

Hierarchical somatosensory processing

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Recent studies of the postcentral and additional somatosensory cortices support a hierarchical scheme for information processing. In the postcentral gyrus, the complexity of receptive field properties increases with caudal progression from area 1. It has been reported that the anterior bank of the intraparietal sulcus, the caudalmost part of the postcentral gyrus, is responsible for the systematic integration of bilateral body parts, as well as of somatic and visual information.

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Abbreviations

fMRI	functional magnetic resonance imaging
IPS	intraparietal sulcus
PET	positron emission tomography
RF	receptive field
SI	first somatosensory cortex
SII	second somatosensory cortex
SEF	somatosensory evoked magnetic field
SEP	somatosensory evoked potential

Introduction

In this review, I will describe the hierarchy involved in information processing within the first somatosensory cortex (areas 3a, 3b, 1 and 2) and area 5 in the postcentral gyrus. I will also discuss the second somatosensory cortex (SII) and surrounding areas in the lateral sulcus, and area 7b in the lateral parietal association cortex.

While recording from the somatosensory cortex, there is a systematic increase in the complexity of neuronal receptive field (RF) properties when the recording site is moved caudally. It is assumed that this increase in complexity results from the convergence of multiple inputs onto single neurons via serial cortico-cortical connections and additional thalamic projections. The presence of hierarchical processing in the postcentral somatosensory cortex was first suggested by Duffy and Burchfiel [1] and by Sakata *et al.* [2] on the basis of single-unit recording studies in the monkey. They showed that RFs of area 5 neurons (both skin and joint) tend to be larger and more complex than those in the first somatosensory cortex (SI), and postulated that the complexity of area 5 neurons was attributable to the convergence of simple RF information from neurons in SI. Later, Hyvarinen and Poranen [3] showed that the increase in the size and complexity of cutaneous RFs does in fact start in area 1.

Complex types of neuronal responses have been found in areas 1 and 2 [4,5], and overlapping representation of different digits has been reported in area 2 [6]. Since then, much knowledge has accumulated to support a hierarchical scheme in this cortical region [7,8]. The serial cortico-cortical relationships between these cortical areas have been well documented anatomically [8–13].

Here, I will briefly describe the results of these earlier studies, as well as the results of more recent studies that lend support to a hierarchical scheme. I will also try to interpret the results from other studies in the somatosensory cortex in light of this scheme. In my opinion, many of the recent important papers were published in 1996.

Receptive field complexity increases along the anterior–posterior axis of the postcentral gyrus

In SI of primates, direct thalamocortical afferent fibers from the ventrobasal complex project mainly to either area 3b (cutaneous inputs) or area 3a (deep inputs). As area 3a is morphologically a transitional zone from the motor to the sensory cortex, it is difficult to define anatomically. A recent study in human brain has demonstrated that the cytoarchitectonic border between areas 3a and 4 coincides with changes in the distribution patterns of various neurotransmitters and that the ligand-binding patterns of areas 3a and 3b are similar, supporting the somatosensory nature of area 3a [14•].

In the digit region of area 3b, functionally unique parts of digits (i.e. tips, ventral glabrous surfaces, and dorsal surfaces) are represented separately and independently from each other, forming different subdivisions of area 3b [15]. In the subdivision representing digit tips, the RFs are smaller and more variable than in other subdivisions. The interdigital integration seen in the more caudal parts of the gyrus originates from an initial categorization within area 3 [16,17]. A recent anatomical study [18] challenges the hypothesis that the interareal connections directly create RF enlargement, particularly in area 1, because the connections between areas 3b and 1 are weaker than intrinsic ones within area 3b. It should be pointed out, however, that there may be regional differences in extent of interareal connections, as interdigital integration in area 1 occurs more often for ulnar digits than for radial ones [19].

In the caudal part of the gyrus, there are unique neurons that respond selectively to specific features of a stimulus [4,5,20]. In the monkey, some of these neurons are activated better or solely by active hand movements, such as reaching [21]. Tremblay *et al.* [22] have reported that

even though texture-related neurons can be observed in areas 3b, 1 and 2, those in area 2 have no apparent peripheral RFs when tested with a hand-held probe, yet they signal differences in surface texture.

Increase in RF complexity toward the caudal part has also been reported in the proximal arm/trunk region [23**]. Even in cats, the RFs of neurons in area 2 are generally larger and the response characteristics are often more complex than those in area 3 [24,25].

