
Bilateral receptive field neurons and callosal connections in the somatosensory cortex

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Earlier studies recording single neuronal activity with bilateral receptive fields in the primary somatosensory cortex of monkeys and cats agreed that the bilateral receptive fields were related exclusively to the body midline and that the ipsilateral information reaches the cortex via callosal connections since they are dense in the cortical region representing the midline structures of the body while practically absent in the regions representing the distal extremities. We recently found a substantial number of neurons with bilateral receptive fields on hand digits, shoulders–arms or legs–feet in the caudalmost part (areas 2 and 5) of the postcentral gyrus in awake Japanese monkeys (*Macaca fuscata*). I review these results, discuss the functional implications of this bilateral representation in the postcentral somatosensory cortex from a behavioural standpoint and give a new interpretation to the midline fusion theory.

Keywords: postcentral gyrus; bilateral representations; callosal connections; hands; midline fusion theory

1. INTRODUCTION

The somatotopic representation of the body in the primary somatosensory cortex (SI) has been described in relation to the contralateral side of the body based on studies of the subjective experience of patients after direct stimulation of the cortex, or of recording surface evoked potentials or single neuronal activity after peripheral stimulation in animals. However, several studies have recorded single neuronal activity with an ipsilateral or bilateral receptive field (RF) in the SI of monkeys (Schwartz & Fredrickson 1971; Dreyer *et al.* 1975; Conti *et al.* 1986; Manzoni *et al.* 1989; Ogawa *et al.* 1989) or cats (Manzoni *et al.* 1980). These bilateral RFs were related to the body midline, either in the oral cavity, the head or trunk but not to the distal part of the extremities or to the vibrissae. The ipsilateral information for these bilateral RFs is likely to reach the cortex via callosal connections since they are dense in the cortical region representing the midline structure of the body while practically absent in the region representing the distal part of the extremities or vibrissae (Jones & Powell 1968, 1969; Pandya & Vignolo 1969; Karol & Pandya 1971; Shanks *et al.* 1975, 1985; Caminiti & Sbriccoli 1985; Ebner & Myers 1962; Manzoni *et al.* 1980; Innocenti 1986). Thus the midline rule of interhemispheric interaction was proposed (Manzoni *et al.* 1989) in analogy with the midline fusion theory in the visual cortex. At the border between V1 and V2 in the visual cortex, bilateral RFs straddle the vertical meridian, and the callosal connections are responsible for unifying two separated visual hemifields. This formed the basis for the midline fusion theory (Choudhury *et al.* 1965; Berlucchi *et al.* 1967; Berlucchi & Rizzolatti 1968; Hubel & Wiesel 1967; Zeki 1978).

At variance with the earlier conclusions, we recently found a substantial number of neurons with bilateral RFs

on the hand digits clustered in the caudalmost part of the SI (areas 2 and 5) in awake Japanese monkeys (*Macaca fuscata*) (Iwamura *et al.* 1994). Furthermore, we found bilateral or ipsilateral activity also in the caudalmost part of the trunk–shoulder–arm region and in the leg–foot region of the SI (Iwamura *et al.* 1996; Taoka *et al.* 1998a, 1999). In the present communication I will review our own studies on bilateral RF neurons and discuss the implication of these findings in understanding the rule of interhemispheric interactions in the somatosensory cortical areas: our findings are in favour of applying the original midline fusion theory proposed in the visual cortex to the somatosensory cortex.

2. BILATERAL AND IPSILATERAL RECEPTIVE FIELD NEURONS IN THE HAND–FINGER REGION OF THE MONKEY SOMATOSENSORY CORTEX

We had encountered bilateral RF neurons in the hand–finger region in our earlier experiments when we penetrated the caudalmost part of the region (Iwamura *et al.* 1993). We re-examined the same region to look for bilateral RF neurons more carefully and found them along penetrations through the upper bank of the intraparietal sulcus (IPS) (Iwamura *et al.* 1994) ('c' in figure 1a; figure 1b). For example, in one hemisphere we recorded a total of 863 neurons along 50 penetrations. We found neurons with bilateral RFs along 21 out of 27 penetrations which entered into the anterior bank of the IPS while we did not encounter bilateral RF neurons in the other 23 penetrations which entered into the posterior bank of the central sulcus (CS) or the crown of the postcentral gyrus. We found a total of 105 bilateral RF neurons out of 528 neurons recorded along the 21 penetrations. Out of 21 penetrations, 12 entered the finger region while the other nine entered into the more

