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Somatosensory processes subserving perception and action

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Abstract: The functions of the somatosensory system are multiple. We use tactile input to localize and experience the various qualities of touch, and proprioceptive information to determine the position of different parts of the body with respect to each other, which provides fundamental information for action. Further, tactile exploration of the characteristics of external objects can result in conscious perceptual experience and stimulus or object recognition. Neuroanatomical studies suggest parallel processing as well as serial processing within the cerebral somatosensory system that reflect these separate functions, with one processing stream terminating in the posterior parietal cortex (PPC), and the other terminating in the insula. We suggest that, analogously to the organisation of the visual system, somatosensory processing for the guidance of action can be dissociated from the processing that leads to perception and memory. In addition, we find a second division between tactile information processing about external targets in service of object recognition and tactile information processing related to the body itself. We suggest the posterior parietal cortex subserves both perception and action, whereas the insula principally subserves perceptual recognition and learning.

Keywords: body image; body schema; crossmodal; insula; parietal; proprioception; tactile object recognition

1. Introduction

The somatosensory system is involved in many aspects of our behaviour. It provides information about the position of different parts of the body with respect to one another. It allows characterisation and localisation of touch, stroking, and pain, and it is important for all motor action involving the body and limbs. Furthermore, tactile exploration informs us about the characteristics of external objects, resulting in a conscious perceptual experience of the stimulus which may lead to object recognition. The central question addressed in this review is how cortical somatosensory processing is organised to subserve these different functions.

We present a model that specifies the separable functional entities and their neuroanatomical correlates (Fig. 1). We suggest that separate cortical processing streams exist. One projects from the anterior parietal cortex (APC) (Brodmann areas 3a, 3b, 1, and 2) via the secondary somatosensory cortex (SII) to the posterior insula, whereas the second terminates in the posterior parietal cortex (PPC). We propose that action-related processing occurs mainly in the PPC, whereas recognition and perception involve the insula, as well as the PPC. The model also distinguishes *between* somatosensory processing about the body (where you have been touched) and about external stimuli (e.g., surface features of objects). This distinction is reflected in largely separate bodies of literature. A final characteristic of the model is 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.

Our starting point when developing this model was the idea that the anatomical and physiological organisation of the somatosensory system should reflect the eventual use of the somatosensory information rather than the detail of stimulus characteristics. This idea has been proposed previously for the visual system (Goodale & Milner 1992; Jeannerod & Rossetti 1993; Milner & Goodale 1995). An important aspect of this model of visual cortical processing is that, in addition to describing the function of certain brain regions in terms of the perceptual characteristics (e.g., spatial or object-centred), it is just as important to state the way in which we use this information (e.g., to store for later recognition or to program a motor action). We suggest that a similar approach would be useful when describing the processing characteristics of the somatosensory system.

Mishkin and colleagues have described a pathway of higher cortical somatosensory processing running from the APC via the SII to the posterior insula and subserving perceptual learning and memory (Friedman et al. 1986; Mishkin 1979; Murray & Mishkin 1984; Pons et al. 1987), and they have suggested that this pathway might be conceptualised as a somatosensory equivalent of the

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visual ventral stream (Mishkin 1979). We have incorporated this proposed pathway in our model, but have expanded the neural mechanisms involved in tactile object perception to include the PPC, based on more recent patient and functional imaging studies. In addition, we suggest that the posterior insula plays a role in the perceptual representation of the body.

A third source of inspiration about the functional organisation of the somatosensory system has been the work on different body representations. The idea of a body schema as an internal representation for action and a body image involved in perceptual identification of body features, as described by Paillard (1999), was particularly important. The studies of patients with residual tactile processing for action without perceptual awareness, as reported by Paillard et al. (1983) and Rossetti et al. (2001) were *especially* relevant.

Taking these sources together, this article incorporates existing ideas about the organisation of the cortical somatosensory system into one coherent model. In the following sections, we review evidence for this model in more detail. First, in section 2, we describe the characteristics of processing in the anterior parietal cortex (APC). Higher-order somatosensory processing is the focus of the next, section 3; after which, evidence for separate processing for perception and action in healthy individuals is described in section 4. Similarities and differences between the cortical somatosensory system and other sensory modalities are discussed in the following section, 5, while crossmodal interactions form the final topic (section 6). Our intention is to provide a model that incorporates a large body of the currently available evidence, from which testable hypotheses can be derived.

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2. Feature processing in the anterior parietal cortex

The main processing pathways of the somatosensory system from peripheral receptors to the cortex that are concerned with touch and proprioception are well known. Input from peripheral receptors ascends through the dorsal column in the spinal cord and subsequently arrives in the medulla. The fibres then decussate in the medial lemniscus and terminate in the ventral posterior lateral nucleus (VPL) of the thalamus (Martin & Jessell 1991; Mountcastle 1984). In addition, there are projections to the ventral posterior inferior nucleus (VPI) and the posterior nuclei group of the thalamus (Mountcastle 1984). A second ascending system, the anterolateral system, mainly deals with thermal and noxious stimuli, but also relays some pressure information. The anterolateral system also projects to the VPL in addition to smaller projections to VPI and centromedian (CM)/parafascicular complex and the intralaminar nuclei (Berkley 1980; De Vito & Simmons 1976; Sinclair 1981).

Most somatosensory information enters the cerebral cortex through projections from the VPL to the anterior parietal cortex (APC) (Jones & Powell 1970; Jones et al. 1979; Whitsel et al. 1978). This area was originally referred to as the first somatosensory cortex (SI), but more recently it has been suggested that only Brodmann area (BA) 3b can be considered to be the homologue of the primary area SI in non-primates (Kaas 1983; 2004). In addition, there are projections from the ventroposterior superior nucleus (VPS) to areas 3a and 2 (Cusick et al. 1985). Finally, small projections exist between the VPL and other thalamic nuclei to the secondary somatosensory cortex (SII), the posterior parietal and insular cortex (Burton & Jones 1976; Friedman & Murray 1986; Jones et al. 1979; Whitsel & Petrucelli 1969).

The organisation of the APC can be characterised by several principles. First, it consists of four different Brodmann areas, BAs 1, 2, 3a, and 3b, containing several somatotopic maps of the contralateral half of the body (Chen et al. 2005; Kaas et al. 1979). Neurophysiological studies suggest that one somatosensory aspect tends to dominate the input to each area. In area 3a, the dominant input originates in the muscle receptors (Phillips et al. 1971; Tanji & Wise 1981), although the hand and digit areas of BA 3a also contain a significant number of cutaneous neurons. In BA 3b (Tanji & Wise 1981) and BA 1, the main input originates in cutaneous receptors (Whitsel et al. 1971). Within these areas, specific cortical domains are activated by different types of stimulation, such as vibration, pressure, or flutter (Friedman et al. 2004). Lesions in each of these areas cause perceptual impairments on tasks that require processing of the relevant modality. In monkeys, area 3b appears to be involved in most tactile discrimination tasks. Removal of area 3a severely impairs performance on several discrimination tasks, including hard-soft, roughness, concave-convex, and square-diamond discriminations (Randolph & Semmes 1974). The neurons in area 1 are predominantly cutaneous, but respond to more complex stimuli, such as movement

