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## Opinion

## Somatosensation in the Brain: A Theoretical Re-evaluation and a New Model

Edward H.F. de Haan<sup>1,3,5,\*</sup> and H. Chris Dijkerman<sup>2,4,5,@</sup>

The somatosensory system is important for many functions, such as tactile recognition, the perception of our body, and motor actions. We present a comprehensive review of the human and animal literature on somatosensory processing over the past 10 years and evaluate how well existing models can accommodate the new observations. Based on these observations and a survey of the brain structures involved in somatosensation, we suggest that a new model is needed that describes multiple networks involved in separate subfunctions. These networks are highly interconnected and often multimodal in nature. The model includes basic somatosensory processing and five higher-order networks involved in haptic object recognition and memory, body perception, body ownership, affective processing, and action.

## The Role and Early Theories of Somatosensory Processing

Somatosensory processing is central to life; a touch on the shoulder, a soft stroke on the hand – both can say more than words. We use it to be aware of the parts that belong to our body, it has an important social function, and it is crucial for socioemotional development. It is also important for almost every activity during our daily life and forms the basis of all of our motor actions. Furthermore, somatosensory processing allows us to recognize with ease different objects based on touch alone (**haptic object recognition**; see [Glossary](#)). Thus, the processing of touch, temperature, pain, and proprioception are important for survival, for efficient interaction with the environment, and for emotional and social functioning.

A central question is how the somatosensory system is organised to perform these different functions. While the visual system has traditionally received the most attention, the functional and neural organisation of the somatosensory system is increasingly being investigated and the complexity of the system is becoming clearer. About a decade ago, the physiology of the somatosensory input to the brain had been mapped to a detailed level (e.g., [1,2]; [Box 1](#)) and several ideas about cortical processing had been formulated [3]. Single-case studies [4,5] hinted at the possibility of very selective deficits in somatosensory processing. Inspired by this work, as well as studies of bodily illusions and psychophysical and neuroimaging investigations with healthy subjects, several models that specified the separable functional entities and their neuroanatomical correlates were put forward.

## A Need to Revise Previous Models

A central theme in these models, of which ours [6] was one, concerned the idea of two separate body representations: (i) **'body image'**, the perceptual and semantic (related to knowledge about the structure and shape of the body) representation; and (ii) **'body schema'**, which provides a somatosensory basis for action. This distinction was further developed according to the two-pathway model for vision with strict separation in terms of consciousness, memory, spatial reference frames, and susceptibility to illusions. These models have provided a basis for

## Highlights

This Opinion article presents a comprehensive review of the human and animal literature on somatosensory processing of the past 10 years.

We propose a new model of the functional architecture of somatosensory processing, entailing several dedicated pathways or networks subserving different functions that rely (partly) on somatosensory information.

In contrast to previous models, these pathways or networks are thought to be much less independent or 'information encapsulated' and much more multimodal in nature.

The model includes a 'cylinder block' of basic somatosensory processing and higher-order networks involved in: (i) haptic object recognition and memory; (ii) body perception; (iii) body ownership; (iv) affective processing; and (v) action.

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**Box 1. Physiology of the Somatosensory System**

Inputs from peripheral receptors in the skin, tendons, muscles, and joints ascend through the dorsal column in the spinal cord and subsequently arrives in the medulla where they decussate and terminate in the ventral posterior lateral nucleus (VPL) of the thalamus [85]. A second ascending system, the anterolateral system, mainly deals with thermal and noxious stimuli and some tactile inputs. The anterolateral system also projects to the thalamus. Most somatosensory information enters the cerebral cortex through projections from the VPL to the anterior parietal cortex (APC) [86]. The APC contains several somatotopic maps of the contralateral half of the body [87] with one somatosensory submodality dominating the input to each area as evidenced by neurophysiological and lesion studies. In addition, the c-tactile system contains low-threshold mechanoreceptors that are connected to slow conducting unmyelinated fibres [69]. Interestingly, neurophysiological and neuroimaging studies suggest that input from c-tactile fibres first enters the cortex in the posterior insula [88].

In the early stages of cortical processing, the neuronal responses represent the characteristics of stimuli applied to peripheral nerves relatively accurately [89]. Neurons situated further from the thalamic input have more complex response properties, which suggests that advanced processing occurs. Processing in the APC reflected the perceived rather than the physical location of peripheral stimuli [90].

The APC maintains reciprocal connections with the secondary somatosensory cortex (SII) [91], although the projections from the APC to SII are more important than those from SII to the APC [91]. Neurons in SII have greater stimulus selectivity, larger receptive fields, and reduced modality specificity and respond to ipsilateral as well as contralateral stimulation [92]. The SII is reciprocally connected with the granular and dysgranular fields of the insula [93]. Neurophysiological recordings from the granular insula in rhesus monkeys showed that a major portion of this area is exclusively devoted to somatic processing [94]. SII has additional projections to posterior parietal area 7b, both ipsilaterally and contralaterally, and the premotor cortex in the same hemisphere [93,95]. In monkeys, the posterior parietal cortex (PPC) also receives direct connections from the APC. Brodmann area 5 (BA5) (superior parietal cortex) receives input from areas BA1 and 2 [96,97], whereas area BA7b (inferior parietal cortex) receives direct input from area BA1 [96]. Several thalamic nuclei also project directly to SII [98] and to different parts of the PPC [86]. Major cortical outputs from the PPC project back to SII and to the premotor cortex, the limbic cortex, and the superior temporal sulcus [3].

studies of the somatosensory system (Box 2). While some recent findings are consistent with these earlier proposals [7,8], other findings are not. In particular, there is a growing realization that the perception–action dichotomy may be a too-restrictive distinction. This issue is currently

**Box 2. The Functional Architecture**

A decade ago, several models for somatosensory processing were put forward, such as those by Longo [99], Serino and Haggard [25], and Gallace and Spence [14]. These models highlighted different aspects but converged on the idea that there are different processing streams for functions such as tactile recognition and action planning. As an example, we briefly describe the model that we postulated [6]. This model was based on Paillard's [100] original distinction between the 'body schema' as an internal representation for action and a separate 'body image' involved in perceptual identification of body features, Berlucchi and Aglioti's [51] proposal for a set of different body representations in the brain, and the idea of Mishkin and colleagues [39,93] of a pathway from the APC via SII to the posterior insula for perceptual learning and recognition. Following the basic principle developed for modelling the visual system [101], it was suggested that there are separate routes for processing somatosensory information for action planning and for somatosensory perception and recognition.

A first characteristic of the model was the progressive integration of different stimulus features. Thus, whereas early processing in the APC is mainly concerned with relatively simple features such as stimulus location and duration, subsequent processing involves detection of the direction and velocity of a target moving over the body surface. Higher association areas combine these features to provide information about the shape of an object or integrate it in a representation of the body. Next, we suggested that separate cortical processing streams exist. One projects from the APC via SII to the posterior insula. The second stream terminates in the PPC and is mainly concerned with action-related processing. Recognition and perception involve the insula as well as the PPC, and here the model distinguishes between somatosensory perception of the body (where you have been touched) and of external stimuli (e.g., surface features of objects).

The idea of a 'ventral pathway of somatosensory processing' has since been supported by MRI lesion overlap studies [102], voxel-based lesion symptom mapping [103], and combined fMRI and **electroencephalography (EEG)** [104]. The role of SII in motor behaviour and the idea that segregation of perception and action-related processing may not occur until after SII has also been supported [105]. The idea of separate processing of somatosensory information for action and perception has been endorsed on theoretical grounds [106], in clinical studies [107], and in experiments with healthy subjects [8].