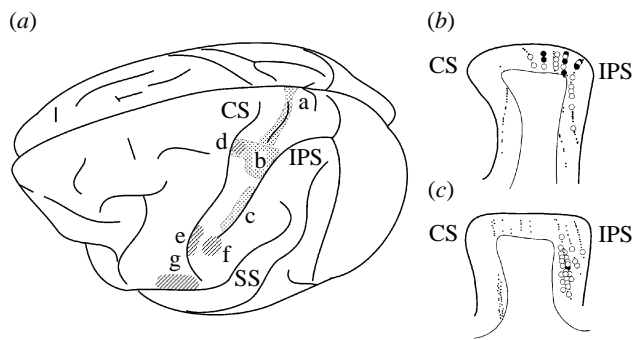


Figure 1. The sites of recording for bilateral RF neurons in the postcentral gyrus of the macaque monkey. (a) A dorsolateral view of the cerebral cortex of a Japanese monkey showing sites of recording of bilateral RF neurons. a, the leg-feet (Taoka *et al.* 1999); b, the trunk-shoulders-arms (Taoka *et al.* 1998a); c, the fingers-hand region (Iwamura *et al.* 1994); d, the midline trunk region by Manzoni *et al.* (1989); e, the face, lips and jaw region by Dreyer *et al.* (1975); f, the midline perioral face and lip region by Schwarz & Fredrickson (1971); g, the intraoral region by Ogawa *et al.* (1989); CS, central sulcus; IPS, intraparietal sulcus; SS, Sylvian sulcus (lateral sulcus). (b) A sagittal section through region b in (a), showing recording sites of neurons and cytoarchitectonic subdivisions in the trunk-shoulder-arm region. (c) A sagittal section through region c in (a), showing recording sites of neurons and cytoarchitectonic subdivisions in the finger region. In (b) and (c) filled circles, ipsilateral RF neurons; open circles, bilateral RF neurons; dots, other types of neurons.

medial part of the cortex where the wrist and forearm were represented.

We found 75 bilateral RF neurons in the finger region. Among them, 48 neurons (64%) were in skin category: 21 neurons had RFs on the finger tip mostly related to the nail, 20 on the glabrous and seven on the dorsal skin of the fingers or hand; 17 neurons (23%) were in the category of deep submodality: 11 neurons were activated by manipulation of finger joints, two by pressure to the finger, and four by the wrist or elbow joint manipulation. In addition, ten neurons (13%) were activated by self-paced movements of the arm of either side. The presence of neurons activated by self-paced arm movements has been described elsewhere (Iwamura & Tanaka 1996). We found 30 bilateral RF neurons in the forearm region, just medial to the finger region. Six neurons were activated by stimulation of the dorsal skin of the hand and/or fingers, and 11 by manipulation of the finger, wrist or elbow joint. Nine neurons had bilateral RFs covering the whole forelimb and/or the trunk. In addition, four neurons were activated by self-paced arm movements.

Among neurons with RFs on fingers, the multiple finger skin (and nail) types were the majority, and in general, the size and orientation of bilateral RFs were symmetrical. The preferred direction of directionally selective neurons as plotted by stimulation of one hand was also symmetrical with the other hand. In many cases, the spatial configuration of the RFs in the two hands was the same, but the intensity of the response was not necessarily the same. We found that among 105 bilateral RF neurons in one hemisphere, 61 (58.1%) responded better to the contralateral side, nine (8.6%) preferred the

ipsilateral side, and 35 (33.3%) responded about equally to either side; their response intensity was estimated by the maximal instantaneous firing rate in the peristimulus histogram.

A few neurons with bilateral RFs were found in the upper part of the bank (area 2), but the majority of them were located in the middle part of the bank, across the border separating area 2 from areas 5 and 7. They were found in both supra- and infragranular layers. We never found any neurons with bilateral RFs in areas 3 and 1.

To learn whether ipsilateral responses are dependent on the contralateral hemisphere, the finger region (areas 3b, 1 and 2) of one hemisphere was ablated completely in one monkey. After identifying the region containing those neurons with bilateral RFs (areas 2 and 5) by multi-unit recording, multiple injections of ibotenic acid were made in another two monkeys. No bilateral RFs were found in the postcentral gyrus of the opposite side after either procedure.

3. BILATERAL AND IPSILATERAL RECEPTIVE FIELD NEURONS IN THE REGIONS FOR THE TRUNK, UPPER ARMS AND SHOULDERS

We subsequently investigated the cortical regions for the proximal arm, shoulder and trunk representation, and found bilateral or ipsilateral RF neurons there as well (Taoka *et al.* 1998a) ('b' in figure 1a; figure 1b). The area we explored included the sites of recording of bilateral RF neurons in the trunk region by Manzoni *et al.* (1989) in areas 3b and 1 of the postcentral gyrus ('d' in figure 1a). We identified RFs of 1162 single cells in areas 3b, 1, 2 and 5 and found a total of 56 ipsilaterally or 107 bilaterally driven neurons. The majority of the bilateral or ipsilateral RF neurons were found in the upper bank of the IPS, and some in the crown of the postcentral gyrus. The distribution of neurons with the ipsilateral RFs overlapped with that of the bilateral neurons. The ipsilateral and bilateral RF neurons of skin submodality ($n=37$) were found in areas 1, 2 and 5. Their RFs were on the trunk, occiput, forelimb, or on both the trunk and arms. Ninety per cent of the neurons had RFs across the midline when they included the trunk, but their RFs were not necessarily confined to the skin area very near to the body midline. Rather they often extended to the forearm, sometimes even to the hand. There were neurons with RFs on both arms, but neurons with RFs confined to the forearm were rare. Many more bilateral neurons responding to joint manipulation ($n=104$) were found in areas 2 and 5. Most of them were activated by manipulation of shoulders or elbows. This class of neurons was not described in previous studies on bilateral RF neurons. The rather high incidence of bilateral RF neurons responding to deep stimulation in this region contrasted with that of bilateral skin neurons in the finger region.