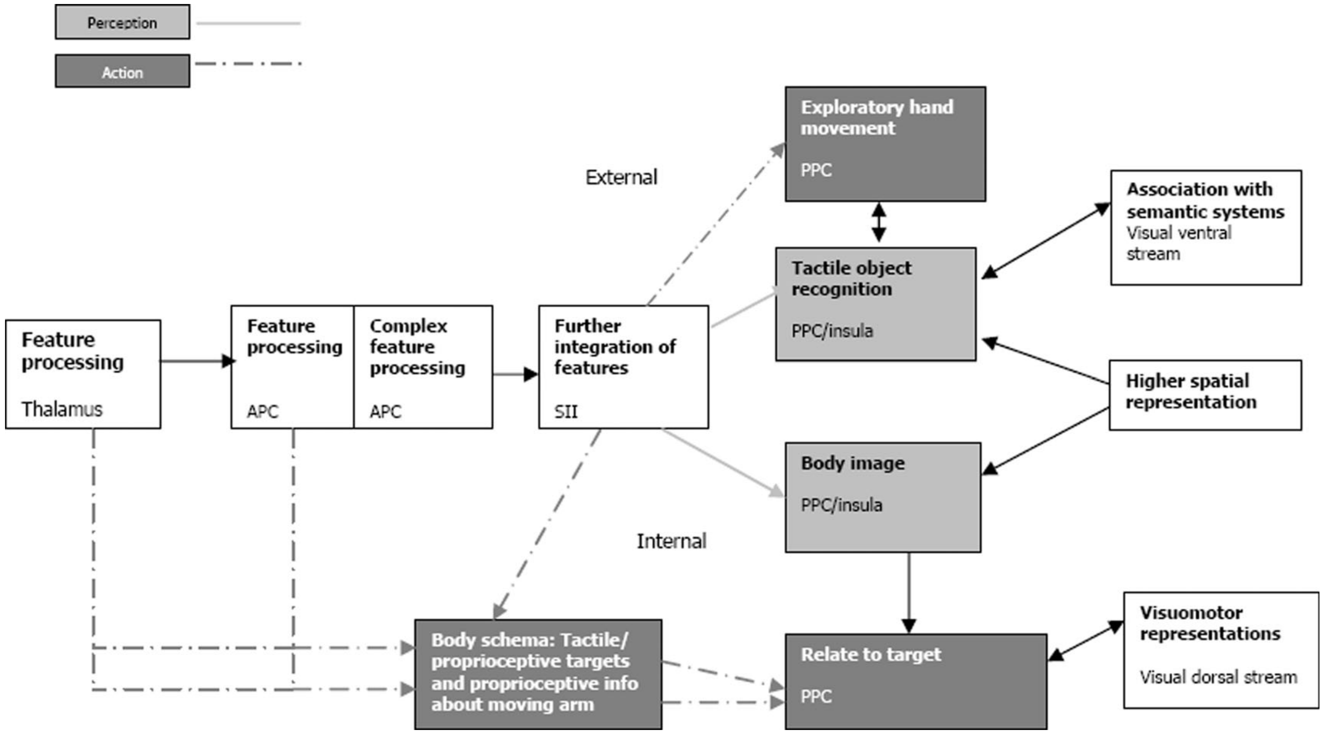

Figure 1. An outline of the proposed model. Dark grey boxes and broken lines depict areas and projections involved in somatosensory processing for action. Light grey boxes and lines show the areas and pathways involved in somatosensory processing for perceptual recognition. Note also the distinction between somatosensory processing pertaining to the body (internal, shown in the bottom of the figure) and tactile processing of information concerning external stimuli such as objects (top). APC, anterior parietal cortex; SII, secondary somatosensory cortex; and PPC, posterior parietal cortex.

detection and the direction sensitivity (Gardner 1988; Hyvärinen & Poranen 1978). In humans, area 1 contains larger representations (Overduin & Servos 2004). Removal of area 1 impairs discriminations involving texture (e.g., roughness, hard-soft) (Randolph & Semmes 1974). The main input to BA 2 originates in deep receptors (joint and muscle afferents; Merzenich et al. 1978). Indeed, removal of this area in primates results in impaired performance on tasks involving kinaesthetic input, such as discrimination of concave versus convex and diamond versus square shapes (Randolph & Semmes 1974). Area 2 also contains modules of cutaneous neurons with complex receptive fields and response properties in the hand and digit areas (Gardner 1988; Hyvärinen & Poranen 1978; Pons et al. 1985). In the early stages of cortical processing, the neuronal responses represent the characteristics of stimuli applied to peripheral nerves relatively accurately (Phillips et al. 1988). Neurons situated further away from the thalamic input have more complex response properties, which suggests that advanced processing occurs. For example, electrophysiological studies showed that direction-sensitive neurons were found less commonly in area 3b, but more densely in areas 1 and 2 (Gardner 1988; Hyvärinen & Poranen 1978). Indeed, lesions of areas 3b, 1 and 2 cause impairments in distinguishing the speed of tactile movement (Zainos et al. 1997). In humans, lesions affecting the postcentral gyrus cause deficits in two-point discrimination; position sense and point localisation; object size, shape, and texture discrimination (Corkin et al. 1970; Kaas 2004; Roland 1987).

The combined lesion and neurophysiological literature suggests that the APC is important for the processing of simple somatosensory features related to both the stimulus and the part of the body that has been stimulated. Moreover, recent optical imaging of a tactile illusion suggests that the APC codes the *perceived* rather than physical location of peripheral stimuli (Chen et al. 2003). This finding suggests that neural processing is related to what the information is processed for (e.g., perception) rather than the stimulus characteristics. Thus, it is consistent with the idea that the *purpose* is at least as important when discussing the neural basis of sensory processing. Indeed, certain types of input may be more important for certain tasks, with proprioceptive input contributing more to action-related processes, and the skin receptors providing more information for perceptual purposes. However, this mapping of different somatosensory submodalities to output is by no means absolute.

With respect to somatosensory processing for the guidance of action, the findings of neuropsychological studies suggest that damage to the APC does not necessarily abolish accurate pointing movements. Several investigators have reported patients with damage to the primary somatosensory cortex who showed severe impairments in tactile perception while their motor deficits were surprisingly mild (Brochier et al. 1994; Halligan et al. 1995; Pause et al. 1989; Volpe et al. 1979). In a seminal study, Volpe et al. (1979) reported four patients with tactile and proprioceptive deficits following a stroke, who were nevertheless able to perform spatially oriented movements with the de-afferented hand. In the study by Pause et al. (1989), the patient, who had a total loss of sensibility and tactile recognition with the contralesional hand, remained able to perform several motor acts, including the pincer grip and exploratory movements. Brochier et al. (1994) observed that their patient could touch the thumb of the insensate hand with each finger individually (similar observations were made also in a patient assessed by Halligan et al. 1995) and could crumble a piece of paper with this hand, while having severe difficulties in recognizing the direction of movements on her skin and letters drawn on her hand.

Spared sensorimotor guidance to targets on the *impaired* arm that were not perceived, has been reported in other studies. In a first description of this kind, Paillard et al. (1983) reported a patient with a left posterior cortical lesion who could point to tactile targets on her right hand that she was unable to detect. They suggested that there were striking similarities with blindsight. A similar dissociation was reported by Rossetti and colleagues (see Rossetti et al. 1995b; 2001), who investigated a patient with a lesion affecting the thalamic nucleus VPL. They assessed his ability to use touch and proprioception for verbal and pointing localisation responses. Localisation of targets by using both touch and proprioception was above chance only when a pointing response was made aimed directly at the target (see Fig. 2). Verbal responses or pointing responses on a drawing of the arm were at chance. Delaying the motor response also reduced performance to chance levels. Rossetti et al. argued that their patient showed a dissociation between the *what* (object recognition) and the *how* (sensorimotor) systems and coined the term "numbsense" for this phenomenon. Another study, by Aglioti et al. (1996), reported similar findings. In addition, Aglioti et al. found above-chance performance when subjects pointed with their insensate hand to the location of stimulation applied to their normal hand.

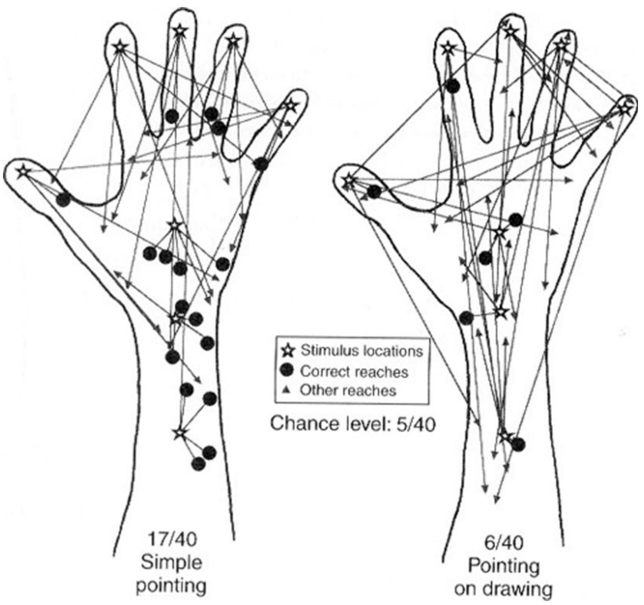

Figure 2. Performance of numbsense patient J.A. on two pointing tasks. In the simple pointing task, the patient pointed with his left hand directly towards a tactile stimulus on the impaired right arm or hand (left picture). He clearly performed this task at above chance levels. In the second task, he was asked to indicate the position of the tactile target by pointing to its location on a drawing of the right hand (right picture). Performance on this task was not different from chance. Reproduced by permission of Oxford University Press (www.oup.com) from Rossetti et al. (2001), Fig. 15.4, p. 275.