**Glossary**

**Anosognosia for hemiplegia:** denial of the paralysis of an arm or leg following brain damage.

**Body image:** indicates a perceptual and semantic (related to knowledge about the structure and shape) body representation.

**Body ownership:** the sense of a body part or whole body as one's own.

**Body schema:** a representation of the body that is mainly used for the guidance of action.

**C-tactile system:** involves unmyelinated c-fibres that respond to low-pressure tactile stimuli, particularly to stroking at a velocity of 1–10 cm/s with the hand or a soft brush. These afferents innervate only the hairy part of the skin (not the palms of the hands, the soles of the feet, or the lips). It has been considered to be particularly involved in social and affective touch.

**Electroencephalography (EEG):** the registration of the electrical activity in the brain via electrodes on the surface of the head.

**Event-related potential (ERP):** registration of the EEG signature in response to a specific stimulus by repeated presentations and averaging of the ensuing signal.

**Functional MRI (fMRI):** registration of brain activity using MRI to detect changes in blood oxygenation.

**Haptic object recognition:** the ability to recognize objects by somatosensory input (tactile, proprioceptive, thermal) alone.

**Magnetic resonance imaging (MRI):** noninvasive method for imaging the brain using a high-power magnetic field.

**N80:** a negative ERP wave occurring about 80 ms after stimulus presentation.

**Somatoparaphrenia:** denial of ownership over a body part following brain damage, attributing it instead to someone else.

**Tactile agnosia:** impairment in recognition of objects by touch, despite intact ability to detect tactile stimuli and to recognise objects through other sensory modalities (e.g., vision).

**Voxel-based lesion symptom**

**mapping:** a statistical procedure based on structural MRI data to infer the brain area responsible for a particular symptom.

heavily debated in vision as well [9,10] and concerns three separate characteristics of the original two-pathway models. First, the idea of ‘independence of processing’ is no longer tenable because there is now convincing evidence for substantial crosstalk between the pathways. The interactive symbiosis between the two pathways was, of course, obvious – and already mentioned in our model for somatosensory processing – for active haptic object recognition using exploratory hand movements where the two pathways must work together. However, it is now clear that dissociations between the two routes depend on the precise task conditions and there are now many examples of ‘perceptual information’ affecting action programming and vice versa. For instance, the induction of a rubber hand illusion (RHI) using active movements resulted in larger displacements when pointing movements were performed towards the illusory hand [11], and grasping movements can also be affected by induction of the RHI [12]. It has been suggested that the effects of bodily illusions on motor responses may depend on several factors, including: (i) the type of motor response given and whether this involves a predefined target; (ii) visual versus proprioceptive targets when testing the effect of the illusion on motor responses; and (iii) active induction of the illusion involving movements made by the participant versus passive tactile stimulation etc. [13].

Second, there is now clear evidence for more than two pathways. As in vision, it has become apparent that there are many more specific cognitive systems that rely on different aspects of somatosensory information. These include somatosensory processing not only for perception and the guidance of action, but also for affective and social signalling [14,15], and working and long-term memory [16,17]. With retrospect, it was an oversight that we omitted the frontal cortical areas in our original model, and it is increasingly clear that they play an important role in many aspects of somatosensory function [18], such as **body ownership** [19] and the haptic recognition of, and memory for, objects [20]. The same holds for subcortical structures such as the cerebellum and basal ganglia that play a central role in sensing body ownership, as demonstrated in various patient [21,22] and neuroimaging studies [23,24]. Combined, recent studies suggest that there are several different but overlapping networks that are active depending on the specific task at hand. These networks are less encapsulated than originally proposed. Besides perception influencing action, there is evidence that body representations influence object and space perception [25,26] and affective tactile processing influences body ownership [27,28].

Third, earlier models tended to focus specifically on the processing of somatosensory information in a particular modality. However, it is clear that somatosensory processing contributes to functions that are inherently multimodal in nature and involves cortical regions that process input from various modalities. For example, body perception has been proposed to depend on a ‘body matrix’, a dynamic neural representation including various cortical regions in the occipital [the extrastriate body area (EBA)], the inferior parietal cortex, the ventral premotor cortex, and the insula, all of which are multimodal [29]. Similarly, haptic feature perception, such as texture or shape perception, involves multimodal neural areas in the occipital and parietal cortex [30], sensory processing about the hand during action is influenced by visual and somatosensory signals in the occipital and parietal cortex [31], and tactile memory involves multimodal processing in posterior parietal and frontal areas [16,17].

### A Framework for New Models

Here we describe a revised proposal for the various networks involved in the many aspects of somatosensory function and provide some pointers for how to investigate these. Our starting point was a survey of the different brain structures that are involved in somatosensory processing. This review was based on lesion data [18], functional imaging [32], and neurostimulation [33]. The first observation concerned the substantial number of structures that we had omitted in our

previous model. Second, we noted that these different units are all highly interconnected, suggesting either one comprehensive or several overlapping networks. Based on an appraisal of the different functions that (partly) rely on somatosensory input, we subsequently, identified a (not necessarily exhaustive) number of networks. Overall, we propose a more interactive, distributed framework. This framework does show functional specificity that is, the purpose of the somatosensory processing at hand controls which network is activated (e.g., affective experience is more related to the insular cortex, somatosensory processing for the guidance of action is more linked to posterior parietal areas) – but somatosensory processing in its broadest sense is subserved by a network of cortical and subcortical areas that shows a more flexible organization than we previously assumed. Adding additional networks with more subunits and brain structures increases the number of different phenomena that can be explained, but of course, it also increases the degrees of freedom of the model. The power of the two-pathway models was in the small number of assumptions (i.e., its simplicity). With this in mind, we want to postulate what is still a relatively condensed model as a first approximation of our new approach.

Note that we do not review the recent findings on pain perception as this is now an expanding field on its own that has been reviewed relatively recently [34].

### The Cylinder Block

First, we suggest that there is a basic somatosensory processing unit involving the thalamus and the primary and secondary somatosensory areas (SI and SII). This 'cylinder block' is dominated by somatosensory input. There is a hierarchical structure; early processing in SI [located in the anterior parietal cortex (APC)] is mainly concerned with relatively simple features such as stimulus location and duration, while subsequent processing involves detection of the direction and velocity of a target moving over the body surface. Higher association areas combine these features. The connections between the constituents are both serial and parallel (e.g., [35]). The functioning and connectivity of SI and SII have been extensively discussed in a recent review [36], including a description of how the different basic features interact to achieve different functions. We suggest that this cylinder block provides the input for five major overlapping networks (i.e., haptic object recognition, body perception, body ownership, affective processing, and action).