Neurons with bilateral activity were found more often in areas 2 and 5 than in area 1, and those found in area 5 were more complex in their RF properties than those in areas 1 and 2. This finding is consistent with analogous finding in the finger region, indicating the presence of a hierarchy along the anteroposterior axis of the postcentral gyrus also in the trunk-arm-shoulder region. The presence of bilateral RF neurons in area 5 was reported earlier by Sakata *et al.* (1973).

4. BILATERAL RECEPTIVE FIELD NEURONS IN THE LEG AND FOOT REGIONS

We also investigated the leg and foot region looking for bilateral activity (Iwamura *et al.* 1996; Taoka *et al.* 1999). We examined single cells in the most medial part of the postcentral gyrus including its medial surface in three hemispheres (areas 3b, 1, 2 and 5) ('a' in figure 1a). We found 24 bilateral and seven ipsilateral RF neurons among 1050 neurons which had RFs including the leg or foot. These bilateral or ipsilateral neurons were found in areas 2 and 5. Out of the 31 neurons, 26 had RFs on the legs or feet and five had RFs extending from the leg to the trunk; eleven were skin neurons with RFs on the feet or legs, and 20 were deep neurons including one neuron which responded both to the foot skin and the ankle movements. Their RFs were symmetrical. Thus the bilateral or ipsilateral RF neurons were found in the leg and foot region also although they were much more sparse than in the hand region, being scattered widely in areas 2 and 5. Armstrong-James & George (1988) found neurons with bilateral RFs in the foot region of rat somatosensory cortex. Their RFs were also precisely symmetrical.

5. BILATERAL RECEPTIVE FIELD NEURONS IN THE HEAD, FACE AND ORAL CAVITY REGION

Previous studies demonstrated the presence of ample bilateral RF neurons in the postcentral face or oral cavity region. Dreyer *et al.* (1975) penetrated microelectrodes into the principal trigeminal projection field of the postcentral gyrus (area 3) ('c' in figure 1a), and found neurons with ipsilateral or bilateral RFs on the lower lip or jaw at the midline. Schwartz & Fredrickson (1971) studied a restricted region of the trigeminal projection field in area 2 at the lateral end of the IPS ('f' in figure 1a), and found neurons with the perioral or intraoral RF of which the centre was always located exactly in the midline. Ogawa *et al.* (1989) studied the laterality of neurons in the gustatory area where the oral cavity is represented. This cortical region is located in the exposed and buried parts of the frontal operculum containing areas 3 and 1–2 in the Old World monkey ('g' in figure 1a). They found ipsi- or bilateral neurons with RFs on the tongue, palate or periodontium, but not on the lip. Almost all neurons were bilateral when their RFs were on multiple sites such as on both the tongue and periodontium. RFs of the bilateral neurons were not necessarily related to the midline. The bilateral RF neurons were distributed widely in areas 3, 1 and 2.

6. ARE CALLOSAL CONNECTIONS RESTRICTED TO MIDLINE STRUCTURES IN THE POSTCENTRAL GYRUS?

Earlier degeneration as well as tracer injection studies in cats (Ebner & Myers 1962; Jones & Powell 1968; Manzoni *et al.* 1980; Innocenti 1986) and monkeys (Jones & Powell 1969; Pandya & Vignolo 1969; Karol & Pandya 1971; Shanks *et al.* 1975, 1985; Caminiti & Sbriccoli 1985) stated that callosal connections were limited to areas corresponding to the axial or midline representation of the trunk, face or head, devoid of the distal portion of the limbs. This statement could be revised by a careful

re-examination of published data, to reconcile it with our present findings that bilateral RFs neurons are not restricted to the midline structures.

Jones & Hendry (1980) in combined anatomical and electrophysiological experiments examined the hand region and compared the distribution of callosal fibres among four different cytoarchitectonic subareas. They concluded that all four (areas 3a, 3b, 1 and 2) representations of the hand and forearm in the SI were without callosal connections. However, their data indicate that a part of area 2 in the finger and forearm region project transcallosally to the opposite side. Some connections are seen in the shoulder–arm region too.

Killackey *et al.* (1983) studied callosal connections in physiologically defined cortical regions and concluded that cortical fields varied in density of callosal connections among different cytoarchitectonic areas: area 3b had few, area 1 had more, and area 2 had relatively dense callosal connections. Within each of these fields, connections were much less dense for the representations of the glabrous hand and foot and much more dense for representations of the face and trunk. They also showed that callosal connections are not necessarily restricted to the zones representing the body midline and that callosally projecting cells were more broadly distributed than callosal terminations. The latter observation was confirmed by Conti *et al.* (1986). Our own study on the callosal connections (Toda *et al.* 1996) confirmed the presence of callosal projections (both degenerated terminals and retrogradely marked cell bodies) in the trunk–shoulder–arm region where we found off-midline bilateral RF neurons.

In grey squirrels, callosal terminations are unevenly distributed in the SI (Gould & Kaas 1981). Similar to the situation in other animals, callosal projections terminate within the representation of the body midline, most clearly the midline of the representation of the upper and lower face. Most or all of the SI cortex away from the midline on the upper and lower lips, the mystacial vibrissae and the glabrous forepaw was almost free of direct callosal terminations. However, callosal terminations were seen also in the architectonically distinct 'unresponsive zone' which may correspond to the sensory association areas in macaque brains. Thus the authors surmised that all parts of the SI (and thus all body parts) are directly or indirectly connected via the callosum with the other hemisphere after all.