Observations in favor of serial hierarchical processing

The response latency of neurons to a vibration stimulus is longer in area 2 neurons than in area 3 or 1 neurons [26]. Dipoles that generate P7, P10, N10, P12, P18 (N and P indicate positive and negative polarity; the numbers indicate the approximate peak latency in milliseconds) somatosensory evoked potentials (SEPs) in response to median nerve stimulation in anesthetized monkeys have been located in the thalamus and areas 3, 1, 2 and 5, respectively [27].

Dalezios *et al.* [28] found that the metabolic activity of SI during a visually guided reaching task is most intense in area 3; they argue that it is because the representation of body parts is most intense and clearcut in area 3.

Ablation of area 3 impairs performance in all somesthetic tasks, whereas ablation of area 1 or 2 impairs only discrimination of roughness or angles, respectively [29]. Injection of muscimol into area 3 results in earlier and more severe deficits in manipulative behavior [30]. Ablations of specific parts of hand representations (e.g. digits 1 and 2) in areas 3a and 3b immediately deactivate neurons in the corresponding part of the hand representation in area 1 [31]. Direct thalamic inputs to area 1 should remain but apparently do not work to activate area 1 neurons after the peripheral stimulation. In contrast, ablation of the regions in area 1 representing digits 1 and 2 has no detectable effect on the activity of neurons in the corresponding regions of area 3. Zainos *et al.* [32] found that removal of SI affects an animal's ability to categorize stimulus speed but does not affect its capacity to detect the stimuli, suggesting that either serial or parallel processing operates, depending on the task.

Diversity in the receptive field of cortical neurons along a perpendicular array

It has been pointed out that the RFs of neighboring neurons diversify in conjunction with an increase in RF size and the complexity of neuronal properties in the crown of the postcentral gyrus, areas 1 and 2 [33]. Fovorov and Kelly [34] used a model cortical network to study the diversity of a cell's complex temporal behaviors evoked by peripheral stimuli, and they demonstrated that the diversity arises even among neurons with similar inputs. Cross-correlation analysis revealed laminar differences in

thalamo-cortical interactions in the cat somatosensory cortex [35], providing a theoretical basis for an earlier finding showing that neurons in deep layers tend to have larger and more complex RFs [33].

Human studies consistent with the serial and hierarchical scheme within the postcentral gyrus

Among the short latency SEPs of humans, the time differences and spatial distribution of various components are explained by the serial and hierarchical information processing based on cortico-cortical connections [36]. Analysis of cortical somatosensory evoked magnetic fields (SEFs) in humans has indicated that occlusion or inhibition is greater in N20 than in P25 when two digits are stimulated simultaneously: N20 is generated in area 3b, whereas P25 is generated in area 1. Thus, the weaker interdigital interaction in P25 has been interpreted as being related to the greater convergence of digits in area 1 [37].

Plastic changes in the representation of digits

Multidigit RFs have been observed in area 3b of owl monkeys trained extensively to use three fingers together, but not in untrained animals [38]. Similarly, the size of the cortical area representing the fingers of the left hand is larger in string players than in controls, as measured by magnetic source imaging [39]. Blind people who use three fingers together to read Braille frequently misperceive which of the fingers actually touches the text [40]. Using magnetic source imaging, Sterr *et al.* [40] found that Braille readers have an expanded and dislocated SI hand representation. Using functional magnetic resonance imaging (fMRI), which has better spatial resolution, Kurth *et al.* [41*] demonstrated somatotopic representation of digits (II and V) in area 3b in 8 out of 20 naive human subjects. Reversed or overlapped representation of these fingers were observed in certain subjects. It is not clear whether the irregularity in somatotopy is attributable to some unidentified plastic changes based on individual experiences. It will be interesting to discover how these manipulations affect the neuronal activity in the more caudal areas of the postcentral gyrus, where RFs covering multifingers are common (and thus the somatotopy is irregular even in naive condition) and are supposed to be more dynamic and plastic in information processing.

SII: a higher level of processing?

