 | 94 |
| Deep | 80.0 | 72 | 23.2 | 132 | 24.8 | 162 | 25.9 | 254 | 22.9 | 83 | 26.5 | 703 |
| Joint manipulation | 67.8 | 61 | 12.1 | 69 | 11.6 | 76 | 14.2 | 139 | 13.8 | 50 | 14.9 | 395 |
| Deep others | 11.1 | 10 | 10.2 | 58 | 10.2 | 67 | 10.6 | 104 | 5.5 | 20 | 9.8 | 259 |
| Joint and deep others |  | 0 |  | 0 | 0.2 | 1 | 0.4 | 4 | 0.3 | 1 | 0.2 | 6 |
| Pacini type | 1.1 | 1 | 0.9 | 5 | 2.8 | 18 | 0.7 | 7 | 3.3 | 12 | 1.6 | 43 |
| Skin and deep |  | 0 | 0.9 | 5 | 1.2 | 8 | 4.4 | 43 | 2.2 | 8 | 2.4 | 64 |
| Skin and joint manipulation |  | 0 | 0.5 | 3 | 0.9 | 6 | 3.3 | 32 | 1.7 | 6 | 1.8 | 47 |
| Skin and deep others |  | 0 | 0.4 | 2 |  | 0 | 0.4 | 4 | 0.3 | 1 | 0.3 | 7 |
| Nail and joint manipulation |  | 0 |  | 0 |  | 0 | 0.6 | 6 |  | 0 | 0.2 | 6 |
| Hair and joint manipulation |  | 0 |  | 0 | 0.3 | 2 | 0.1 | 1 | 0.3 | 1 | 0.2 | 4 |
| Submodality not specified | 5.6 | 5 | 13.2 | 75 | 14.5 | 95 | 30.1 | 295 | 56.7 | 206 | 25.5 | 676 |
| Total | 100.0 | 90 | 100.0 | 568 | 100.0 | 654 | 100.0 | 980 | 100.0 | 363 | 100.0 | 2655 |

Data from six hemispheres of four monkeys. dIPS, deep part of intraparietal sulcus

ceptive field also on the contralateral forelimb. Although the total number of such neurons is small, 90% of them were found in the dIPS (Table 1, Fig. 8A). We are currently studying the response characteristics of these neurons in more detail and will describe them in a separate paper.

In Fig. 8B and Table 2 we summarize the results of classification of postcentral neurons in terms of submodality. They indicate that the skin submodality neurons were the majority in areas 3b and 1, that the deep submodality neurons were similarly distributed except in area 3a, that a small number of neurons responding to both skin and deep stimuli were found mostly in area 2,

and that submodality-unspecified neurons increased posteriorly, reaching as many as 60% in the dIPS.

## Discussion

### The rostrocaudal differences in neuronal receptive field properties

In the present paper we showed rostrocaudal changes in the receptive field properties of postcentral neurons: toward the caudal part of the gyrus the ratio of unspecified neurons increased gradually and continuously; the ratio of single-locus-type neurons decreased, while the ratio of

composite-type neurons increased. We also examined the relative distribution of neuronal submodality classes along the rostrocaudal axis and among different cytoarchitectonic subareas. The ratio of skin neurons was largest in area 3b and decreased gradually toward the caudal part of the gyrus. The ratio of deep submodality neurons was largest in area 3a, as expected from previous studies (Jones and Porter 1980). It was around 20% in area 3b and stayed almost constant caudally from there. The results are at variance with the results of Powell and Mountcastle (1959b), who reported that more than 90% of area 2 neurons were of deep submodality. The discrepancy may be explained by the regional difference: Powell and Mountcastle recorded neurons in the more medial part of the gyrus (those with receptive fields on the forearm, arm, shoulder, trunk, thigh, leg, and very few on the finger), while we recorded neurons in the finger region, which may be a highly specific area for cutaneous inputs. Another difference between the study of Powell and Mountcastle and ours is in the ratio of submodality-unspecified neurons. It is likely that in their study the ratio of neurons unresponsive to peripheral stimuli (and thus their submodality was unspecified) was underestimated – the presence of these neurons are noticed only through the spontaneous activity which might have been reduced or suppressed under the anesthetized condition, especially in area 2. It is also likely that some of them were activated only in relation to the animal's active movements of the arm or hand.