In rats, callosal connections are distributed mainly in the dysgranular zone, outside of what can be defined as the SI (Akers & Killackey 1978; Killackey 1985). However, Pidoux & Verley (1979) reported the presence of callosally mediated ipsilateral potentials in the barrel region, and Hayama & Ogawa (1997) recently found callosal connections in a distinct granular zone for the representation of the jaw.

7. IS THE CORPUS CALLOSUM THE ONLY PATHWAY TO CONVEY IPSILATERAL INPUTS?

Manzoni *et al.* (1980) in cats and Conti *et al.* (1986) in monkeys attributed ipsilateral sensory inputs to callosal connections: neurons with the bilateral RFs in the body midline were recorded in bands of cortex containing

dense patches of callosal neurons and terminals. Pidoux & Verley (1979) reported that callosally mediated ipsilateral potentials in the barrel region disappeared after making a lesion in the contralateral sensory cortex. Results of our studies in the hand–finger region (Iwamura *et al.* 1994) are in favour of this notion that after destruction of the homotopic part of the contralateral hemisphere, the neurons with bilateral RFs disappeared. We also demonstrated the presence of patchy zones with dense callosal connections in the crown of the postcentral gyrus (area 2) and the anterior bank of the IPS (areas 2 and 5) of the trunk–shoulder–arm region, where we found a dense distribution of bilateral or ipsilateral neurons (Toda *et al.* 1996). Thus callosal connections are likely to be responsible for ipsilateral inputs to bilateral RF neurons.

Conti *et al.* (1986) pointed out a possibility that the bilaterality of RFs of midline neurons in monkeys depends on thalamocortical input from the ipsilateral ventrobasal complex, because the bilateral RFs crossing the trunk midline were found in the cat ventrobasal neurons (Barbaresi *et al.* 1984). This possibility may not be excluded in monkeys too, but there have been no reports so far on the bilateral representation in the ventrobasal complex of macaque monkeys except for the trigeminal representation (Jones *et al.* 1986; Rausell & Jones 1991). Thalamocortical projections from the ventrobasal complex are most dense to area 3b, less in area 1 or 2, and rare in area 5 (Jones & Powell 1970; Jones *et al.* 1979; Shanks & Powell 1981). Since bilateral or ipsilateral neurons were scarce in area 3b and were found mostly in areas 2 and 5 in our studies, the contribution of this nucleus to the ipsilateral inputs is less likely, at least in those samples found in areas 2 and 5. However, the possibility that very specific projections from certain thalamic association nuclei to the IPS bank is responsible for the bilateral activity cannot be excluded. For example it has been reported that the anterior pulvinar projects to area 2 and the lateral posterior nucleus projects to rostral areas 5 and 7 (Pons & Kaas 1985). Yet there have been no indication at present that neurons in these nuclei have bilateral RFs. The possible contribution of bilateral innervation from the periphery or integration at the sub-cortical levels were also mentioned by others (Schwartz & Fredrickson 1971; Manzoni *et al.* 1989; Armstrong-James & George 1988). Injection of lidocaine into the contralateral hemisphere did not abolish the ipsilateral responses for bilateral RF neurons in the foot region of rats (Armstrong-James & George 1988). Ipsilateral inputs for these neurons are more likely to come through pathways other than the callosal connection since their RFs were also precisely symmetrical: they argued that if final convergence from the two RFs occurs high up the neuroaxis there will have been much opportunity for divergence and convergence at successive relays in the largely independent routes, with greater probability in mismatch of RFs and greater difference in latency.

8. DIVERSE ROLES OF CALLOSAL CONNECTIONS

The role of callosal connections may not be simply for combining excitatory signals of two hemispheres to yield bilateral RFs. Lidocaine injection into the contralateral

hemisphere reduced the neuronal activity in rats suggesting that the afferent sensory transmission to the SI cortex is under subthreshold interhemispheric influences (Shin *et al.* 1997). On the other hand, disinhibitory effects were reported after cooling homotopic cortical sites of the contralateral hemisphere in flying fox or macaque monkeys: cooling of area 3 resulted in the augmentation of activity and enlargement of RFs of neurons in the homotopic cortical part of the opposite hemisphere suggesting that one of the roles of callosal fibres is inhibitory (Clarey *et al.* 1996). Crossed inhibition between the two sides of the periphery was demonstrated in rats also (Armstrong-James & George 1988).

9. NEW INTERPRETATION OF THE MIDLINE FUSION THEORY IN THE SOMATOSENSORY CORTEX

Our studies described above demonstrated that the bilateral representation in the postcentral gyrus is not restricted to the midline structures such as described earlier (Manzoni *et al.* 1989). Manzoni *et al.* (1989) proposed the midline rule to explain the presence of bilateral RF neurons in the SI in analogy with the visual cortex. In the visual cortex, callosal fibres are very sparse or absent in V1, and are remarkable at the border between areas V1 and V2. There, bilateral RFs straddle the vertical meridian, and the callosal connections are responsible for unifying two separated visual hemifields. This formed the basis for the midline fusion theory (Choudhury *et al.* 1965; Berlucchi *et al.* 1967; Berlucchi & Rizzolatti 1968; Hubel & Wiesel 1967; Zeki 1978).