The notion that SII is higher than SI in hierarchy was proposed on the basis of their anatomical relationships: SI sends projections to SII, while SII projects back to the superficial layers of SI [8,42,43]. Physiological studies have shown that compared to SI neurons, SII neurons tend to have larger and more complex RFs, including bilateral ones [8]. SII has been viewed as being composed of at least two parts [42,44], with area 3b having greater connections to the anterior part [42]; however, it is not yet known whether there is a hierarchical relationship between the

two parts of SII with regard to the RF properties of their neurons. Two representations of the hand have been demonstrated by recording SEPs and SEFs directly from the cortical surface of human perisylvian cortex (SII) [45].

Jiang *et al.* [46•] have shown that neurons in SII signal a change in texture but not its magnitude; thus, SII neurons are of a higher-order than SI neurons, which show a graded change in discharge when the spatial periods of test gratings are increased. Huttunen *et al.* [47] recorded SEFs in response to median nerve stimulation so as to measure changes in responsiveness during finger movements. The changes did not parallel those in SI, suggesting that the changes depended on additional modulatory inputs to SII rather than those from SI. The long latency component of SEF in response to stimulation of the posterior tibial nerve is affected by movement imagery of a toe in bilateral SII [48]. Painful stimulation first activates contralateral SI and then bilateral SII, although it is not clear whether SII receives signals through SI or directly from the thalamus [49]. SEFs in response to median nerve stimulation in SII are enhanced during thenar muscle contraction, possibly by decreasing inhibition from SI [50]. Enhanced SII activation might be related to the tuning of SII neurons towards the relevant tactile input arising from the muscle [50]. On the other hand, neural activity in SII of marmoset monkey and cat is not completely abolished by reversible inactivation of SI [51,52], leading to the suggestion that the strict serial processing scheme is in need of revision.

Attention to tactile objects alters responsiveness of SI and SII neurons

In monkeys, some SI or SII neurons are activated only when the animal actually touches an object [21,53,54]. The active process may involve mechanisms of efference copy or motor set; in addition, attentional processes may facilitate neuronal activation. Recent studies have identified neurons in monkey somatosensory cortex with enhanced sensitivity and selectivity for stimuli to which an animal is directing its attention [53–57,58••]. The authors argue that SII, rather than SI, plays a role in tactile attention because a larger number of neurons in SII is related to attention.

Burton *et al.* [58••] found that tactile and auditory cues correlate with enhanced or suppressed average firing rates of SII or area 7b neurons (45–50% of neurons) in response to vibrotactile stimuli. These modulations are consistent with a model of possible neural mechanisms associated with selective attention and confirm earlier suggestions that SII plays a role in tactile attention. The authors also suggest that area 7b might play a similar role.

Iriki *et al.* [59] have recently reported a correlation between neuronal activity in the postcentral gyrus and pupil size, which is used as an indicator of the intensity and time course of attention. In many neurons, sensitivity to passive skin stimulation changes in parallel with pupil size,

suggesting that the activity of these neurons is under the control of attention. These neurons were found in areas 3, 1 and 2. The same monkeys were trained for a button-pushing task. The activity of a particular group of neurons was enhanced together with pupil size when the monkeys attended to keep a distance between the digits and the button to wait a go-signal to push a button. Most of the attention-related neurons of the latter type were recorded in areas 2 and 5, in the anterior bank of the intraparietal sulcus (IPS), some in area 1, but none in area 3.

Bilateral representation of the hand, upperarms, shoulders and the trunk in the postcentral gyrus

It has long been thought that digits are represented only in the contralateral side of the postcentral somatosensory cortex and that the integration of bilateral digits takes place in SII [60–62]. However, there is a substantial number of neurons with bilateral or ipsilateral RFs clustered in the caudalmost part (areas 2 and 5) of the postcentral digit region [63]. Bilateral RFs are surprisingly symmetrical and large—the largest and the most complex types represent the hands; therefore, they support the notion that the highest level of processing takes place in this gyrus. Bilateral RFs disappear after lesioning the opposite hemisphere, indicating their dependence on callosal connections. Bilateral neurons for the upperarm and trunk have also been found in the more medial part of the postcentral gyrus [23••,64]. Previous studies have demonstrated the existence of bilateral neurons with RFs for the skin of the trunk across the midline [61] and for the bilateral joints [1,2,65]. Taoka *et al.* ([23••]; M Taoka, T Toda, Y Iwamura, *Soc Neurosci Abstr* 1997, 23:1007) have shown that the RF properties of bilateral neurons are more complex in the anterior bank of IPS (the majority in area 5) than in the crown of the postcentral gyrus, suggesting the presence of a hierarchy among these bilateral neurons.