Thus, lesion studies suggest that somatosensory information can be used for the guidance of movements after lesions to the APC or the VPL, although the stimuli cannot be detected consciously. While some "numbsense" studies assessed pointing to proprioceptive or tactile targets on the insensate arm (Aglioti et al. 1996; Rossetti et al. 1995b), others showed that movements with the impaired arm were still possible despite the absence of proprioceptive feedback (Brochier et al. 1994; Pause et al. 1989; Volpe et al. 1979).

Regarding the neural substrate of these unconscious residual sensorimotor abilities, several possibilities have been suggested. Brochier et al. (1994) and Rossetti and colleagues proposed that thalamic projections to the PPC, bypassing the APC and the VPL, may be responsible (Rossetti 1998; Rossetti et al. 2001). Brochier et al. (1994) and Rossetti et al. (2001) identified projections from the posterior lateral nucleus and medial portion of the posterior complex to the PPC (cf. Jones et al. 1979; Pearson et al. 1978) as possible substrate. A second possibility may be that direct projections from the VPL to the motor cortex are involved (Jeannerod et al. 1984), although this may be less likely in the case of Rossetti et al. because their patient's lesion primarily affected this thalamic nucleus. A final suggestion is that small ipsilateral pathways to the intact hemisphere may be responsible (Rossetti et al. 1995b; 2001). Supportive evidence for this notion comes from studies with hemispherectomized patients who usually do retain some crude somatosensory function on the side contralateral to the removed hemisphere (Dijkerman 1996; Holloway et al. 2000; Muller et al. 1991). Whether these pathways are also involved in certain basic aspects of conscious perception, such as stimulus detection, remains as yet to be determined.

The main lesson to be learned for the issue at hand is that – as is the case for the visual system – the execution of a motor action towards a spatially defined target does not necessarily depend on conscious awareness of that target. This observation supports the idea of two separate somatosensory pathways for action and conscious perception.

3. Higher somatosensory cortical processing

Processing of somatosensory input beyond the APC occurs in several cortical areas. These include the secondary somatosensory area (SII), the insula, and the PPC. Overall, somatosensory projections involving these areas are characterised by serial, as well as parallel, processing (Iwamura 1998; Knecht et al. 1996). The APC maintains reciprocal connections with the SII (Barbaresi et al. 1994; Disbrow et al. 2003; Friedman et al. 1980; Pons & Kaas 1986), although the projections from the APC to the SII are more important than those from SII to the APC (Pons et al. 1987). Neurons in the SII have greater stimulus selectivity, larger receptive fields, reduced modality specificity, and respond to ipsilateral, as well as contralateral, stimulation (Disbrow et al. 2001; Lin &

Forss 2002; Ruben et al. 2001; Sinclair & Burton 1993). The SII is reciprocally connected with granular and dysgranular fields of the insula (Friedman et al. 1986). Neurophysiological recordings from the granular insula in rhesus monkeys showed that a major portion of this area is exclusively devoted to somatic processing (Schneider et al. 1993).

The SII has additional projections to the posterior parietal area 7b, both ipsilaterally and contralaterally, and the premotor cortex in the same hemisphere (Disbrow et al. 2003; Friedman et al. 1986). In monkeys, the PPC also receives direct connections from the APC. Area 5 (superior parietal cortex) receives input from areas 1 and 2 (Pearson & Powell 1985; Pons & Kaas 1986), whereas area 7b (inferior parietal cortex) receives direct input from area 1 (Pons & Kaas 1986). Several thalamic nuclei also project directly to the SII (Disbrow et al. 2002) and to different parts of the PPC (Friedman & Murray 1986; Jones et al. 1979). Major cortical outputs from the PPC project back to the SII and to the premotor cortex, the limbic cortex, and the superior temporal sulcus (Kaas 2004).

An important question is whether two processing streams can be discerned in this network of connections, analogous to the visual system (Milner & Goodale 1995; Ungerleider & Mishkin 1982). Indeed, it has been suggested that the projections from the APC via the SII to the granular and dysgranular fields of the insula are involved in tactile perception and learning (and thus would constitute the somatosensory equivalent to the visual "what" pathway; see sect. 3.1) (Friedman et al. 1986; Mishkin 1979). The tactile "dorsal stream" would involve projections from the APC to the PPC (Westwood & Goodale 2003), either directly or through the SII. In a study of anatomical connections of two areas within the SII (the SII proper and the parietal ventral area [VP]) in monkeys, Disbrow et al. (2003) suggested that the interconnections between these two areas in the SII overlapped considerably. They suggested that this was inconsistent with the idea of two separate processing streams. Indeed, Disbrow et al. (2003) indicated that the SII may be involved in somatosensory processing for both perception and action. In our view, the data of Disbrow et al. are not at all inconsistent with the idea of separate processing pathways for perception and action, as segregation may not occur until after the SII.

In a recent fMRI study, Reed et al. (2005) investigated whether a "what" versus "where" dissociation also exists for somatosensory processing. They compared tactile object recognition with tactile object localisation while controlling for differences in exploratory finger movements. Differential activation patterns were observed with tactile object recognition activating frontal, as well as bilateral, inferior parietal areas. In contrast, the tactile object location task was associated with activation in bilateral superior parietal areas. Note that these authors link their investigations with to the distinction between spatial and object vision made by Ungerleider and Mishkin (1982). Indeed, Reed et al. (2005) specifically controlled for differences in the action component, e.g., exploratory finger movements.

In the present review, instead of the "what" versus "where" distinction, we discuss evidence from patient, functional imaging, and neurophysiology studies for separate processing for somatosensory perception and action ("what" vs. "how"). As action and perception are both broadly defined functions that can include many different aspects, a further subdivision is made between processing of external target features (e.g., for object recognition) and somatosensory input about the body (e.g., the body representations). Indeed, functional differences have been found between judgements pertaining to the position of the stimulus on the body and in external space (Kitazawa 2002). Differences in perception and action are therefore reviewed separately for internal and external somatosensory information, respectively.

3.1. Tactile object recognition

One major function of the somatosensory system is the recognition of external stimuli, such as objects. We frequently make use of tactile perception to recognize objects in our daily lives, for example, when retrieving keys from our pockets. Recognizing objects by touch is usually not a passive process (Gibson 1962). The stimulus is typically explored actively by using finger and hand movements to build a perceptual object representation. The results of psychophysical studies suggest that the finger and hand movements made are not random, but depend on the object characteristics that need to be identified. Lederman and Klatzky (1987) observed that when subjects were asked to discriminate a particular dimension (e.g., texture, hardness, and weight), different types of hand movements, named *exploratory procedures*, could be identified. The exploratory procedures used depended on the dimension to be discriminated. For example, texture was mainly explored through sideway movements between skin and object surface (lateral motion), whereas hardness was determined by pressing the object. When identifying objects, sequences of exploratory procedures are executed that would enable a representation to be built that can be matched with object representations in memory (Lederman & Klatzky 1993). The selection of the exploratory procedures depends on a number of factors, including its duration, breadth of sufficiency (number of features that can be extracted through this particular exploratory procedure), and compatibility with other exploratory procedures. These findings suggest a close relation between perceptual processes and finger and hand movements that support these perceptual processes. On the basis of these behavioural characteristics, one would perhaps also expect the neural pathways involved in tactile object recognition and the performance of exploratory finger movements to be highly interrelated. Evidence from monkey-lesion, neuropsychology, and functional imaging studies suggests that dissociable neural processes can be identified for the sensory guidance of the exploratory finger movements and for tactile object recognition.