Manzoni *et al.* (1989) confirmed the presence of relatively dense callosal connections in areas 3 and 1 of the SI in the region where they found neurons with bilateral receptive fields on the trunk straddling the body midline. It had been generally accepted that callosal connections are dense in the region for the representation of the axial body parts such as the trunk, head, or oral cavity while they are sparse in the region for the distal extremities and face. However, it was later noted that callosal connections are found even in the finger region, in its caudalmost part such as area 2 and 5. This is exactly the region where we found neurons with bilateral RFs on the finger. In the finger region, this caudal zone could be an analogue of the border zone between V1 and V2 in the visual cortex in that the callosal fibres first appear. Similar coexistence of bilateral RF neurons and callosal termination in the caudalmost part of the postcentral SI was confirmed also in the region for the shoulder/arm representation (Toda *et al.* 1996).

It is important to realize that the vertical meridian includes the retinal fovea. In the somatosensory system the body midline includes the oral cavity, which has the highest spatial resolution power. Hands are also organs with strong spatial resolving ability. Thus our findings that bilateral RF neurons are found also in the hand–finger region encourages us to adopt the midline fusion theory to the somatosensory cortex in analogy to the visual cortical system. Hands are the body parts which are geographically well separated, but when hands are used together, they can easily join at the midline, and work together to manipulate objects, yielding a single unified image of objects. On the other hand, the bilateral

RF neurons activated by the movement of bilateral shoulders and upper arms in various different combinations may represent various postures and movements of the both arms, and part of these activities may also be related to the bilateral use of hands since the use of two hands necessarily requires the cooperation of both shoulders and arms bilaterally. Callosal connections as well as the bilateral activities become more common in the second somatosensory cortex (SII) and the more caudal parietal association cortices. The same is true for the prestriate visual association cortices.

Apart from our demonstration that bilateral representation in the postcentral gyrus is not restricted to midline structures, we confirmed that the midline structures do have bilateral RF neurons. Among the midline structures, the integration of bilateral information may be particularly important for body parts such as the oral cavity, which works bilaterally as one entity in food ingestion. The bilateral RFs across the midline over the dorsal fur of the trunk and occiput may have a special behavioural relevance in quadrupedal mammals such as cats since it is these body parts which detect the upper limit of a hole to pass through. It is possible to assume that bilateral RF neurons are more often found in the representation of the body parts which work bilaterally in a similar behavioural context. Shoulders are not, strictly speaking, structures of the body midline, but they work or move together. Similarly and more importantly, two hands are absolutely far from the midline but work together and deserve being united. On the other hand feet are not used together but mostly used in reciprocal ways. The fact that bilateral neurons with RFs restricted to the toe were less common than those to fingers may reflect such a functional difference between the hands and feet.

10. BILATERAL NEURONS AND HIERARCHICAL INFORMATION PROCESSING IN THE SOMATOSENSORY CORTEX

Iwamura *et al.* (1993) compared RF properties of neurons in different cytoarchitectonic subdivisions of the postcentral finger region and found an increase of RF complexity towards the caudal part of the gyrus. Bilateral hand neurons found by Iwamura *et al.* (1994) in the anterior bank of the IPS had the most complex RFs, suggesting that the bilateral integration of hands takes place at a late stage of the hierarchical processing in the postcentral gyrus. Taoka *et al.* (1998a) demonstrated that (i) the number of bilateral RF neurons in the trunk–shoulder–arm region increases towards the caudal part of the gyrus, (ii) the complexity of bilateral RFs increases towards the caudal part of the gyrus and that there are bilateral neurons with RFs which cover the trunk, shoulder and proximal forelimb.

The bilateral RFs were generally of the most complex type among all neurons found in this gyrus, in either the finger region or the trunk–shoulder–arm region. In the finger region, RFs often covered multiple fingers, and in the shoulder–arm region, RFs often covered both the trunk and arms. Thus they were considered to be at the higher level of the hierarchical chain (Hyvarinen & Poranen 1978; Iwamura *et al.* 1983a,b, 1985a,b, 1993, 1994; Iwamura 1998). Our interpretation is that in the finger

region, the bilaterality, possibly conferred by the callosal connections, is postponed until the very end of the hierarchical processing in this gyrus.

11. COMPARISON WITH BILATERAL RECEPTIVE FIELD NEURONS IN THE SII

In earlier studies, neurons with bilateral RFs were related exclusively to the body midline, either in the oral cavity, the head or trunk but not to the distal part of the extremities or to the vibrissae, and it was postulated that the interhemispheric integration did not take place to keep the purity of the information processing in the distal part of the extremities.

However, activity recorded within the corpus callosum or in the SII contradicted this rule (Innocenti 1986; Innocenti *et al.* 1974), and it was concluded that interhemispheric integration of information from the distal parts of the body could be an attribute of the SII, a hierarchically higher station than the SI, and not of the SI (Manzoni *et al.* 1989). Our studies, however, demonstrated that it occurs in the postcentral gyrus too, as I have just described.