## The presence of proximal neurons in the finger region

We showed that within the hand–finger region were intermingled neurons with proximal receptive fields, especially in the rostralmost and caudalmost parts of the gyrus. The nature of the neurons with proximal receptive fields differed between the two parts. In the rostral region the proximal neurons were found mostly in the medial half of the finger representation. They were mostly of single-locus type and their respective receptive fields localized to the forearm. In the caudal region, neurons with proximal receptive fields were distributed more widely. Most of these neurons were of multifoci type, including a number of elbow or shoulder neurons. Functional significance of the presence of neurons with proximal receptive fields is not clear yet, but it may be interpreted as reflecting the close relationship between the proximal and distal parts of the forelimb in the hand manipulation and reaching actions.

## The caudal border of area 2

The present study covered various parts of the gyrus, including the depth of the rostral bank of the IPS. The area caudal to area 2 was designated as area 5 by Brodmann (1909) and area PE by Bonin and Bailey (1947). Powell and Mountcastle (1959a) described area 5 or PE as being much thinner in the lateral part of the gyrus where fingers or the face are represented and found that in the finger region area 2 directly shifts to area 7 without area 5 interposed between them. Seltzer and Pandya

(1986) also showed that at the lateral pole of the IPS area PE does not exist.

The difficulty in defining the caudal border of area 2 cytoarchitectonically has been pointed out (von Bonin and Bailey 1947; Powell and Mountcastle 1959a; Mountcastle et al. 1975; Jones et al. 1978; McKenna et al. 1982; Pons and Kaas 1985; Pons et al. 1985; Wannier et al. 1991): no consistent architectonic feature clearly identified the caudal border of area 2 throughout its mediolateral extent. Pons et al. (1985) tried to define the boundary of area 2 by physiological means. They mapped the SI in anesthetized monkeys with multiunit recording. They stated that cortex within 3–4 mm of the area 1 border was generally responsive to somatosensory stimuli, while more caudal cortex usually was not. Their physiological border is likely to be placed between +4.5 (at the corner of the IPS bank) and +5.5 mm in our coordinates (Fig. 1).

Our data indicated that neurons with a finger receptive field of single-locus type are found in the region rostral to 5.5 mm from the reference point. On the other hand, neurons responding to the manipulation of the proximal forelimb invaded the lateral part of the finger region, starting at around 4.5 mm from the reference point. The relative number of neurons of which receptive field positions were not identified increased most sharply between 6 and 7 mm from the reference point. Neurons related to face, the ipsilateral hand, or visual input were found also mostly in the deeper part of the bank caudal to 6–7 mm from the reference point. All these observations indicate that the shift of neuronal receptive field properties in the rostral bank of IPS is gradual and variable depending on parameters. The physiological border of area 2 as defined by Pons et al. (1985) may correspond roughly to the caudal limit of neurons representing single loci of the hand in our observation. The coincidence appears reasonable, since small receptive fields localized to single fingers may imply that these particular neurons receive inputs directly from the specific thalamic relay nuclei, and since it is most likely that in multiunit recording techniques in anesthetized animals the record reflects mainly the activity of direct thalamic inputs.

## A hierarchical model

The present results are in line with the hierarchical scheme, i.e., within the postcentral gyrus sensory information is processed from the primary sensory receiving stage to integrative and more associative stages (Iwamura et al. 1983b). This model fits better to the gradual shift of the cytoarchitectonic characteristics along the rostrocaudal axis of the postcentral gyrus. Rich intrinsic corticocortical connections are demonstrated within the postcentral gyrus, starting with area 3b and projecting to areas 1 and 2 (Jones and Powell 1970; Jones 1975; Jones and Burton 1976; Vogt and Pandya 1978; Jones et al. 1978; Shanks and Powell 1981). These corticocortical connections may be the main route of inputs to area 2 and further caudal regions where the majority of neurons did not respond to the stimulation of the periphery. The

direct thalamic inputs from the shell of the ventroposterior nuclei (Jones and Friedman 1982; Pons and Kaas 1985) to area 2 may be subordinate, if not minimal, among various inputs to area 2. On the other hand, additional inputs from thalamic association nuclei such as anterior pulvinar reach area 2 as well as areas 5 and 7 (Pons and Kaas 1985). Such inputs may also contribute to a blurring of the distinction between the SI and the posterior association cortices.

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