With respect to perceptual processes, Mishkin and coworkers (Friedman et al. 1986; Murray & Mishkin 1984) proposed that, in monkeys, the cortical pathway projecting from the APC via the SII to the insula is involved in tactile discrimination and recognition (see also Burton & Sinclair 2000). Several studies suggest a distinct involvement of each area in tactile memory. Recent studies implicate the APC in working memory and learning of simple stimulus features such as vibration, pressure, and roughness in humans (Harris et al. 2001a; 2001b; 2002). With respect to the SII, monkeys with damage to the SII exhibit impairments in tactile discrimination learning (Garcha & Ettlinger 1980; Murray & Mishkin 1984), and, in humans, lesions including the SII may cause tactile agnosia (Caselli 1991, 1993; Reed et al. 1996). Furthermore, functional imaging studies report activation in the SII after application of simple stimuli (Hagen & Pardo 2002; Hodge et al. 1998; McGlone et al. 2002; Ruben et al. 2001), as well as during recognition of objects (Reed et al. 2004). Evidence for insular involvement in tactile object recognition is mixed. Studies with human patients reported tactile agnosia after lesions that included the insula or the retroinsular cortex (Bohlhalter et al. 2002; Caselli 1993). However, in all these cases, the PPC was at least partly damaged, as well. Furthermore, lesions sparing the insula, but affecting the PPC, may also cause tactile object recognition deficits (Knecht et al. 1996; Reed & Caselli 1994; Reed et al. 1996). Similarly, tactile discrimination deficits have been observed following PPC lesions in monkeys (Moffett et al. 1967). Neurophysiological and functional imaging studies suggest that the anterior part of the intraparietal sulcus (AIP) is particularly involved in tactile, but also visual, representations of objects and object manipulation (Binkofski et al. 1999b; Grefkes et al. 2002; Seitz et al. 1991). A study by Stoeckel et al. (2004) observed differences between right and left superior parietal involvement in tactile object discrimination. Activation on the right was associated with kinaesthetic attention, whereas maintenance of tactile information for subsequent object discrimination activated left superior parietal areas. Functional imaging studies also provide some evidence for insular involvement in tactile object recognition. Reed et al. (2004) observed insular activation when comparing object recognition with palpation of nonsense shapes. In addition, activation in the insula and central opercular region has been reported during tactile long-term and short-term memory tasks (Bonda et al. 1996; Burton & Sinclair 2000) during relatively simple stimulations, such as being stroked, thermal stimulation (Davis et al. 1998), and vibrotactile stimulation (Hodge et al. 1998; McGlone et al. 2002).

Overall, these results suggest that the PPC as well as the insula are involved in tactile object recognition. A possible explanation is that, in contrast to the visual system which is inherently spatial, tactile object recognition requires integration of spatial somatosensory information over time. Damage to the inferior PPC may impair temporal integration of spatial somatosensory information, which is crucial for tactile object recognition. In an earlier study, Semmes (1965) found that tactile object recognition deficits without primary sensory impairment were frequently accompanied by spatial deficits. Vallar (1997) also suggested that high-level spatial representations contribute to somatosensory performance and linked this to the right PPC. Indeed, spatial distortions have been found in tactile size matching in patients with hemispatial neglect, which usually results from right inferior parietal lesions (Bisiach et al. 2004). However, not all tactile agnosias are a consequence of right parietal damage, nor do they all exhibit spatial impairments (Reed & Caselli 1994; Reed et al. 1996). Saetti et al. (1999) suggested that tactile agnosia could be caused by disruption to two distinct mechanisms. It may arise from contralesional parietal lesions, damaging somatosensory processing that culminates in the structural description of the object. Or it may be caused by a profound derangement of spatial skills, affecting both hands to the same degree. The latter is associated with right PPC damage.

With respect to the interrelatedness of tactile recognition and manual exploration suggested earlier, neuropsychological studies show that impairments in tactile object recognition can occur both with and without deficient tactile exploration. Several studies reported impaired tactile object recognition together with deficient manual exploration after lesions affecting the PPC (Binkofski et al. 2001; Knecht et al. 1996; Pause et al. 1989). However, others reported patients whose tactile agnosia was independent of exploratory hand movement deficits (Platz 1996; Reed & Caselli 1994; Reed et al. 1996). Basic somatosensory function was normal in all these patients.

Exploratory hand movements can also be impaired while tactile perception remains relatively preserved. Pause et al. (1989) observed that patients with posterior parietal lesions were severely disturbed in their ability to perform exploratory movements, while having only mild to moderate somatosensory perceptual disturbances. Remarkably, these patients could produce the exploratory movements imitatively. This suggests that the disturbance of the posterior parietal patients is one of sensorimotor transformation for the guidance of exploratory hand movements that normally provide information required for the identification of objects.

Valenza et al. (2001) described a patient with an intact ability to perceive passively applied stimuli, but with severe impairments when required to use exploratory finger movements for object identification. The lesion of this patient affected, among other regions, the inferoposterior parietal lobe, including the intraparietal sulcus. Functional magnetic resonance imaging (fMRI) recordings with this patient showed a lack of activation in the superior temporal and inferoparietal regions, compared to control subjects during passive somatosensory stimulation.

Functional imaging studies also indicate a role for the PPC in exploratory hand movements. Seitz et al. (1991) found increased regional cerebral blood flow (rCBF) in the superior PPC during tactile discrimination of unfamiliar objects. fMRI recordings during manipulation and exploration of complex meaningless objects showed activation of the superior parietal cortex (area 5), the opercular parietal cortex, including the SII, and the AIP (Binkofski et al. 1999b; Jäncke et al. 2001).

Overall, the studies reviewed here suggest an overlap, as well as dissociation, between the neural mechanisms involved in exploratory hand movements and those responsible for perception of objects. Both the PPC and the insula have been implicated in the perception of objects. The PPC has been implicated in exploratory hand movements, and patient studies suggest that exploratory finger movements are dissociable from perceptual recognition of objects. We suggest that the APC–SII–Insula route is responsible for conscious somatosensory perception and recognition of objects, with the right inferior PPC contributing to spatio-temporal integration. However, often exploratory movements are necessary to recognize an object and at this point the APC–PPC cortex route is called upon to program these movements that constitute specific, well-rehearsed action sequences depending on the type of information that is required. This route may involve superior parietal areas (particularly area 5). AIP seems to be involved in both perceptual representation of the object and exploratory finger movements. It, therefore, may act as an interface between perceptual and motor-related processes and could be involved in temporal and spatial integration of input obtained during tactile exploration into an object representation. Thus, recognition via hand and finger movements depends on an intricate collaboration between the parietal and the insular systems.

3.2. Cortical processing of somatosensory information pertaining to the body

Perhaps an even more important function of the somatosensory system is informing us about the position of our different body parts with respect to one another. To achieve this, tactile and proprioceptive input needs to be integrated with visual and vestibular input into a representation of the body. Evidence concerning body representations comes from different sources. Studies of neurological patients show that a variety of lesions to the peripheral and central nervous systems can result in changes of body representations. For example, some limb amputees report that their phantom limb can change in size and form over time (Berlucchi & Aglioti 1997). Lesions to the central nervous system can produce disorders such as anosognosia (denial of symptom) for motor and sensory deficits after a stroke (Berlucchi & Aglioti 1997; Levine et al. 1991), denial of ownership of a body part, and misplegia (hatred of hemiparetic limbs) (Berlucchi & Aglioti 1997; Moss & Turnbull 1996). These disorders usually, but not always, are found after right hemisphere lesions and may be accompanied by reports of supernumerary limbs (Halligan & Marshall 1995), suggesting that negative and positive syndromes share common neural mechanisms. Left posterior parietal brain lesions can result in other impairments of body representations, such as autotopagnosia (inability to localise body parts), finger agnosia, and left-right disorientation (Denes 1999).

The important question for the present review is whether different representations of the body are used for the guidance of movements, as compared to perceptual judgements about the spatial relations of the different body parts. Several authors have suggested that this indeed may be the case. For example, Paillard (1999) distinguished between *body schema* and *body image. Body image* was described as a "perceptual identification of body features" related to an internal representation of sensory and motor input of corporeal origin. This internal representation would be accessible to conscious experience. In contrast, the *body schema* refers to the location of different body parts in a sensorimotor map of body space, which is not accessible to consciousness. In addition to the two body representations described by Paillard, other authors also distinguished a third representation containing conceptual and semantic knowledge about the body (Buxbaum & Coslett 2001; Guariglia et al. 2002; Schwoebel et al. 2001; Sirigu et al. 1991).

Evidence for separate body representations from neuropsychological studies was first described almost a century ago (Head & Holmes 1911–1912). More recently, Paillard (1999) suggested that the "numbsense" patients mentioned earlier in this review have a specific deficit in the perceptual representation of target (body image), while the sensorimotor representation (body schema) remains unaffected. He described the opposite dissociation in a patient who suffered from peripheral deafferentation, but with an intact motor system. She was able to verbally identify the location of tactile stimuli, but was poor at pointing towards the stimulus (see Fig. 3). This would be consistent with an impairment in body schema, with preserved body image. A similar pattern (impaired pointing in combination with intact verbal report) has also been reported by Halligan et al. (1995).