In rats, injection of lidocaine into one hemisphere reduces neuronal activity in the contralateral hemisphere [66], suggesting that afferent sensory transmission to the SI cortex is under subthreshold interhemispheric influences. In the flying fox, disinhibitory effects have been reported after the lesion of homotopic cortical sites of the contralateral hemisphere; the RFs expanded after the lesion [67], suggesting that the callosal influences may not be solely excitatory.

Bilateral representation of hands in human SI, SII and posterior parietal cortex

Bilateral projections from hands, feet and lips have been characterized in human SI and posterior association cortex by measuring SEFs [47–49,68–72] or SEPs [73]. After median nerve stimulation, ipsilateral SEPs are lower in amplitude and longer in latency than contralateral ones [73]. The ipsilateral/contralateral latency difference is too short for it to occur through callosal connections.

Ipsilateral activation by tactile stimuli has been observed using positron emission tomography (PET) [74•] and fMRI [37,75,76]. Kakigi and colleagues [71,77] report that the contralateral hand interferes with the middle latency component of SEF in SI. It is possible that bilateral integration of tactile pattern recognition takes place at a higher level in the hierarchy [78]. An interesting recent paper by Canavero [79] reports a case of bilateral pain disorder.

Convergence of somatosensory and visual inputs in the postcentral gyrus

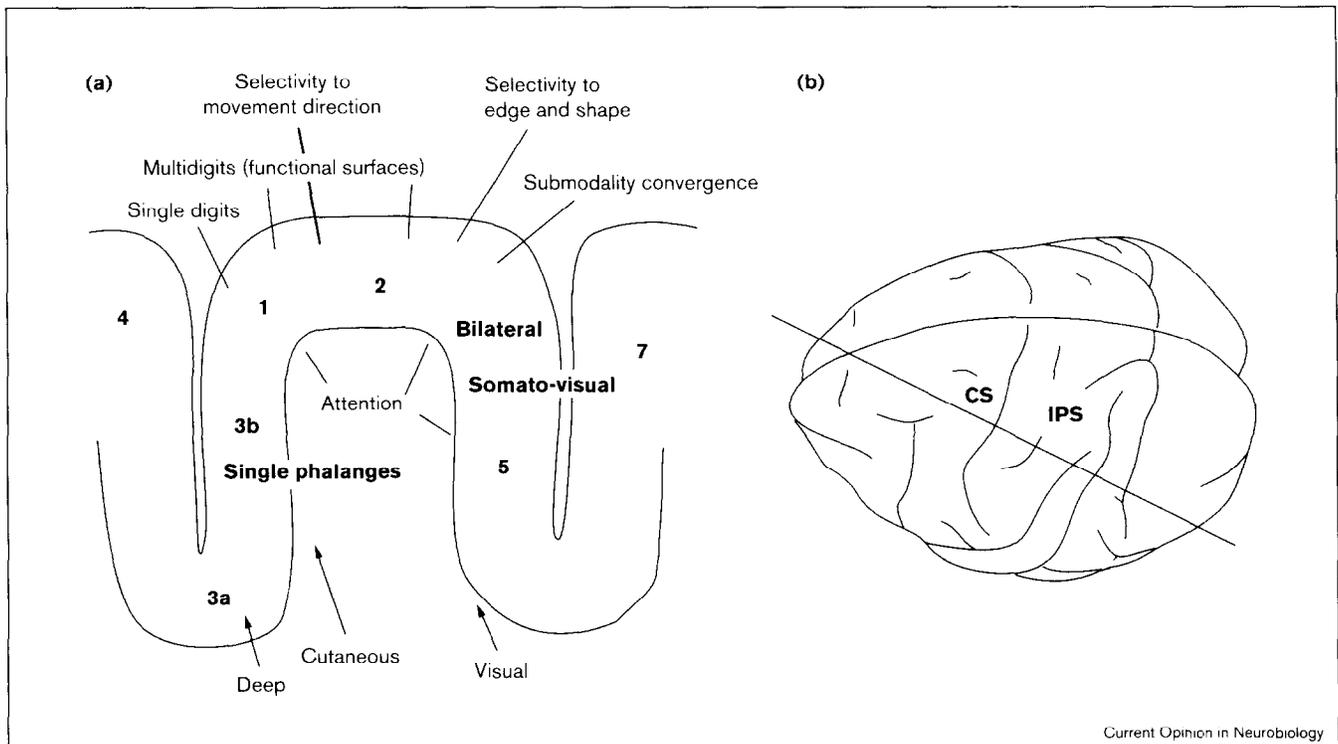
Iriki *et al.* [80] found that a substantial number of neurons in the arm/hand region of monkey postcentral gyrus is activated by both somatosensory and visual stimulation. The effective visual stimulus was to move an object or the experimenter's hand in the space over or near the somatosensory RF of the neurons. Visual responses were dependent on the monkey's arm position, or visual stimuli presented within the reaching distance of the hand evoked responses. After the monkey held a rake and repeated food-retrieving actions for 5 min, the visual RF became elongated along the axis of the tool, as if the image of the tool was incorporated into that of the hand. Responses to somatosensory stimulation were not modified after