### Haptic Object Recognition and Tactile Memory

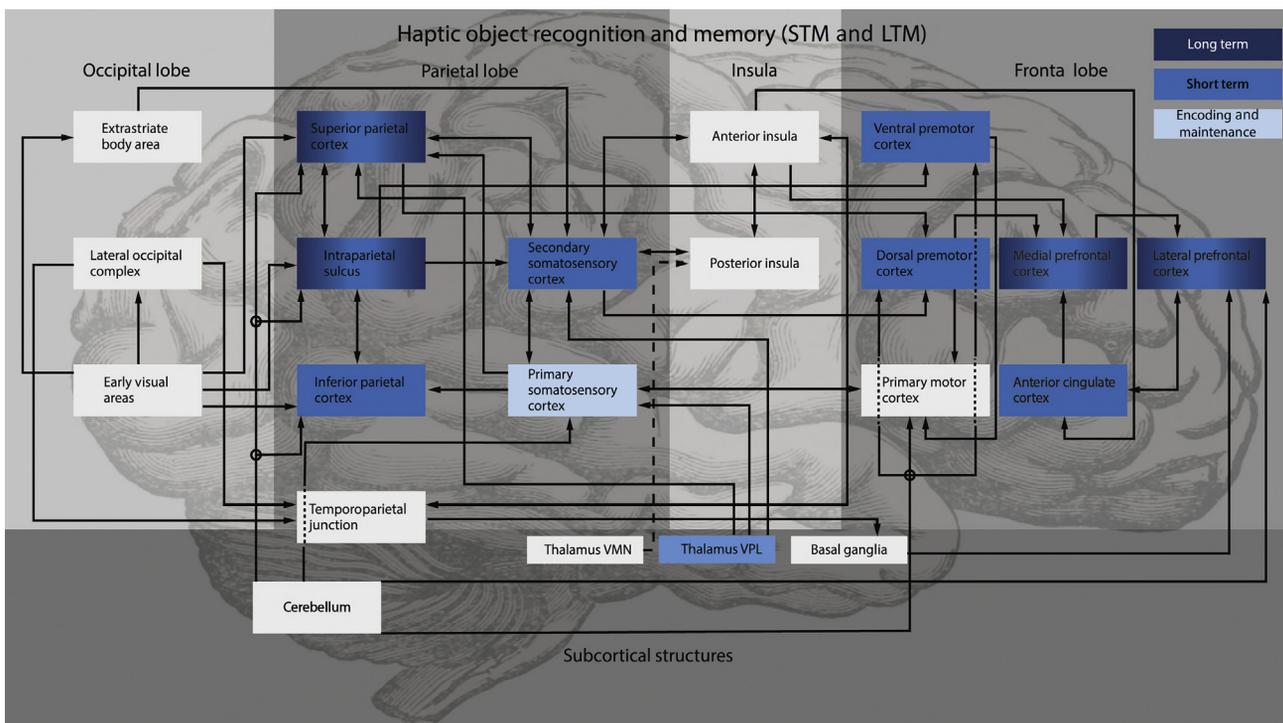
Recognizing objects by touch is a complex skill involving several different subcomponents. First, it involves learning (e.g., storing haptic information in short- and long-term memory and associating it with object knowledge). Second, haptic object recognition involves active exploration. Subjects use specific finger and hand movements to extract information about the object and these movements are dependent on the task and the object characteristics [37]. However, these processes are separately instantiated in the brain as indicated by neuroimaging. **fMRI** activation was observed in the left posterior parietal lobe and premotor cortex for sensory-guided motor activity but in the left superior parietal lobe and the right cuneus for the perception and memory of shape characteristics [21]. This fractionation can be observed in relatively basic tasks; for instance, a dissociation between active haptic exploration of surfaces for roughness discrimination versus the detection of the orientation of 2D patterns [38].

In contrast to our previous proposal, which was based in part on an early monkey lesion study [39], recent neuroimaging and lesion evidence suggests that the insular cortex is not involved in object recognition or that its role is limited to the affective aspects of objects. In addition, **tactile agnosia**, the inability to recognize objects by touch, may be caused exclusively by lesions including SII [5,40]. Patients with lesions in the postcentral gyrus may show impaired texture recognition due to poor sequential processing while patients with damage to the superior parietal lobule and

the intraparietal sulcus had impaired shape recognition. Note that the insula was not implicated in any of these patients [26]. Based on the available evidence, we now suggest that, in addition to posterior parietal areas, the frontal lobes also play a role in haptic recognition beyond programming exploratory movements (Figure 1). For instance, a recent fMRI study [20] on passive shape recognition found activation in a somatosensory network as well as in the prefrontal and premotor cortex.

There are relatively few studies looking at tactile memory. With respect to working memory, early work with monkeys showed that damage to SII may cause impairments in tactile discrimination learning [41,42]. fMRI studies in humans have subsequently suggested that there is good evidence for anterior and superior parietal cortex, supplementary motor area (SMA), and dorsolateral and anterior cingulate cortex involvement in tactile working memory [43–45]. Furthermore, there is also MRI [46] evidence for multimodal working memory mechanisms, where memorizing visual and tactile spatial matrices both activated posterior parietal, dorsolateral prefrontal, and anterior cingulate networks.

Regarding long-term tactile memory, as mentioned earlier, based on the work of Mishkin and coworkers we had hypothesized that the cortical pathway projecting from the APC via SII to the insula is involved in tactile memory (Box 2). However, we now suggest prefrontal and parietal involvement in long-term tactile memory as well as a multimodal memory representation. For example, a recent fMRI study [16] used a paired associate learning paradigm to investigate the recall of visually and haptically presented objects and locations after a delay of 1 day. Besides modality-specific activations in vision and somatosensory areas, a conjunction analysis with



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Figure 1. Areas Involved in Memory and Object Recognition. Abbreviations: STM, short-term memory; LTM, long-term memory; VMN, ventromedial nucleus; VPL, ventral posterior lateral nucleus.

data collapsed over modalities showed activations in the medial and superior frontal gyrus and the superior parietal lobe including the intraparietal sulcus.