Other evidence for separate body representations involved in the guidance of action and perceptual recognition of objects comes from patients with autotopagnosia. Buxbaum and Coslett (2001) described a patient who was unable to point to any of his body parts, or to those of another person, yet could perform visually guided grasping movements. The latter suggests that his impairment was unlikely to be the consequence of an impairment in body schema. Furthermore, he was able to point to objects attached at different locations to the body (see also Sirigu et al. 1991). Buxbaum and Coslett suggested that their patient had an impaired "system of structural descriptions of the body and its parts which defines the position of body parts relative to one another in a perceptual . . . format" (p. 302). In a recent study of body representation disorders in a group of 70 stroke patients, Schwoebel and Coslett (2005) observed a triple dissociation between measures of three putative body representations (body schema,

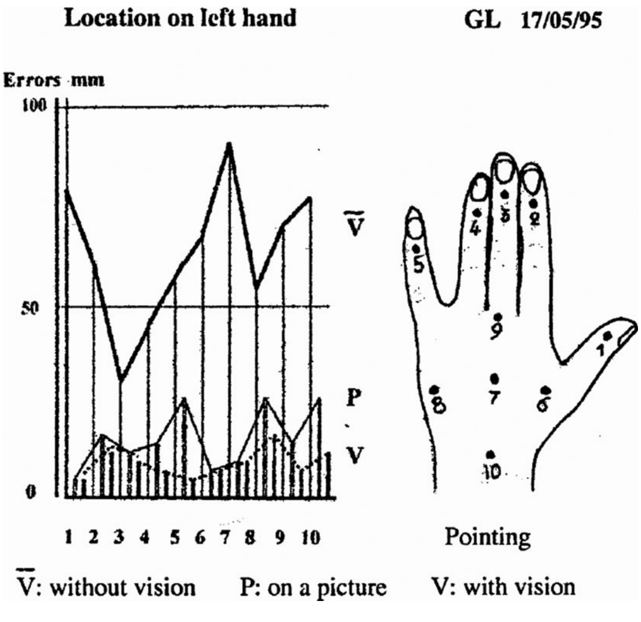

Figure 3. Performance of peripherally de-afferented patient G.L. on three pointing tasks. Cold tactile stimuli were applied to various locations on her left hand. In the "without vision" condition, GL was greatly impaired in pointing towards the stimuli. Performance was considerable better when allowed vision of her left hand. Remarkably, her performance was similar to the "vision" condition when asked to point to the location of the stimulus on a picture of the left hand. From Paillard (1999) with permission from Academic Publishing House, Sofia, Bulgaria.

body structural description, and body semantics). They linked the left temporal cortex to structural and semantic knowledge, and the dorsolateral frontal and posterior parietal lesions to body schema.

Other authors have implicated a network that includes the APC, the PPC, and the insula to be involved in bodily awareness and perception (Berlucchi & Aglioti 1997; Melzack 1990). Each area is supposed to play a different role. Thus, lesions to the APC result in tactile and proprioceptive impairments, but not in higher-order body-awareness deficits. The SII appears to be important for integration of information from the two body halves (Hari et al. 1998; Lin & Forss 2002). Lesions to the PPC can result in alterations in higher-order body awareness, as mentioned previously, with lesions to the left and the right PPC producing different types of deficits. Functional imaging studies also suggest that the PPC is involved in body representations. A positron emission tomography (PET) study showed activation in the superior PPC, intraparietal sulcus, and adjacent inferior parietal lobule during mental transpositions of the body in space (Bonda et al. 1995) In a more recent study, Ehrsson et al. (2005b) used the vibrotactile illusion to study the neural basis of body representations and, specifically, body image. Participants were asked to hold their waist while vibrotactile stimulation was applied to the wrist extensors. They experienced predictable changes in waist size. This illusion was related to activation in the left postcentral sulcus, but also in the anterior part of the left intraparietal sulcus, suggesting that this area is involved in the perceptual experience of body size.

In addition to the PPC, the insula may be involved in corporeal awareness. Patients with insular lesions may experience somatic hallucinations (Roper et al. 1993) or somatoparaphrenia (Cereda et al. 2002). A recent lesion overlap study implicated the posterior insula in bodily awareness (Karnath et al. 2005). Functional imaging studies also suggest that the insula activation may be related to a sense of ownership and agency (Farrer et al. 2003). Others have related the insula to subjective awareness and affective processing of bodily signals (Craig 2002, 2004). Craig has proposed a separate pathway relaying input regarding the ongoing condition of different organs of the body (viscera, muscles, joints, skin, etc.). This pathway mainly relays information through small-diameter afferent fibres to the spinal dorsal horn and the solitary nucleus in the medulla as part of the autonomic nervous system. It not only provides input as part of homeostatic mechanisms to the hypothalamus and brain stem, but also projects through the ventral medial nucleus of the thalamus to the posterior insula (see also Olausson et al. 2002). Further projections exist from the posterior insula to the anterior insula. Craig has suggested that this pathway is related to our subjective awareness of our body and bodily emotions (“how you feel”). Thus, in this model, emotional processing is related to activity of the autonomic nervous system. Craig (2005) has additionally suggested different roles for the left and the right insulae. The right insula is suggested to be related to “aroused” emotions linked to the sympathetic system. In contrast, the left insula is considered to be involved in “parasympathetic” or “enrichment” emotions.

Overall, the studies reviewed here suggest that the insula is concerned with higher-order somatosensory processing of the body that is either related to a sense of ownership or to emotional experience. In contrast, the posterior parietal cortex may be more concerned with metric aspects of the body, such as its spatial configuration and size. Although the data are not entirely consistent, the overall picture that emerges is that the anterior part of the intraparietal sulcus is consistently involved.

With respect to the neural basis of action-related body representations, again a network of different neural structures appears to be involved. Activity related to arm movement occurs already early in the somatosensory system. Neurons in the postcentral gyrus have been found to modulate their responsiveness to arm movement, depending on whether the arm movement was made passively or actively (Prud’Homme & Kalaska 1994). Furthermore, different sensorimotor channels can be detected in the APC. Iwamura and Tanaka (1996) reported that certain neurones in area 2 were activated only by self-generated hand actions to reach or to grasp objects. These neurones were preferentially active during reaching, a precision grip, or a whole hand grasp. A recent fMRI study confirmed the involvement of the APC in somatosensory-guided movements in humans (Wenderoth et al. 2006). These areas may provide kinaesthetic information to the multimodal visuomotor neurones in the PPC, although another possibility may be the direct connections to the motor cortex (Johnson et al. 1996; Marconi et al. 2001; Rizzolatti et al. 1998) Of course, we also know that information about the movement of the arm can bypass the postcentral gyrus (see sect. 2).

The SII also seems to play a role in proprioception. Activation of the SII is modulated by isometric muscle contraction (Lin et al. 2000) and activation after electric median nerve stimulation is enlarged bilaterally when accompanied by exploratory finger movements (Huttunen et al. 1996).

A third area that plays a particularly important role is the PPC. Neurophysiological studies suggest that particularly area 5 is involved in somatosensory processing concerning the body during goal-directed arm movements. Neurones in this area respond to somatosensory stimulation that is reach-related (Colby 1998; Gregoriou & Savaki 2001), whereas others have been found active during prehension (Debowy et al. 2001; Gardner et al. 1999; Ro et al. 2000). Furthermore, integration of tactile, and especially proprioceptive, input about the movement of the arm with sensory information about the target probably occurs in the posterior parietal lobe. There is considerable evidence that the PPC is involved in the transformation of visual signal into motor commands (Jeannerod et al. 1995; Kalaska et al. 1997; Milner & Dijkerman 1998). Neurophysiological studies (Colby 1998; Sakata et al. 1973; Savaki et al. 1997) and neuroimaging studies (Clower et al. 1996; Kertzman et al. 1997) suggest particular involvement of the area 7 in the integration of visual target information with proprioceptive limb information (see also sect. 6).

4. Behavioural dissociations in studies of healthy subjects

While the review so far suggests that there is considerable evidence for dissociated neural processing for somatosensory perception and action, relatively few studies have investigated possible behavioural dissociations in healthy participants. Westwood and Goodale (2003) assessed the effect of a haptic version of a visual size-contrast illusion on perceptual size matching and grasping responses. Subjects were required to explore with the left hand a flanker object placed underneath a table and subsequently hold a target object positioned adjacent to the flanker object. The flanker object could be smaller, larger, or identical to the target object. They were then asked to either perceptually estimate the size of the target object by varying the index finger–thumb distance of the right hand, or grasp an object identical to the target object on the table with that hand. Although the size estimates were influenced by the flanker object (smaller for the larger flanker object), no effect was found for the maximum grip aperture during grasping.