It was known that neurons with bilateral RFs on the hands or arms exist in the SII (Whitsel *et al.* 1969), its surroundings (Robinson & Burton 1980a,b), and in the parietal association cortices (Duffy & Burchfiel 1971; Sakata *et al.* 1973; Mountcastle *et al.* 1975; Burbaud *et al.* 1991; Leinonen *et al.* 1979). All these cortical regions have dense callosal connections. Thus it is interesting to compare the complexity of the RFs of the bilateral neurons found in the postcentral gyrus with those of neurons in the SII or parietal association cortices. We studied the SII region (Taoka *et al.* 1998b), and found neurons with RFs on bilateral hands and feet, bilateral hands and face, and bilateral hands, feet and face etc. These findings indicate that the RF properties of bilateral neurons in the SII are more complex than those found in the postcentral gyrus where bilaterality was confined to a single body part.

The intraparietal zone receives intrinsic corticocortical projections from the more rostral region (Seltzer & Pandya 1986) and projects to the SII and its surrounding region (Pandya & Seltzer 1982). Previous reports (Ogawa *et al.* 1989) as well as our own observations indicate that bilateral RF neurons in the SII region have more complex RF properties than those in the IPS bank supporting another sequential and hierarchical scheme of information processing in the somatosensory system, placing the SII and the surrounding regions at an even higher station than the SI including the IPS bank. On the other hand it is possible that the postcentral region where we found bilateral hand neurons is a part of the caudal somatosensory association cortices.

The region of bilateral hand representation would be the station for integrating information necessary for the cooperative actions of the two hands, which includes the unitary perception of objects explored by the two hands in unison. It would also be the station for interhemispheric information transfer for tactile discrimination. Such transfer is lost after callosal sections (Ebner & Myers 1962; Hunter *et al.* 1975). It has been thought that the SII is the most likely candidate for this function

(Manzoni *et al.* 1989; Berlucchi 1990; Ridley & Ettlinger 1978). The present results indicate that the intraparietal zone may be another candidate for this function. Alternatively the bilateral RF neurons in the trunk and shoulder region may project to more medial parts of the parietal association cortex, areas 5 and 7, where the combinations of limbs and postures or their positions within space are represented (Sakata *et al.* 1973).