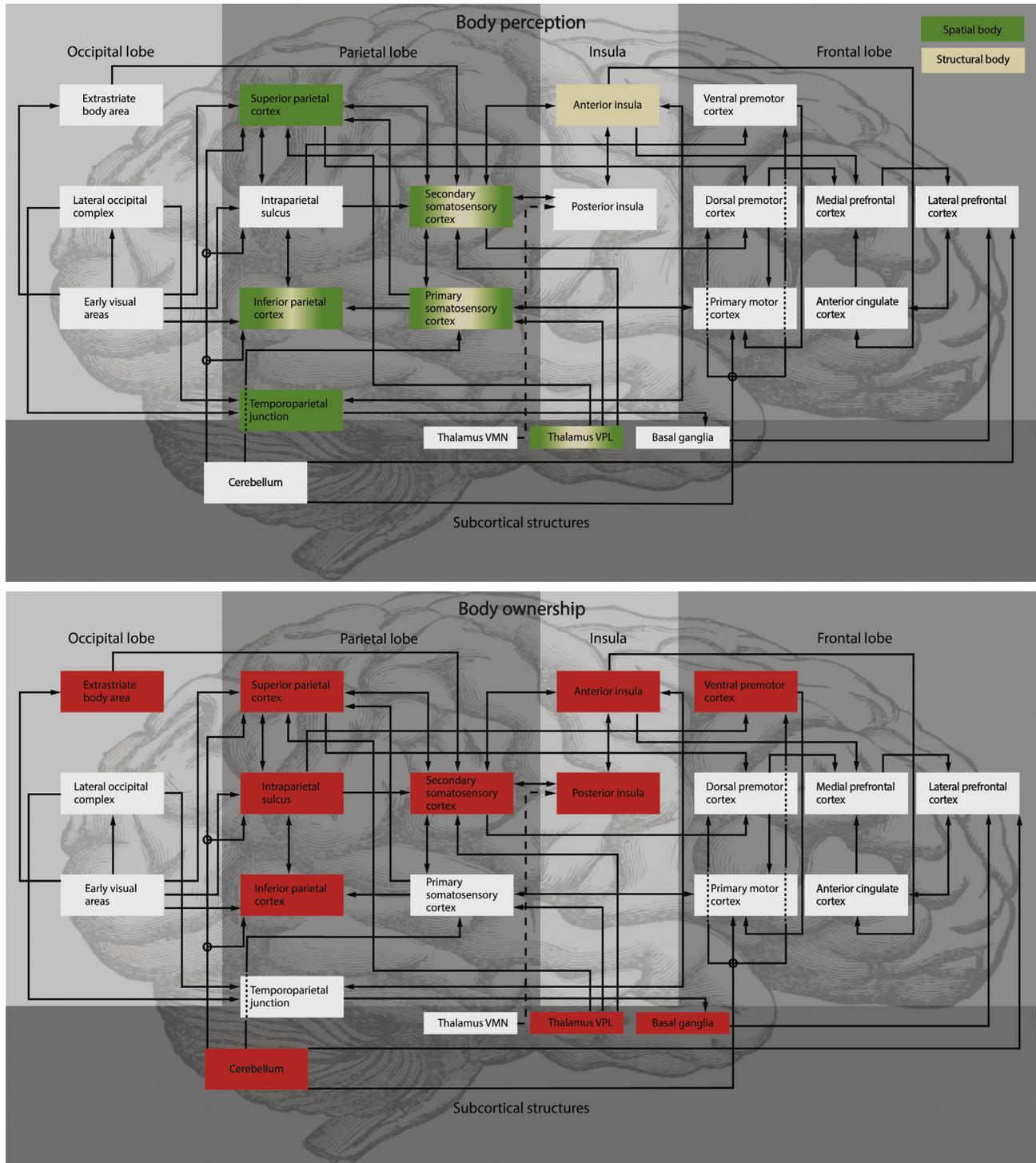
Imagery may be another way to activate stored somatosensory representations. Evidence from behavioural and neuroimaging studies suggests modality-specific as well as multimodal representations. For example, imagining the tactile features of an object can accelerate reaction times to tactile, but not to auditory, stimuli, suggesting modality-specific representation [47]. Moreover, somatotopic specific activations in SI can be observed during tactile imagery for different body parts [48]. A study on the neural basis of tactile imagery using vibrotactile patterns [49] showed activation in the primary somatosensory cortex and in the retrosplenial cortices, the precuneus, and the prefrontal cortex. The former finding supports the notion that sensory areas provide a modality-specific basis for mental imagery. The latter finding confirms the idea of an additional modality-independent construction network. The prefrontal activation was also related to top-down activation of a visual representation of a haptically explored object, emphasizing the multimodal nature of haptic object recognition [50].

### Body Perception and Body Ownership

In addition to basic proprioception, touch, temperature, and pain, body perception depends on several higher-order representations. We can distinguish ‘spatial’ (e.g., location of, distance between, speed of touch sensation) and ‘structural’ (knowledge and awareness of the positions of body parts, knowing the left and right side of the body) body information. Moreover, somatosensory processing, together with visual, vestibular, and interoceptive input, leads to body awareness and more specifically to body ownership. Several authors have suggested that networks of cortical and subcortical areas underlie different bodily representations [29,51,52]. Based on the recent literature, we suggest that structural and spatial representations are dissociable [4,53]. However, the few studies on their underlying neural substrate suggest that they share to some extent similar underlying neural networks and show related functional representations (Figure 2, top).

For example, a behavioural study [54] investigated the effect of body segmentation between hand and arm on tactile and visual perception. This study found that two tactile stimuli felt farther apart when they were applied across the wrist than when they were both administered within a single body part (palm or forearm). This suggests that a mental body representation exists in which the body is structured in categorical body parts with the joints as boundaries and that this categorical representation influences the perception of spatial tactile stimuli [55]. An **event-related potential (ERP)** study [56] showed that presenting somatosensory stimuli across structural boundaries between body parts affected the **N80** (thought to originate from the contralateral SI), suggesting that structural aspects of body representation affect early somatosensory processing. Furthermore, structural body representation deficits such as finger agnosia and left–right disorientation are generally related to inferior parietal lobe damage. In a recent study, the ability to distinguish between left and right was investigated in a group of subacute stroke patients [26]. **Voxel-based lesion symptom mapping** showed that impaired performance on left–right discrimination was related to damage to the right anterior insula, extending the network of areas involved in structural body representations.

Spatial aspects of body representations are often investigated using a tactile distance estimation task in which participants are asked to judge the distance between two tactile stimuli applied to, for example, the arm. Performance on this task depends both on lower-level somatosensory processing and high-level stored body size representation, to correct for differences in receptor density between body parts [57]. Neurostimulation [58] and fMRI [59] studies showed the



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Figure 2. Areas Involved in Body Perception (Top) and Body Ownership (Bottom). Abbreviations: VMN, ventromedial nucleus; VPL, ventral posterior lateral nucleus.

involvement of bilateral inferior and superior parietal areas as well as the right parieto-occipitotemporal junction. Thus, parietal areas appear to be mainly responsible for processing spatial input.

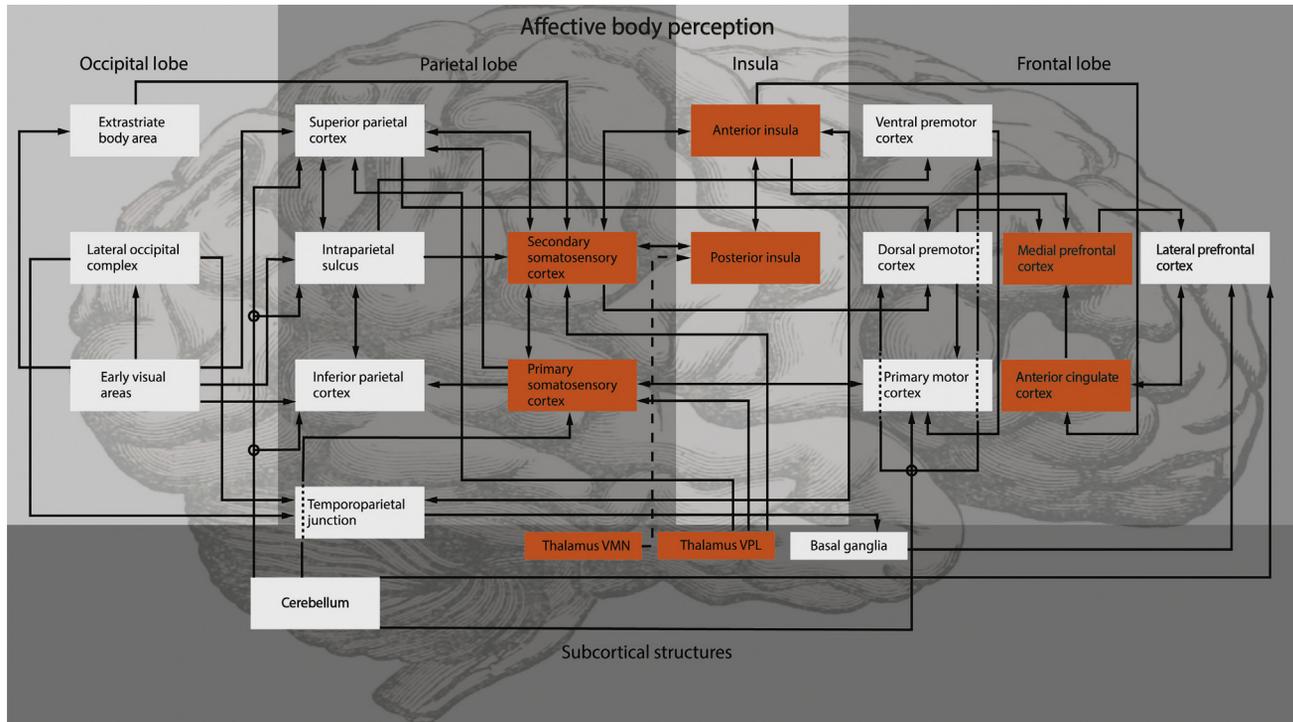
Another aspect of body representation is body ownership – the feeling that a body (or part of it) belongs exclusively to you (Figure 2, bottom). Several conditions exist in which ownership over a body part is disrupted. **Anosognosia for hemiplegia** after stroke was found to be related to right posterior insula and premotor lesions [60]. Importantly, a recent study shows that disruptions to three networks, the premotor loop, the limbic system and the ventral attentional network, contribute in particular to anosognosia for hemiplegia [61]. This is consistent with our suggestions that distributed networks are responsible for various body-related perceptions. Another body ownership problem is **somatoparaphrenia**, in which patients often attribute their affected arm to another person (doctor, sister, etc.). With respect to the neuroanatomical correlates, a review [62] reported that somatoparaphrenia mainly occurs after right hemispheric damage, usually posterior (temporoparietal) or insular but occasionally subcortically. Furthermore, recent lesion overlap studies have suggested that frontal (middle and inferior frontal gyrus) and subcortical (amygdala, hippocampus, thalamus, basal ganglia, white matter, internal capsule posterior limb) structures are involved in somatoparaphrenia in addition to the postcentral gyrus [21,63,64]. Other evidence comes from illusion studies. In the RHI, a subject experiences a rubber hand as part of his/her body. This experience arises when an unseen real hand and seen rubber hand are stroked simultaneously. Regarding the neural substrate during this illusory feeling of ownership over the rubber hand, several studies consistently found the ventral premotor and posterior parietal areas, the EBA, the cerebellum, and the putamen to be involved [19,24,65–67]. Others also point to involvement of the insula [19,24,68].