Whereas Westwood and Goodale (2003) investigated somatosensory processing of external objects, Kammers et al. (2006) used a vibrotactile illusion to explore differences between matching and reaching involving the position of a body part. The vibrotactile illusion is evoked by repetitive stimulation of a tendon of a muscle in one of the extremities. This stimulation induces the subjective experience of a movement of that extremity congruent with relaxation of that muscle. Two conditions were used. The *direct* condition, in which the biceps brachii tendon of the dominant arm was vibrated, created an illusory extension of the underarm. The *indirect* condition, wherein the ipsilateral knee was held with the vibrated arm, caused an illusion of lowering of the leg. In each condition, subjects were asked to make a reaching response (point with the index finger of the non-stimulated arm to the felt location of the ipsilateral index fingertip or top of the kneecap), as well as a matching response (mirroring the position of the non-stimulated arm or knee to the perceived position of the stimulated arm or kneecap). The illusion was significantly larger for the matching as compared to the reaching response, with the largest difference observed in the direct condition, suggesting that body representations underlying perception and action may be differentially sensitive to the illusion in healthy individuals. In an earlier study, Sittig and colleagues observed that subjects continued to reach to the correct target position when vibrotactile stimulation was applied to the moving arm (Sittig et al. 1985). In a more recent study, Marcel (2003) also observed a difference in sensitivity to the vibrotactile illusion between the perceptual report and motor response. In addition, he reported that, after several seconds, the motor responses also became influenced by the vibrotactile illusion. This intriguing observation suggests that, with time, cognitive perceptual representations of limb position become dominant.

Overall, the findings of these behavioural studies are consistent with the idea that somatosensory processing for perception can be dissociated from those underlying action, although the Marcel (2003) study suggests that interactions between the two representations can occur.

5. Comparison with other sensory modalities

As mentioned before, the idea that the guidance of action requires different sensory processing than does recognition is not new and was first proposed about 15 years ago for the visual cortical system (Goodale & Milner 1992; Jeannerod & Rossetti 1993; Milner & Goodale 1995). Separate processing streams have been also been proposed for the auditory system (Belin & Zatorre 2000; Rauschecker 1998). These similarities in proposed cortical organisation of the different sensory systems may suggest a common plan of how sensory input is processed by the brain (Belin & Zatorre 2000; Rauschecker 1998). In this section, we compare the cortical organisation of the somatosensory system with that of other sensory systems. Although there are many similarities, some important differences exist, as well.

One of the central premises of the "separate visual cortical processing streams for perception and action" model is that neural processing is related to the way in which we use this information – for example, to store for later recognition or to program a motor action (Milner & Goodale 1995). Support for this idea, rather than for a distinction in terms of input characteristics (e.g., spatial vs. object vision), was based on mainly two lines of evidence. First, monkey neurophysiology suggested that posterior parietal regions also process non-spatial characteristics (size) for guidance of the hand (Sakata et al. 1995). Second, it has been argued that patients with neurological lesions indicate a double dissociation between visual processing for perception and for action. Patient D.F., who suffers from visual form agnosia, was impaired when required to give a perceptual judgement about the size or orientation of a visual stimulus, but was able to use the same stimulus characteristics for the guidance of hand movements (Goodale et al. 1991). In contrast, optic ataxic patient A.T. was impaired when required to grasp an object, while remaining able to judge the size of the object perceptually (Jeannerod et al. 1994). More recent fMRI evidence also seems consistent with this idea (Culham et al. 2003; James et al. 2003). Milner and Goodale (1995) further suggested that perceptual and action-related responses require different processing characteristics. The visuomotor system requires information about the position of the target in relation to the observer that is continuously updated. As a consequence, dorsal stream processing is characterised by egocentric reference frames and real-time computation with an inability to store the input for longer than a few seconds. In contrast, the perceptual system is able to recognize objects irrespective of its viewpoint, and it stores this information over long periods of time.

The visual ventral stream also plays a role in visuomotor control when it involves aspects that are characteristic for ventral stream processing, such as holding visual information during a delay or retrieval of object knowledge (Goodale 2001). Indeed, visual form agnosic patient D.F. was impaired when required to wait for as little as 2 seconds after stimulus presentation when grasping an object (Goodale et al. 1994). In contrast, optic ataxic patients improved their performance after a delay (Milner et al. 2001; 2003), consistent with the idea that such patients are able to use to intact ventral stream to overcome their visuomotor deficit when a delay is introduced. A second example is that optic ataxic patient A.T. improved in ability-to-grip scale when grasping familiar as compared to unfamiliar objects (Jeannerod et al. 1994), whereas visual agnosic patient D.F. failed to take into account stored knowledge about the characteristics of well-known objects when programming her grip (Carey et al. 1996). Other studies suggest that the ventral stream is also active when subjects must consciously identify the visual context and decide on the appropriate action (Passingham & Toni 2001). Together, these findings are consistent with the idea of two separate, but interacting, visual cortical streams. The dorsal stream is involved in the visual guidance of immediate goal-directed hand and arm movements. The visual ventral stream is primarily associated with visual perception and recognition; however, it is also involved in certain aspects of the visual guidance of movement that require delayed action, object knowledge, or conscious decision making.

To what extent are similar processing characteristics applicable to the cortical somatosensory system as proposed here? As already described by others, for both the somatosensory and the visual systems, response characteristics become increasingly more complex the further away the neurones are from the thalamic input into the cortex. This involves increasing receptive fields (Lin & Forss 2002; Ruben et al. 2001; Sinclair & Burton 1993), more complex stimuli required to activate the neurones (Gardner 1988; Hyvärinen & Poranen 1978), and so on. A second similarity is that residual unconscious processes can occur after lesions affecting primary cortical areas or the main thalamic relay station. Thus, implicit processing of tactile stimuli for action in the numbsense patients is very similar to the findings observed in the visual equivalent, that is, blindsight (Perenin & Rossetti 1996; Weiskrantz 1996) – as was indeed observed by the original investigators (Paillard et al. 1983; Rossetti et al. 2001). Third, there is some evidence that introducing a delay between stimulus presentation and response has similar effects in the visual and the somatosensory system. Rossetti et al. (2001) reported that performance of their numbsense patient reverted to chance levels when a delay was introduced. Similar findings were reported for action blindsight (Perenin & Rossetti 1996). In a study with healthy participants, Zuidhoek et al. (2003) observed that the introduction of a delay reduced errors on a haptic parallel-setting task. They attributed the improved performance to a shift from the egocentric towards the allocentric reference frame during the delay period. These findings are consistent with a shift from dorsal to ventral stream processing in the visual system.

Perhaps one of the most striking differences between the two-visual-cortical-streams model and the present proposal is the inclusion of body-related representations. Whereas the two-visual-cortical-streams model deals only with visual input concerning external stimuli, the somatosensory system first and foremost provides information about our own body. A model of somatosensory cortical processing, in our opinion, would be incomplete without incorporating ideas about the neural basis of body representations. In contrast, a model of the visual cortical processing does not necessarily include body representations, as the optical array can provide direct information about the structure and position of external stimuli. Nevertheless, visual input about the observer's body is an important source of information, both during the guidance of movements and for perceptual awareness and recognition of your body. With respect to the neural basis of visual body representations, there is ample evidence for egocentric coding of external targets in a reference frame linked to specific body parts (Andersen 1997; Colby 1998; Graziano et al. 2000); however, the neural correlates of visual representations of the observer's *own* body has received less attention. Recent functional imaging studies have reported activation in the extrastriate body area (EBA) when body stimuli have been viewed (Downing et al. 2001). While activation in this area is modulated by the position of the observer's body (Arzy et al. 2006b) and movement with the observer's (unseen) arm (Astafiev et al. 2004), activation responds mainly to pictures of other people's body and is therefore not specifically involved in *own* body representations.