REFERENCES

- Akers, R. M. & Killackey, H. P. 1978 Organization of cortico-cortical connections in the parietal cortex of the rat. *J. Comp. Neurol.* **181**, 513–538.
- Armstrong-James, M. & George, M. J. 1988 Bilateral receptive fields of cells in rat SmI cortex. *Exp. Brain Res.* **70**, 155–165.
- Barbaresi, P., Conti, F. & Manzoni, T. 1984 Topography and receptive field organization of the body midline representation in the ventrobasal complex of the cat. *Exp. Brain Res.* **54**, 327–336.
- Berlucchi, G. 1990 Commissurotomy studies in animals. In *Handbook of neuropsychology*, vol. 4 (ed. F. Boller & J. Grafman), pp. 9–46. Amsterdam: Elsevier.
- Berlucchi, G. & Rizzolatti, G. 1968 Binocularly driven neurons in visual cortex of split-chiasm cats. *Science* **159**, 308–310.
- Berlucchi, G., Gazzaniga M. S. & Rizzolatti, G. 1967 Microelectrode analysis of transfer of visual information by the corpus callosum. *Arch. Ital. Biol.* **105**, 583–596.
- Burbaud, P., Doegle, C., Gross, C. & Bioulac, B. 1991 A quantitative study of neuronal discharge in areas 5, 2, and 4 of the monkey during fast arm movements. *J. Neurophysiol.* **66**, 429–443.
- Caminiti, R. & Sbriccoli, A. 1985 The callosal system of the superior parietal lobule in the monkey. *J. Comp. Neurol.* **237**, 85–99.
- Choudhury, B. P., Whitteridge, D. & Wilson, M. E. 1965 The function of the callosal connections of the visual cortex. *Q. J. Exp. Physiol.* **50**, 214–219.
- Clarey, J. C., Tweedale, R. & Calford, M. B. 1996 Interhemispheric modulation of somatosensory receptive fields: evidence for plasticity in primary somatosensory cortex. *Cerebr. Cortex* **6**, 196–206.
- Conti F., Fabri, M. & Manzoni, T. 1986 Bilateral receptive fields and callosal connectivity of the body midline representation in the first somatosensory area of primates. *Somatosens. Res.* **3**, 273–289.
- Dreyer, D. A., Loe, P. R., Metz, C. B. & Whitsel, B. L. 1975 Representation of head and face in postcentral gyrus of the macaque. *J. Neurophysiol.* **38**, 714–733.
- Duffy, F. H. & Burchfiel, J. L. 1971 Somatosensory system: organizational hierarchy from single units in monkey area 5. *Science* **172**, 273–275.
- Ebner, F. F. & Myers, R. E. 1962 Corpus callosum and the interhemispheric transmission of tactual learning. *J. Neurophysiol.* **25**, 380–391.
- Gould III, H. J. & Kaas, J. H. 1981 The distribution of commissural terminations in somatosensory areas I and II of the grey squirrel. *J. Comp. Neurol.* **196**, 489–504.
- Hayama, T. & Ogawa, H. 1997 Regional differences of callosal connections in the granular zones of the primary somatosensory cortex in rats. *Brain Res. Bull.* **43**, 341–347.
- Hubel, D. H. & Wiesel, T. N. 1967 Cortical and callosal connections concerned with the vertical meridian of visual fields in the cat. *J. Neurophysiol.* **30**, 1561–1573.
- Hunter, M., Ettlinger, G. & Maccabe, J. J. 1975 Intermanual transfer in the monkey as a function of amount of callosal sparing. *Brain Res.* **93**, 223–240.
- Hyvarinen, J. & Poranen, A. 1978 Receptive field integration and submodality convergence in the hand area of the post-central gyrus of the alert monkey. *J. Physiol.* **257**, 199–227.
- Innocenti, G. M. 1986 General organization of callosal connections in the cerebral cortex. In *Cerebral cortex. 5. Sensory-motor areas and aspects of cortical connectivity* (ed. E. G. Jones & A. Peters). New York: Plenum.
- Innocenti, G. M., Manzoni, T. & Spidalieri, G. 1974 Patterns of the somesthetic messages transferred through the corpus callosum. *Exp. Brain Res.* **19**, 447–466.
- Iwamura, Y. 1998 Hierarchical somatosensory processing. *Curr. Opin. Neurobiol.* **8**, 522–528.
- Iwamura, Y. & Tanaka, M. 1996 Representation of reaching and grasping in the monkey postcentral gyrus. *Neurosci. Lett.* **214**, 147–150.
- Iwamura, Y., Tanaka, M., Sakamoto, M. & Hikosaka, O. 1983a Functional subdivisions representing different finger regions in area 3 of the first somatosensory cortex of the conscious monkey. *Exp. Brain Res.* **51**, 315–326.
- Iwamura, Y., Tanaka, M., Sakamoto, M. & Hikosaka, O. 1983b Converging patterns of finger representation and complex response properties of neurons in area 1 of the first somatosensory cortex of the conscious monkey. *Exp. Brain Res.* **51**, 327–337.
- Iwamura, Y., Tanaka, M., Sakamoto, M. & Hikosaka, O. 1985a Diversity in receptive field properties of vertical neuronal arrays in the crown of the postcentral gyrus of the conscious monkey. *Exp. Brain Res.* **58**, 400–411.
- Iwamura, Y., Tanaka, M., Sakamoto, M. & Hikosaka, O. 1985b Vertical neuronal arrays in the postcentral gyrus signaling active touch: a receptive field study in the conscious monkey. *Exp. Brain Res.* **58**, 412–420.
- Iwamura, Y., Tanaka, M., Sakamoto, M. & Hikosaka, O. 1993 Rostrocaudal gradients in neuronal receptive field complexity in the finger region of alert monkey's postcentral gyrus. *Exp. Brain Res.* **92**, 360–368.
- Iwamura, Y., Iriki, A. & Tanaka, M. 1994 Bilateral hand representation in the postcentral somatosensory cortex. *Nature* **369**, 554–556.
- Iwamura, Y., Iriki, A., Tanaka, M., Taoka, M., Toda, T. 1996 Bilateral receptive field neurons in the postcentral gyrus: two hands meet at the midline. In *Pergamon studies in neuroscience. Perception, memory and emotion: frontier in neuroscience* (ed. T. Ono, B. L. McNaughton, S. Molotchnikoff, E. T. Rolls & H. Nishijo), pp. 33–44. Oxford, UK: Elsevier.
- Jones, E. G. & Hendry, S. H. C. 1980 Distribution of callosal fibers around the hand representations in monkey somatic sensory cortex. *Neurosci. Lett.* **19**, 167–172.
- Jones, E. G. & Powell, T. P. S. 1968 The commissural connexions of the somatic sensory cortex in the cat. *J. Anat.* **103**, 433–455.
- Jones, E. G. & Powell, T. P. S. 1969 Connections of the somatic sensory cortex of the rhesus monkey. II. Contralateral cortical connections. *Brain* **92**, 717–730.
- Jones, E. G. & Powell, T. P. S. 1970 Connections of the somatic sensory cortex of the rhesus monkey. III. Thalamic connections. *Brain* **93**, 37–56.
- Jones, E. G., Coulter, J. D. & Wise, S. P. 1979 Commissural columns in the sensory-motor cortex of monkeys. *J. Comp. Neurol.* **188**, 113–136.
- Jones, E. G., Schwark, H. D. & Callahan, P. A. 1986 Extent of the ipsilateral representation in the ventral posterior medial nucleus of the monkey thalamus. *Exp. Brain Res.* **63**, 310–320.
- Karol, E. A. & Pandya, D. N. 1971 The distribution of the corpus callosum in the rhesus monkey. *Brain* **94**, 471–486.
- Killackey, H. P. 1985 The organization of somatosensory callosal projections. A new interpretation. In *Epilepsy and corpus callosum* (ed. A. G. Reeves), pp. 41–53. New York: Plenum.