### Social and Affective Touch

Somatosensory information is central for social interaction and affective experience. A recent review [14] suggests that touch is an effective way of communicating social signals and influencing others' social behaviour (social touch) and is an important way of experiencing and communicating emotions (affective touch). While the latter can be related to both pleasant and unpleasant (pain, itch) experiences, as mentioned earlier, here we limit ourselves to pleasant affective touch.

An important, but by no means the only, sensory channel for the positive affective aspect of touch is the **c-tactile system**. Unmyelinated c-fibres in hairy skin respond best to slow (1–10 cm/s) stroking with a soft brush or hand and at skin temperature (about 34°C), suggesting sensitivity for skin-on-skin contact [69]. It is perceived as very pleasant and has been linked to affiliative behaviour and social and emotional development. C-tactile stroking activates the posterior insular cortex [69] (Figure 3), with subsequent activation in a network of cortical areas including the superior temporal sulcus, anterior cingulate gyrus/medial prefrontal cortex, and orbitofrontal cortex [70,71].

A recent meta-analysis of fMRI studies showed dissociable but overlapping regions of activation for affective and discriminatory tactile stimuli [15]. The discriminative touch network involved SI, SII, the left lateral inferior premotor cortices, the inferior parietal cortex, the SMA, and bilateral angular gyri and medial prefrontal areas. Affective touch was subserved by a bilateral network encompassing the posterior and anterior insula, the postcentral primary and secondary somatosensory cortex, the putamen, the thalamus, the frontal operculum, and the medial prefrontal cortex. In addition, it has been shown that feeling affective touch activates the posterior insula, while imagining affective touch activated the anterior insula. This suggests that the anterior insula is particularly important for the affective interpretation of touch [72].



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Figure 3. Areas Involved in Affective Body Perception. Abbreviations: VMN, ventromedial nucleus; VPL, ventral posterior lateral nucleus.

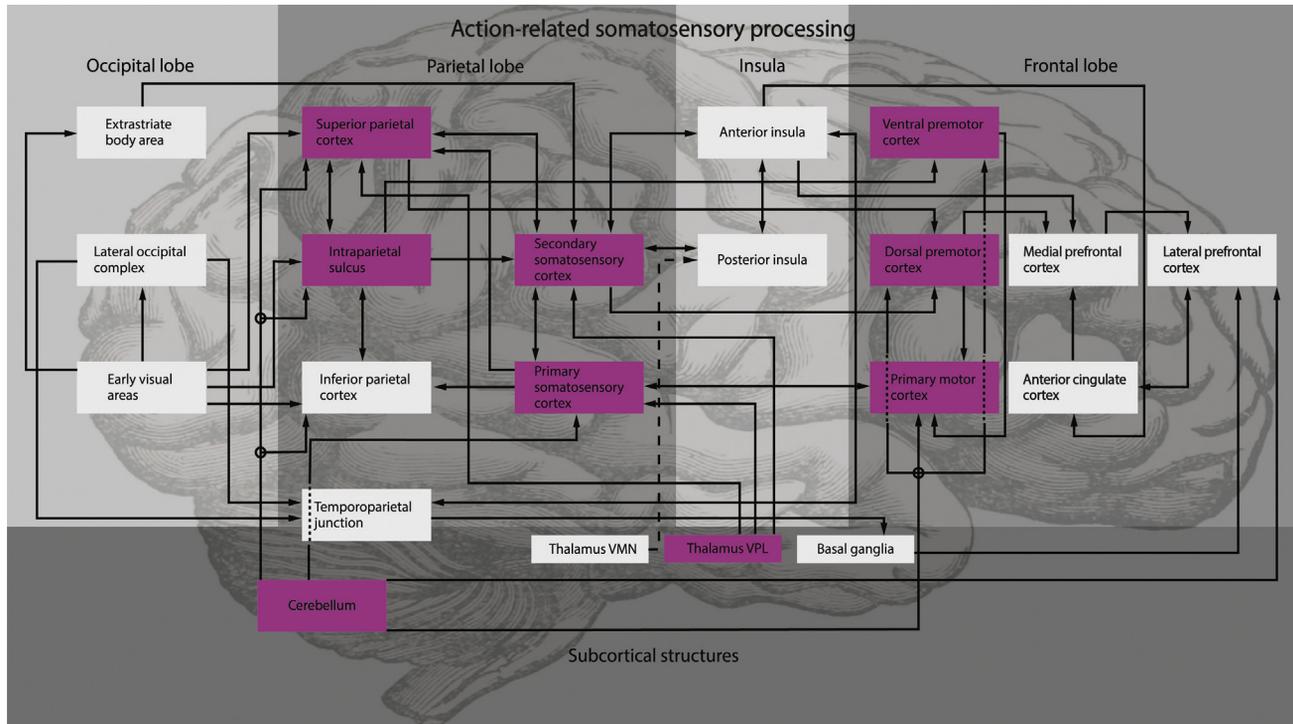
In addition to c-tactile stimulation, there are many other tactile stimuli that are socially relevant [14] including holding hands, hugging, squeezing, etc. There appears to be a substantial overlap of the neural mechanisms underlying social and affective touch [73]; both involve activation of somatosensory as well as social brain areas [74].

Finally, future research will reveal whether we need to distinguish between the affective input, such as the c-tactile system, and cortical networks that are informed by other (cognitive) function domains, such as expression recognition, reward computation, and decision-making, to maintain the affective body. It is possible that these constitute two different networks that are not necessarily connected but are both involved in what we call 'affect'.