A second possible difference between the visual and somatosensory systems pertains to the degree of separation in the two cortical processing streams and the amount of spatio-temporal integration that is required. In the visual system, processing for action and for perception is clearly linked to separate cortical processing streams. Although more recent work suggests that the two processing streams are probably more interconnected than originally was thought and the ventral stream plays a (specific) role in several aspects of visuomotor processing, functional characteristics can, nevertheless, be related to separate neural processing streams. Our review of the literature suggests that the separation between action-related and perception-related processes may be less distinct in the somatosensory system. We found evidence for the involvement of both the PPC and the insula in perception and again the PPC for action-related processes. The involvement of posterior parietal processing for somatosensory perception may be related to a fundamental difference between somatosensory and visual systems. Whereas the visual array enables simultaneous processing of different stimuli and stimuli features, tactile exploration of stimulus features occurs in a more sequential manner. Increased temporal and spatial integration may be required in order to be able to integrate the tactile input into a coherent representation of the stimuli. The inferior parietal cortex seems particularly important for such integration (Saetti et al. 1999). The role of the PPC in somatosensory perception may be related to these increased demands on spatio-temporal integration. Interestingly, higher-order visual spatial functions have also been related to inferior posterior parietal processing. This has also been described as the ventro-dorsal stream (Pisella et al. 2006; Rizzolatti & Matelli 2003) and has been related to disorders such as hemispatial neglect (after right hemisphere lesions) and apraxia (after left hemisphere lesions) (Milner & Goodale 1995; Pisella et al. 2006; Rizzolatti & Matelli 2003). Several investigators have noted that somatosensory deficits often co-occur with impairments in higher spatial processing such as neglect (Semmes 1965; Vallar 1997). This indeed may be the consequence of increased higher-order spatial processing that may influence visual, as well as somatosensory, spatial representations (Saetti et al. 1999; Vallar 1997).

A third sensory modality for which separate processing streams have been proposed concerns the auditory system. These suggestions are based on recent neurophysiological data discerning separable cortical areas for the processing of auditory input. These areas involve a core, a belt, and parabelt regions arranged in a concentric manner in the superior temporal gyrus (Kaas et al. 1999).

An important model of the functional architecture of auditory processing was proposed by Rauschecker and Tian (2000), who argued that a ventral pathway running from the auditory core area in a forward direction is involved in analysing the stimulus characteristics. This route is important for object identification (e.g., a voice) and hence called the "what" pathway. A second, more posterior dorsal, pathway is thought to be sensitive to spatial location (the "where" path). This distinction is further supported by patient studies (Clarke et al. 2000) and neuroimaging experiments (e.g., see Romanski et al. 1999). This model has been challenged by Zatorre and colleagues (e.g., Belin & Zatorre 2000), who agree with the conceptualisation of the ventral "what" pathway. However, they object to the idea that the posterior dorsal route is mainly involved in spatial localisation, because, among other reasons, there is little evidence for spatial maps in the auditory system. In contrast, they claim that the dorsal pathway is primarily involved in perceiving the "evolution in time of the signal emitted by one or several auditory objects" (Belin & Zatorre 2000, p. 965). Hence, the processing characteristic is likened to that of the visual area V5 or MT, processing time-related change in the signal. According to Zatorre and colleagues, the dorsal pathway processes the verbal message, whereas the ventral route is responsible for the recognition of the voice. In addition, they propose a lateralisation of function with the left hemisphere system being better tuned for speech perception (time sensitivity) and the right hemisphere system for music perception (pitch sensitivity; Zatorre et al. 2002).

Overall, there are clear similarities between the organisation of the auditory and the somatosensory systems. These systems share the increasing complexity of the information processing while moving away from the primary cortical areas (APC and the auditory core [Heschl's gyrus]). There is a reasonable agreement in the literature that two distinct pathways can be discerned in the auditory system. The equivalent of the "what" pathway is comparable in that it is involved in the recognition of external objects (as in vision), but there is no active exploration of the objects as is the case in tactile object recognition. The status of the "where" pathway is controversial, with different competing views. So far, there is little evidence for spatially organised cortical maps in the auditory system and a link with action-related processes.

Taken together, there appears to be substantial support for the idea that the different cortical sensory systems share overall organisational principles (Belin & Zatorre 2000; Rauschecker 1998). In addition, there are clear indications for a common organisational principle in the development of the morphology, architecture, and connections in the different modalities (e.g., see Pandya & Yeterian 1990). These include specialisation of function, subserved by separate processing routes. This distinction is, however, relative, because there are also clear differences resulting from the input (nature of the sensory signal) and the output characteristics (perception, action) of the particular modality.

6. Crossmodal interactions

Traditionally, the study of sensory systems has focused on the processes and structure within a single modality. More recent studies have demonstrated that the different senses work closely together and strongly influence one another. Neuroanatomy supports the notion of integration and mutual influence. An example at a relative basic level concerns the structure of the superior colliculus with close proximity and common organisation among visual, auditory, and somatosensory processing (May 2005).

Crossmodal processes have been found to affect a variety of tasks. Early perceptual processing in one modality may be modulated by input from another modality presented shortly prior to or simultaneously with the first stimulus. A dramatic example of this phenomenon is the observation that a single light flash is perceived as two flashes when the subject simultaneously hears two short auditory stimuli. The effect of the auditory stimulus alters processing in the primary visual cortex (Watkins et al. 2006). There is now a substantial literature on crossmodal links between auditory, tactile, and visual stimuli in spatial attention (Maravita et al. 2003; Schmitt et al. 2001). There are indications, however, that the links between vision and audition are perhaps stronger than between these modalities and touch (Eimer et al. 2002). Furthermore, cross-modality presentation may influence the "experience of ownership." Studies have shown that normal subjects experience a rubber hand as their own when it is stroked in a synchronous, but irregular, manner with their own unseen hand (Botvinick & Cohen 1998; Tsakiris & Haggard 2005). Functional imaging studies suggest that the ventral premotor cortex, the intraparietal sulcus, and the lateral cerebellum are involved in this illusion (Ehrsson et al. 2004; 2005a).

In another study, subjects experienced the hand seen on a screen as their own when their hand and the one on the screen are touched simultaneously. Using magnetoencephalography (MEG), it was demonstrated that the activity in the APC was modulated depending on whether the subject experienced ownership of the hand on the monitor (Schaefer et al. 2006a).

Crossmodal interactions have also been observed for somatosensory tasks in which non-informative vision was provided. Non-informative vision has been found to influence performance on a variety of perceptual tasks, ranging from spatial acuity (Kennett et al. 2001) to size constancy (Taylor-Clarke et al. 2004) and parallel setting of bars (Newport et al. 2002; Zuidhoek et al. 2004). The visual information provided varied, from a view of the stimulated body part (Kennett et al. 2001; Taylor-Clarke et al. 2004), to the environment excluding the stimuli (Newport et al. 2002; Zuidhoek et al. 2004). Fewer studies have investigated crossmodal interactions with respect to sensorimotor action. Newport et al. (2001) showed that impaired proprioceptive target information in a patient could be ameliorated during a pointing movement through non-informative vision of the surrounding environment.

The question relevant for this review is whether a certain specificity in the visual-tactile interaction can be observed. That is, are visual influences on somatosensory processing for action different from visual-tactile interactions during perceptual recognition? At a behavioural level, this topic has received little attention, even though neurophysiological and functional imaging studies suggest that these crossmodal interactions involve different neural processes. For example, a functional imaging study by Prather et al. (2004) showed that mental rotation of tactile forms activates the visual dorsal stream, whereas tactile form discrimination is associated with ventral stream activation. Furthermore, several fMRI studies showed activation of the lateral occipital complex (LOC, part of the visual ventral stream) during visual and tactile object recognition (Amedi et al. 2001; James et al. 2002; Reed et al. 2004). On the other hand, neurophysiological studies and functional imaging studies show multimodal activation in the PPC that is related to motor action (Clower et al. 1996; Kalaska et al. 1997; Kertzman et al. 1997; Savaki et al. 1997). Indeed, it could be argued that the two processing streams in both modalities project to the same higher-order cortical areas that are involved in multimodal sensory integration for the guidance of action (PPC) or perception (LOC).

With respect to the PPC in action, different areas within the superior parietal cortex and the intraparietal sulcus appear to be related to different visuomotor channels, including grasping, reaching, saccade, and pursuit eye movements (Hyvärinen & Poranen 1974; Milner & Dijkerman 1998; Mountcastle et al. 1975). Some of these areas contain neurones that have bimodal response properties and are active during reaching (Colby 1998). Multimodal processing in the PPC also appears to be related to distinct reference frames. For example, the bimodal responsive neurones in area VIP appear to code stimuli particularly in a head-centred reference frame (Duhamel et al. 1998), while bimodal activity in area MIP is related to arm-centred spatial representations (Colby 1998; Duhamel et al. 1998; Graziano et al. 2000). In humans, the PPC appears to be active when a conflict is created between visual and proprioceptive signals during a reaching movement (Clower et al. 1996). Overall, these findings suggest the PPC to be involved in multimodal coding of body-related and arm-related configurations used for the guidance of action.