- Killackey, H. P., Gould III, H. J., Cusick, C. G., Pons, T. P. & Kaas, J. H. 1983 The relation of corpus callosum connections to architectonic fields and body surface maps in sensorimotor cortex of new and old world monkeys. *J. Comp. Neurol.* **219**, 384–419.
- Leinonen, L., Hyvarinen, J., Nyman, G. & Linnankoski, I. 1979 Functional properties of neurons in lateral part of associative area 7 in awake monkeys. *Exp. Brain Res.* **34**, 299–320.
- Manzoni, T., Barbaresi, P., Bellardinelli, E. & Caminiti, R. 1980 Callosal projections from the two body midlines. *Exp. Brain Res.* **39**, 1–9.
- Manzoni, T., Barbaresi, P., Conti, F. & Fabri, M. 1989 The callosal connections of the primary somatosensory cortex and the neural bases of midline fusion. *Exp. Brain Res.* **76**, 251–266.
- Mountcastle, V. B., Lynch, J. C., Georgopoulos, A., Sakata, H. & Acuna, C. 1975 Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. *J. Neurophysiol.* **38**, 871–908.
- Ogawa, H., Ito, S. & Nomura, T. 1989 Oral cavity representation at the frontal operculum of macaque monkeys. *Neurosci. Res.* **6**, 283–298.
- Pandya, D. N. & Seltzer, B. 1982 Intrinsic connections and architectonics of posterior parietal cortex in the rhesus monkey. *J. Comp. Neurol.* **204**, 196–210.
- Pandya, D. N. & Vignolo, L. A. 1969 Interhemispheric projections of the parietal lobe in the rhesus monkey. *Brain Res.* **15**, 49–65.
- Pidoux, B. & Verley, R. 1979 Projections on the cortical somatic I barrel subfield from ipsilateral vibrissae in adult rodents. *EEG Clin. Neurophysiol.* **46**, 715–726.
- Pons, T. P. & Kaas, J. H. 1985 Connections of area 2 of somatosensory cortex with the anterior pulvinar and subdivisions of the ventroposterior complex in macaque monkeys. *J. Comp. Neurol.* **240**, 16–36.
- Rausell, E. & Jones, E. G. 1991 Histochemical and immunocytochemical compartments of the thalamic VPM nucleus in monkeys and their relationship to the representational map. *J. Neurosci.* **11**, 210–225.
- Ridley, R. M. & Ettlinger, G. 1978 Further evidence of impaired tactile learning after removals of the second somatic sensory projection cortex (SII) in the monkey. *Exp. Brain Res.* **31**, 475–488.
- Robinson, C. J. & Burton, H. 1980a Somatotopic organization in the second somatosensory area of *M. fascicularis*. *J. Comp. Neurol.* **192**, 043–067.
- Robinson, C. J. & Burton, H. 1980b Organization of somatosensory receptive fields in cortical areas 7b, retroinsula, postauditory and granular insula of *M. fascicularis*. *J. Comp. Neurol.* **192**, 069–092.
- Sakata, H., Takaoka, Y., Kawarasaki, A. & Shibutani, H. 1973 Somatosensory properties of neurons in the superior parietal cortex (area 5) of the rhesus monkey. *Brain Res.* **64**, 85–102.
- Schwartz, D. W. F. & Fredrickson, J. M. 1971 Tactile direction sensitivity of area 2 oral neurons in the rhesus monkey cortex. *Brain Res.* **27**, 397–401.
- Seltzer, B. & Pandya, D. N. 1986 Posterior parietal projections to intraparietal sulcus of the rhesus monkey. *Exp. Brain Res.* **62**, 459–469.
- Shanks, M. F. & Powell, T. P. S. 1981 An electron microscopic study of the termination of thalamocortical fibres in areas 3b, 1 and 2 of the somatic sensory cortex in the monkey. *Brain Res.* **218**, 35–47.
- Shanks, M. F., Rockel, A. J. & Powell, T. P. S. 1975 The commissural fibre connections of the primary somatic sensory cortex. *Brain Res.* **98**, 166–171.
- Shanks, M. F., Pearson, R. C. A. & Powell, T. P. S. 1985 The callosal connections of the primary somatic sensory cortex in the monkey. *Brain Res. Rev.* **9**, 43–65.
- Shin, H.-C., Who, C.-K., Jung, S.-C., Oh, S., Park, S. & Sohn, J.-H. 1997 Interhemispheric modulation of sensory transmission in the primary somatosensory cortex of rats. *Neurosci. Lett.* **230**, 137–139.
- Taoka, M., Toda, T. & Iwamura, Y. 1998a Representation of the midline trunk, bilateral arms, and shoulders in the monkey postcentral somatosensory cortex. *Exp. Brain Res.* **123**, 315–322.
- Taoka, M., Toda, T., Iriki, A., Tanaka, M. & Iwamura, Y. 1998b Hierarchical organization of bilateral neurons in the second somatosensory cortex of awake macaque monkeys. *Soc. Neurosci. Abstr.* **24**, 1381.
- Taoka, M., Toda, T., Iriki, A., Tanaka, M. & Iwamura, Y. 1999 Bilateral representation of the hindlimb in the postcentral somatosensory cortex of awake macaque monkeys. *Soc. Neurosci. Abstr.* **25**, 2196.
- Toda, T., Taoka, M. & Iwamura, Y. 1996 Transcallosal connections of the upperarm/shoulder region of the monkey postcentral somatosensory cortex. *Jap. J. Physiol.* **46**(Suppl.), S159.
- Whitsel, B. L., Petrucelli, L. M. & Werner, G. 1969 Symmetry and connectivity in the map of the body surface in somatosensory area II of primates. *J. Neurophysiol.* **32**, 170–183.
- Zeki, S. 1978 Functional specialization in the visual cortex of rhesus monkey. *Nature* **274**, 423–428.