### Somatosensory Processing for Action

The final pathway concerns the action route'. Somatosensory (proprioception) information is used to determine the starting position of the body and limbs from where the action is being planned and to determine the end position when we move towards a target location on the body. This processing route receives input from the somatosensory 'cylinder block' (Figure 4) but operates closely with other modalities as the targets to which motor action are being planned are also often defined in vision or audition.

The nature of somatosensory processing for action guidance has been studied in the context of various questions. First, with reference to the two visual streams model, it has been hypothesised that somatosensory processing differs for perception and action [7]. Initial studies showed that, comparable with the visual domain, somatosensory perception was susceptible to illusions but actions were not [75]. More recently, it has been shown that this dissociation is not as clear cut



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Figure 4. Areas Involved in Motor Action. Abbreviations: VMN, ventromedial nucleus; VPL, ventral posterior lateral nucleus.

and that, for instance, the RHI also affects motor actions [12]. This suggests that there is substantial crosstalk between the networks involved in action and perception.

Second, a number of recent studies have specifically looked at the interplay between somatosensation and other sensory domains. For instance, it has been shown that the visual form agnostic patient D.F. is poor at the visual perception of size, while grip scaling (the aperture between thumb and index finger) during grasping was not affected [76]. A recent study [77] subsequently suggested that D.F. was impaired on grip scaling during grasping when haptic feedback at the end of the movement was withdrawn. The implication is that action to external visual targets is modulated by tactile feedback and that both somatosensory and visual processing are used during the guidance of action [78].

The reverse effect of visual representations on somatosensory guided action has also been reported. For example, reaching towards tactile targets on an unseen arm is influenced by eye fixation [79]. Evidence for the close intertwining of visual and somatosensory processing for the guidance of action also comes from neuroimaging studies. For instance, kinaesthetically guided movements activated superior parietal and anterior intraparietal areas in a way similar way to visually guided movements [72].

Third, in the visual domain, there is evidence for a dissociation between grasping and reaching movements in the dorsal stream [80]. There is evidence for a similar type of dissociation in the haptic domain as well [81], with reaching showing different trajectory characteristics compared with grasping.

A related aspect that has received considerable attention in the visual two-stream model is that vision for action is not accessible for conscious report. Similarly, we [6] suggested that somatosensory input underlying sensorimotor guidance may also not be consciously perceived. Several studies have now shown that detection of tactile stimuli during goal-directed movements is attenuated [82,83], arguably to allow greater resources for task-relevant somatosensory processing [84]. At this point, we do not feel that it is warranted to postulate a separate network for somatosensory consciousness. It is clear that parts of the overall network operate outside consciousness and that other parts are involved as precursors or even neural correlates of consciousness. It appears prudent at this point to assume that consciousness is embedded within components of the overall somatosensory network.

### Concluding Remarks

Somatosensory processing has gained increasing research interest in the cognitive neurosciences in the past 10 years. Several important new insights have emerged that necessitate adaptations to the earlier neurocognitive models (although of course many questions remain; see [Outstanding Questions](#)). There is now clear evidence for a multitude of brain structures involved in somatosensation and these structures appear to be organized in several networks (we have identified five). In addition, somatosensory information is, from an early stage onwards, processed in a much more multimodal fashion than previously thought. For instance, the concept of body image is now conceptualized as a network of different cortical regions in the occipital (EBA), the inferior parietal cortex, and the posterior insula, and all of these areas are multimodal in nature.

Overall, we propose a more interactive, distributed framework. This framework does show functional specificity (e.g., affective experience is more related to insular cortex and somatosensory processing for the guidance of action is more linked to posterior parietal areas), but somatosensory processing in its broadest sense involves a network of cortical and subcortical areas that shows a more flexible organization than we previously assumed. Adding more networks with more subunits and more brain structures increases the explanatory power, but the strength of the two-pathway models was in the small number of assumptions. With this in mind, we have postulated a more condensed model as a first approximation of our new approach. The descriptive merit of the methodology we used in this review [i.e., an overview of the functional architectures of different cognitive functions that rely (partly) on somatosensory information] lies in the framework it provides for more specified models.

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### References

- Burton, H. and Jones, E.G. (1976) The posterior thalamic region and its cortical projection in New World and Old World monkeys. *J. Comp. Neurol.* 168, 249–302
- Berkley, K.J. (1980) Spatial relationships between the terminations of somatic sensory and motor pathways in the rostral brainstem of cats and monkeys. I. Ascending somatic sensory inputs to lateral diencephalon. *J. Comp. Neurol.* 193, 283–317
- Kaas, J.H. (2004) Somatosensory system. In *The Human Nervous System* (2nd edn) (Paxinos, G. and Mai, J.K., eds), pp. 1059–1092. Academic Press
- Sirigu, A. *et al.* (1991) Multiple representations contribute to body knowledge processing. Evidence from a case of autotopagnosia. *Brain* 114, 629–642
- Reed, C.L. *et al.* (1996) Tactile agnosia. Underlying impairment and implications for normal tactile object recognition. *Brain* 119, 875–888
- Dijkerman, H.C. and de Haan, E.H.F. (2007) Somatosensory processes subserving perception and action. *Behav. Brain Sci.* 30, 189–239
- Hömke, L. *et al.* (2009) Analysis of lesions in patients with unilateral tactile agnosia using cytoarchitectonic probabilistic maps. *Hum. Brain Mapp.* 30, 1444–1456
- Jones, S.A.H. *et al.* (2012) A task-dependent effect of memory and hand-target on proprioceptive localization. *Neuropsychologia* 50, 1462–1470
- Schenk, T. and McIntosh, R.D. (2010) Do we have independent visual streams for perception and action? *Cogn. Neurosci.* 1, 52–62
- de Haan, E.H.F. *et al.* (2018) Where are we now with 'what' and 'how'? *Cortex* 98, 1–7
- Kammers, M.P.M. *et al.* (2009) Specificity and coherence of body representations. *Perception* 38, 1804–1820

### Outstanding Questions

The first question is whether this new conceptual framework will stimulate new research that will lead to an overall better description of the somatosensory system. This theoretical framework does, however, produce clear-cut hypotheses. For instance, the networks can be investigated using meta-analyses of functional imaging data by looking at the network of areas that show co-activation with a particular cortical area deemed central for that function (e.g., the superior parietal cortex for action planning). Lesion studies can elucidate whether the postulated parallel processing routes can lead to predicted selective deficits.

A central thesis here is the multimodal aspect of the networks that are informed by somatosensory information. The question is now to delineate the extent to which different networks and their constituent processing units combine the information from different sensory sources.

The role of C-fibres is currently a hotly debated issue and many laboratories are currently investigating its characteristics and neuroanatomical basis. However, affective somatosensory processing is not reliant on C-fibres only, and we need to look into the interaction between these systems.

Finally, our contention is that various neural areas are flexibly combined into networks to perform the task at hand. An important question concerns the time course of the activation of the different networks. Which areas are first activated and how does the activation of the rest of the network evolve? EEG or MEG possibly combined with TMS may provide some insight into these questions.