tool-use. Neurons whose visual RFs were modified after tool use were found most frequently in the anterior bank of the IPS, down to its very fundus, but some were even found in the crown of the gyrus, area 2. The presence of somatosensory/visual bimodal neurons had been reported previously in VIP (ventral intraparietal) cortex, the fundus of the IPS [81], and area 7b [82], but not in the anterior bank of the IPS. Neuronal activity in the somatosensory cortex possibly reacting to visual stimuli has also been found in a cross-modal memory task [83].

Serial or parallel processing of tactile information in humans: beyond SI and SII

Knecht *et al.* [84] found a correlation between deficits in two-point discrimination and a loss of SEP N20 in patients with parietal cortical lesions. The data suggested that a serial processing of somesthetic information underlies the perception of different haptic features in humans. Exceptions to this are sensing temperature, pain and vibration, which are processed in parallel in various areas, including subcortical structures. In a recent PET study, Roland *et al.* [85] concluded that separate processing streams exist for roughness discrimination and for shape and length discrimination within the parietal cortex.

Figure 1



Hierarchical processing in the postcentral gyrus. (a) Lateral view of a schematized histological section of the postcentral gyrus, with various RF characteristics assigned to different sites. There is a hierarchical order in the rostro-caudal direction relating to the complexity of RF characteristics. The numbers represent cytoarchitectonic areas of Brodmann. (b) A dorsal view of monkey cortex, illustrating the position of the postcentral gyrus between the central sulcus (CS) and the intraparietal sulcus (IPS). The diagonal line indicates the direction of the nearly sagittal histological sectioning shown in (a).

SEFs evoked by median nerve stimulation have been recorded in SI, posterior parietal, parietal opercular (SII), and frontal regions [86]. On the basis of latency differences, it is assumed that the higher-order areas receive signals from SI through serial feedforward projections. Manguiere and Isnard [87] report that all known cases of tactile agnosia also have sensory disturbances or problems with naming. These results will need to be addressed in light of the observations by Caselli [88]. Moreover, these higher-order disorders are accompanied by abnormalities in SEP N20 or P27, indicating a serial processing in the postcentral gyrus.

Platz [89] recently reported a patient with a lesion in the right postcentral and supramarginal gyrus, who had difficulty in tactile object recognition but had no primary motor or sensory impairment. Reed *et al.* [90] examined a similar patient and concluded that tactile shape perception can be disrupted independent of general or tactile spatial ability, manual shape exploration, or even the precise perception of metric length in the tactile modality.

Conclusions

Figure 1 summarizes the major neurophysiological findings described above, in that potential RF characteristics have been assigned loosely to various portions of the postcentral gyrus. The hierarchical structure of the gyrus is evident, as the complexity increases along the its rostro-caudal axis. The hierarchical scheme was proposed nearly 30 years ago in the somatosensory cortex on the basis of neurophysiological studies (see [1–3]), but it has been developed much slower than in the visual system because it was set against the prevailing scheme of parallel and segregated representation of different submodalities in different cytoarchitectonic subdivisions of the postcentral gyrus. In my opinion, the hierarchical scheme has made a more substantial contribution to our understanding of information processing in this cortical region because it can be applied to the interrelationship between SI and SII as well as to other cortical regions; however, more studies need to focus on SII.

Recently, there have been many studies performed in human subjects using new imaging techniques. Although their findings will clearly contribute to our understanding of somatosensory processing, I would like to emphasize the importance of making isolated single-unit recordings in awake animals and of studying the information processed by single neurons.

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