12. Kammers, M.P.M. *et al.* (2010) How many motoric body representations can we grasp? *Exp. Brain Res.* 202, 203–212
13. Riemer, M. *et al.* (2013) Action and perception in the rubber hand illusion. *Exp. Brain Res.* 229, 383–393
14. Gallace, A. and Spence, C. (2010) The science of interpersonal touch: an overview. *Neurosci. Biobehav. Rev.* 34, 246–259
15. Morrison, I. (2016) ALE meta-analysis reveals dissociable networks for affective and discriminative aspects of touch. *Hum. Brain Mapp.* 37, 1308–1320
16. Stock, O. *et al.* (2009) Cortical activation patterns during long-term memory retrieval of visually or haptically encoded objects and locations. *J. Cogn. Neurosci.* 21, 58–82
17. Kaas, A.L. *et al.* (2013) The neural substrate for working memory of tactile surface texture. *Hum. Brain Mapp.* 34, 1148–1162
18. Rullmann, M. *et al.* (2019) Prefrontal and posterior parietal contributions to the perceptual awareness of touch. *Sci. Rep.* 9, 16981
19. Ehrsson, H.H. *et al.* (2004) That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science* 305, 875–877
20. Savini, N. *et al.* (2010) Passive tactile recognition of geometrical shape in humans: an fMRI study. *Brain Res. Bull.* 83, 223–231
21. Moro, V. *et al.* (2016) Motor versus body awareness: voxel-based lesion analysis in anosognosia for hemiplegia and somatoparaphrenia following right hemisphere stroke. *Cortex* 83, 62–77
22. Hänggi, J. *et al.* (2017) Structural and functional hyper-connectivity within the sensorimotor system in xenomelia. *Brain Behav.* 7, e00657
23. Brozzoli, C. *et al.* (2012) That's near my hand! Parietal and premotor coding of hand-centered space contributes to localization and self-attribution of the hand. *J. Neurosci.* 32, 14573–14582
24. Petkova, V.I. *et al.* (2011) From part- to whole-body ownership in the multisensory brain. *Curr. Biol.* 21, 1118–1122
25. Serino, A. and Haggard, P. (2010) Touch and the body. *Neurosci. Biobehav. Rev.* 34, 224–236
26. van Stralen, H.E. *et al.* (2018) Body representation disorders predict left right orientation impairments after stroke: a voxel-based lesion symptom mapping study. *Cortex* 104, 140–153
27. van Stralen, H.E. *et al.* (2014) Affective touch modulates the rubber hand illusion. *Cognition* 131, 147–158
28. Crucianelli, L. *et al.* (2013) Bodily pleasure matters: velocity of touch modulates body ownership during the rubber hand illusion. *Front. Psychol.* 4, 703
29. Moseley, G.L. *et al.* (2011) Bodily illusions in health and disease: physiological and clinical perspectives and the concept of a cortical 'body matrix'. *Neurosci. Biobehav. Rev.* 36, 34–46
30. Stilla, R. and Sathian, K. (2008) Selective visuo-haptic processing of shape and texture. *Hum. Brain Mapp.* 29, 1123–1138
31. Limanowski, J. and Friston, K. (2019) Attentional modulation of vision versus proprioception during action. *Cereb. Cortex* 30, 1637–1648
32. Hong, K.S. *et al.* (2017) Classification of somatosensory cortex activities using fNIRS. *Behav. Brain Res.* 333, 225–234
33. Gogulski, J. *et al.* (2017) Neural substrate for metacognitive accuracy of tactile working memory. *Cereb. Cortex* 27, 5343–5352
34. Haggard, P. *et al.* (2013) Spatial sensory organization and body representation in pain perception. *Curr. Biol.* 23, R164–R176
35. Klingner, C.M. *et al.* (2016) The processing of somatosensory information shifts from an early parallel into a serial processing mode: a combined fMRI/MEG study. *Front. Syst. Neurosci.* 10, 103
36. Delhaye, B.P. *et al.* (2018) Neural basis of touch and proprioception in primate cortex. *Compr. Physiol.* 8, 1575–1602
37. Lederman, S.J. and Klatzky, R.L. (1987) Hand movements: a window into haptic object recognition. *Cogn. Psychol.* 19, 342–368
38. Master, S. and Tremblay, F. (2010) Differential modulation of corticospinal excitability during haptic sensing of 2-D patterns vs. textures. *BMC Neurosci.* 11, 149
39. Mishkin, M. (1979) Analogous neural models for tactual and visual learning. *Neuropsychologia* 17, 139–151
40. Caselli, R.J. (1991) Rediscovering tactile agnosia. *Mayo Clin. Proc.* 66, 129–142
41. Garcha, H.S. and Ettlinger, G. (1980) Tactile discrimination learning in the monkey: the effects of unilateral or bilateral removals of the second somatosensory cortex (area SII). *Cortex* 16, 397–412
42. Murray, E.A. and Mishkin, M. (1984) Relative contributions of SII and area 5 to tactile discrimination in monkeys. *Behav. Brain Res.* 11, 67–83
43. Harris, J.A. *et al.* (2001) The topography of tactile working memory. *J. Neurosci.* 21, 8262–8269
44. Kaas, A.L. *et al.* (2007) The neural correlates of human working memory for haptically explored object orientations. *Cereb. Cortex* 17, 1637–1649
45. Numminen, J. *et al.* (2004) Cortical activation during a spatio-temporal tactile comparison task. *Neuroimage* 22, 815–821
46. Ricciardi, E. *et al.* (2006) Neural correlates of spatial working memory in humans: a functional magnetic resonance imaging study comparing visual and tactile processes. *Neuroscience* 139, 339–349
47. Anema, H.A. *et al.* (2012) Thinking about touch facilitates tactile but not auditory processing. *Exp. Brain Res.* 218, 373–380
48. Schmidt, T.T. and Blankenburg, F. (2019) The somatotopy of mental tactile imagery. *Front. Hum. Neurosci.* 13, 10
49. Schmidt, T.T. *et al.* (2014) Imaging tactile imagery: changes in brain connectivity support perceptual grounding of mental images in primary sensory cortices. *Neuroimage* 98, 216–224
50. Lacey, S. and Sathian, K. (2014) Visuo-haptic multisensory object recognition, categorization, and representation. *Front. Psychol.* 5, 730
51. Berlucchi, G. and Aglioti, S. (1997) The body in the brain: neural bases of corporeal awareness. *Trends Neurosci.* 20, 560–564
52. Riva, G. (2018) The neuroscience of body memory: from the self through the space to the others. *Cortex* 104, 241–260
53. Schwoebel, J. and Coslett, H.B. (2005) Evidence for multiple, distinct representations of the human body. *J. Cogn. Neurosci.* 17, 543–553
54. de Vignemont, F. *et al.* (2009) Segmenting the body into parts: evidence from biases in tactile perception. *Q. J. Exp. Psychol.* 62, 500–512
55. Gálvez-García, G. *et al.* (2011) An attentional approach to study mental representations of different parts of the hand. *Psychol. Res.* 76, 364–372
56. Shen, G. *et al.* (2018) Neuropsychology of human body parts: exploring categorical boundaries of tactile perception using somatosensory mismatch responses. *J. Cogn. Neurosci.* 30, 1858–1869
57. Taylor-Clarke, M. *et al.* (2004) Keeping the world a constant size: object constancy in human touch. *Nat. Neurosci.* 7, 219–220
58. Spitoni, G.F. *et al.* (2013) Right but not left angular gyrus modulates the metric component of the mental body representation: a tDCS study. *Exp. Brain Res.* 228, 63–72
59. Spitoni, G.F. *et al.* (2010) Two forms of touch perception in the human brain. *Exp. Brain Res.* 207, 185–195
60. Baier, B. and Karnath, H.-O. (2008) Tight link between our sense of limb ownership and self-awareness of actions. *Stroke* 39, 486–488
61. Pacella, V. *et al.* (2019) Anosognosia for hemiplegia as a tripartite disconnection syndrome. *eLife* 8, e46075
62. Vallar, G. and Ronchi, R. (2009) Somatoparaphrenia: a body delusion. *Exp. Brain Res.* 192, 533–551
63. Gandola, M. *et al.* (2011) An anatomical account of somatoparaphrenia. *Cortex* 48, 1165–1178
64. Invernizzi, P. *et al.* (2012) What is mine? Behavioral and anatomical dissociations between somatoparaphrenia and anosognosia for hemiplegia. *Behav. Neurol.* 25, 139–150
65. Ehrsson, H.H. *et al.* (2005) Touching a rubber hand: feeling of body ownership is associated with activity in multisensory brain areas. *J. Neurosci.* 25, 10564–10573
66. Limanowski, J. and Blankenburg, F. (2015) Network activity underlying the illusory self-attribution of a dummy arm. *Hum. Brain Mapp.* 36, 2284–2304

67. Guterstam, A. *et al.* (2019) Direct electrophysiological correlates of body ownership in human cerebral cortex. *Cereb. Cortex* 29, 1328–1341
68. Tsakiris, M. *et al.* (2007) Neural signatures of body ownership: a sensory network for bodily self-consciousness. *Cereb. Cortex* 17, 2235–2244
69. Morrison, I. *et al.* (2010) The skin as a social organ. *Exp. Brain Res.* 204, 305–314
70. Gordon, I. *et al.* (2013) Brain mechanisms for processing affective touch. *Hum. Brain Mapp.* 34, 914–922
71. Rolls, E.T. *et al.* (2003) Representations of pleasant and painful touch in the human orbitofrontal and cingulate cortices. *Cereb. Cortex* 13, 308–317
72. Fiehler, K. and Rösler, F. (2010) Plasticity of multisensory dorsal stream functions: evidence from congenitally blind and sighted adults. *Restor. Neurol. Neurosci.* 28, 193–205
73. Ebisch, S.J. *et al.* (2014) Touching moments: desire modulates the neural anticipation of active romantic caress. *Front. Behav. Neurosci.* 8, 60
74. Lee Masson, H. *et al.* (2018) The multidimensional representational space of observed socio-affective touch experiences. *Neuroimage* 175, 297–314
75. Kammers, M.P.M. *et al.* (2009) The rubber hand illusion in action. *Neuropsychologia* 47, 204–2011
76. Goodale, M.A. *et al.* (1991) A neurological dissociation between perceiving objects and grasping them. *Nature* 349, 154–156
77. Schenk, T. (2012) No dissociation between perception and action in patient DF when haptic feedback is withdrawn. *J. Neurosci.* 32, 2013–2017
78. Whitwell, R.L. *et al.* (2014) DF's visual brain in action: the role of tactile cues. *Neuropsychologia* 55, 41–50
79. Harrar, V. and Harris, L.R. (2010) Touch used to guide action is partially coded in a visual reference frame. *Exp. Brain Res.* 203, 615–620
80. Gallivan, J.P. and Culham, J.C. (2015) Neural coding within human brain areas involved in actions. *Curr. Opin. Neurobiol.* 33, 141–149
81. Karl, J.M. *et al.* (2013) Nonvisual learning of intrinsic object properties in a reaching task dissociates grasp from reach. *Exp. Brain Res.* 225, 465–477
82. Juravle, G. *et al.* (2010) Changes in tactile sensitivity over the time-course of a goal-directed movement. *Behav. Brain Res.* 208, 391–401
83. Buckingham, G. *et al.* (2010) Gating of vibrotactile detection during visually guided bimanual reaches. *Exp. Brain Res.* 201, 411–419
84. Juravle, G. *et al.* (2013) Context-dependent changes in tactile perception during movement execution. *Front. Psychol.* 4, 913
85. Mountcastle, V.B. (1984) Central mechanisms in mechanoreceptive sensibility. In *Handbook of Physiology, Section 1: The Nervous System* (Vol. III) (Brookhart, J.M., ed.), pp. 789–878, American Physiological Society
86. Jones, E.G. *et al.* (1979) Differential thalamic relationships of sensory-motor and parietal cortical fields in monkeys. *J. Comp. Neurol.* 183, 833–882
87. Kaas, J.H. *et al.* (1979) Multiple representations of the body within the primary somatosensory cortex of primates. *Science* 204, 521–523
88. Olausson, H. *et al.* (2002) Unmyelinated tactile afferents signal touch and project to insular cortex. *Nat. Neurosci.* 5, 900–904
89. Phillips, J.R. *et al.* (1988) Spatial pattern representation and transformation in monkey somatosensory cortex. *Proc. Natl. Acad. Sci. U. S. A.* 85, 1317–1321
90. Chen, L.M. *et al.* (2003) Optical imaging of a tactile illusion in area 3b of the primary somatosensory cortex. *Science* 302, 881–885
91. Pons, T.P. *et al.* (1987) Physiological evidence for serial processing in somatosensory cortex. *Science* 237, 417–419
92. Disbrow, E. *et al.* (2001) Evidence for interhemispheric processing of inputs from the hands in human S2 and PV. *J. Neurophysiol.* 85, 2236–2244
93. Friedman, D.P. *et al.* (1986) Cortical connections of the somatosensory fields of the lateral sulcus of macaques: evidence for a corticolimbic pathway for touch. *J. Comp. Neurol.* 252, 323–347
94. Schneider, R.J. *et al.* (1993) A modality-specific somatosensory area within the insula of the rhesus monkey. *Brain Res.* 621, 116–120
95. Disbrow, E. *et al.* (2003) Cortical connections of the second somatosensory area and the parietal ventral area in macaque monkeys. *J. Comp. Neurol.* 462, 382–399
96. Pons, T.P. and Kaas, J.H. (1986) Corticocortical connections of area 2 of somatosensory cortex in macaque monkeys: a correlative anatomical and electrophysiological study. *J. Comp. Neurol.* 248, 313–335
97. Pearson, R.C. and Powell, T.P. (1985) The projection of the primary somatic sensory cortex upon area 5 in the monkey. *Brain Res.* 356, 89–107
98. Disbrow, E. *et al.* (2002) Thalamocortical connections of somatosensory areas PV and S2 in macaque monkeys. *Thalamus Relat. Syst.* 1, 289–302
99. Longo, M.R. *et al.* (2010) More than skin deep: body representation beyond primary somatosensory cortex. *Neuropsychologia* 48, 655–668
100. Paillard, J. (1999) Body schema and body image – a double dissociation in deafferented patients. In *Motor Control, Today and Tomorrow* (Gantchev, G.N. *et al.*, eds), pp. 198–214, Academic
101. Milner, A.D. and Goodale, M.A. (1995) *The Visual Brain in Action*, Oxford University Press
102. Preusser, S. *et al.* (2015) The perception of touch and the ventral somatosensory pathway. *Brain* 138, 540–548
103. Meyer, S. *et al.* (2016) Voxel-based lesion–symptom mapping of stroke lesions underlying somatosensory deficits. *Neuroimage Clin.* 10, 257–266
104. Goltz, D. *et al.* (2015) Connections between intraparietal sulcus and a sensorimotor network underpin sustained tactile attention. *J. Neurosci.* 35, 7938–7949
105. Taaka, M. *et al.* (2013) Neural response to movement of the hand and mouth in the secondary somatosensory cortex of Japanese monkeys during a simple feeding task. *Somatosens. Mot. Res.* 30, 140–152
106. de Vignemont, F. (2010) Body schema and body image – pros and cons. *Neuropsychologia* 48, 669–680
107. Anema, H.A. *et al.* (2009) A double dissociation between somatosensory processing for perception and action. *Neuropsychologia* 47, 1615–1620