With respect to perceptual recognition of external targets, activation of area LOC during visual as well as somatosensory object recognition has been found. Several possible explanations have been put forward for this finding. Participants may use visual imagery when performing a tactile object recognition task (Deibert et al. 1999). A second possibility is that LOC is a multimodal area related to higher-order perceptual representations of objects (Amedi et al. 2001; James et al. 2002). Amedi et al. (2001) observed that activation in LOC during visual imagery was less than during either tactile or visual object recognition Furthermore, Pietrini et al. (2004) observed similar activation during tactile recognition in congenitally blind subjects, which suggests that visual imagery is less likely to be the principal cause for the involvement of LOC in tactile object perception. Together, these findings suggest that LOC is a multimodal area involved in perceptual representation of object-form features.

7. Conclusions

The present review has discussed physiological, neuropsychological, and neuroimaging evidence concerning somatosensory processing for conscious perception and recognition, and for the guidance of action. Our hypothesis is that separate neural pathways are involved in the processing of somatosensory input for these two functions. Support for dissociations between perception and action has been found at several levels of processing and on a variety of tasks. Numbsense reveals a dissociation between detection of a simple touch and the preserved guidance of action towards the same stimulus based on processes that remained unaware to patients. For higher somatosensory functions, a further distinction can be made between somatosensory processing of internal and external targets. With respect to the latter, tactile recognition of objects may be impaired independent of exploratory finger movements deficits, whereas passive recognition of shape can remain preserved when exploratory hand and finger movements are impaired. In normal circumstances, however, perceptual and action-based processes must operate in a coordinated fashion during tactile object recognition, and damage to either system might lead to deficits. Regarding internal higher-order representations pertaining to the body, there is considerable evidence, especially from neuropsychological studies, that there are at least two different representations: that is, body image and body schema. Body image has been defined as a more stable and internal perceptual representation of the body, whereas the body schema contains a dynamic representation of different body parts that can be used for sensorimotor action.

These functional dissociations suggest that different neural processes may subserve somatosensory action and perception. Indeed, there is evidence for two separate routes of tactile processing, one projecting through the SII to the insula and another terminating in the posterior parietal areas. We suggest that the system responsible for somatosensory processing for the immediate guidance of action is subserved by a route that runs from the APC, either directly or via the SII, to the PPC. This area is subsequently involved in crossmodal integration and the preparation of movements. Somatosensory processing for conscious perception and memory is performed by a system that culminates in the insula. In addition, the right PPC appears to be involved in spatio-temporal integration of somatosensory input during recognition of objects and body configurations, whereas the left PPC has been implicated in structural and semantic body representations.

We have thus developed a model to describe the cortical processing of somatosensory information (see Fig. 1). Although our model is inspired by ideas about the organisation of the visual cortical system, there are some important differences. First, we make a distinction between processing concerning internal and external stimuli, whereas the two-visual-systems model is concerned with external targets only. Second, the two somatosensory processing streams appear less independent than the two visual streams. For example, the PPC appears to be involved in processes subserving perception, as well as action, although the double dissociations found suggest that they involve neural circuits that are at least partly separate. Furthermore, it is clear that, at a behavioural level, normal performance during tactile recognition of external objects requires close coordination between action-related and perception-related processes. Nevertheless, the evidence presented in this review is consistent with dissociable processes, and further studies should be aimed at delineating the specificity and interaction between the functional entities proposed in the model.

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Open Peer Commentary

Tactile agnosia and tactile apraxia: Cross talk between the action and perception streams in the anterior intraparietal area

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Abstract: In the haptic domain, a double dissociation can be proposed on the basis of neurological deficits between tactile information for action, represented by tactile apraxia, and tactile information for perception, represented by tactile agnosia. We suggest that this dissociation comes from different networks, both involving the anterior intraparietal area of the posterior parietal cortex.

Dijkerman & de Haan (D&dH) suggest that, analogous to the organisation of the visual system, somatosensory processing for guiding actions (terminating in the posterior parietal cortex [PPC]) can be dissociated from the processing that leads to perception and memory (going through the secondary somatosensory cortex and terminating both in the insula and in the PPC).

In the visual domain, the clinical conditions of optic ataxia and visual form agnosia stand for two separate streams of visual information: dorsal stream for action and ventral stream for perception. Analogously, in the haptic domain a similar dissociation of information processing for external tactile stimuli can be proposed: an action stream represented by tactile apraxia and a perception stream represented by tactile agnosia. As suggested by D&dH, there is also clinical evidence that, despite the parallel processing, the haptic streams for perception and action interact tightly because of functional and anatomical overlaps inside the PPC. Accordingly, both haptic perception of objects and somatosensory guidance of action are processed in the anterior part of the PPC: the human anterior intraparietal area (AIP).

AIP and action (tactile apraxia): Interaction with the ventral premotor cortex. *Tactile apraxia* is defined as an affection of explorative finger movements in absence of paresis or sensory deficits (Klein 1931). The finger movements seem uncoordinated and inadequate to the size and the shape of objects to be explored (Binkofski et al. 2001). Typically, the intransitive (not object related) and expressive movements (gestures) are well preserved. Functional imaging studies show that manipulative finger movements involve activation of the AIP, the superior parietal lobule, the secondary somatosensory area, and the ventral premotor cortex (vPMC) (Binkofski et al. 1999a; Jäncke et al. 2001). Especially the AIP is processing dynamic parameters of ongoing hand actions (Tunik et al. 2005). Electrophysiology in monkeys showed that AIP neurons discharge during object holding and manipulation (Sakata et al. 1992; 1995) and that those "motor dominant" neurons discharge during hand-related actions in the dark (Murata et al. 1996). The tight interaction between the AIP and the vPMC for coordination of goal-directed hand movements has been already proposed on the basis of monkey data (Jeannerod et al. 1995; for review, see also Rizzolatti & Lupino 2001; Rizzolatti et al. 1998). Studies on human lesion provide another argument in favour of this interaction in the haptic domain. Lesions involving the AIP, contralateral to the affected hand, cause tactile apraxia (Binkofski et al. 2001; Valenza et al. 2001). Furthermore, lesions of the frontal operculum, containing the vPMC, can also impair finely tuned finger movements in a condition resembling tactile apraxia, that is, limb kinetic apraxia (Binkofski & Fink 2005; Binkofski et al. 2001; Dettmers et al. 2003). Thus, there is converging evidence that the AIP constitutes the nodal point of a network for coordination and integration of sensorimotor information for action.

The AIP and perception (tactile agnosia): Links with inferior temporal cortex. For object recognition from tactile stimulation, elementary cutaneous and proprioceptive sensations from the exploratory hand have to be integrated to more complex information reflecting textural and spatial patterns of a specific object. O'Sullivan et al. (1994) and Roland et al. (1998) found evidence for different information streams, depending on the somatosensory submodalities from positron emission tomographic activation studies of the human brain. Roughness discrimination activated the lateral opercular cortex, but shape and length discrimination activated the AIP. Accordingly, Bohlhalter et al. (2002) reported two patients with tactile agnosia. One patient had a lesion that affected mostly the anterior parietal lobe and caused a pure aperceptive agnosia, and the second had agnosia for more complex features (like shape) following a lesion of the anterior intraparietal regions (Hoemke et al., in press). This is consistent with neuroimaging data in human patients showing that the AIP is involved in tactile, visual, and transmodal processing of object features (Grefkes et al. 2002). The lateral occipital cortex (part of the inferotemporal cortex) is known to be important not only for visual, but also for tactile, object recognition (Amedi et al. 2001) and maybe even for the supramodal object recognition (Binkofski et al. 2004). Anatomical connections between the intraparietal and inferotemporal areas have been found by the Van Essen group of researchers (see Lewis & Van Essen 2000) in monkeys, and such connections seem also to exist in people (Figure 1).

AIP the node. Tactile apraxia and tactile agnosia can occur separately, indicating a possible dissociation. Indeed, clinical cases have been reported of patients with tactile agnosia who had intact exploratory hand movements and preserved basic

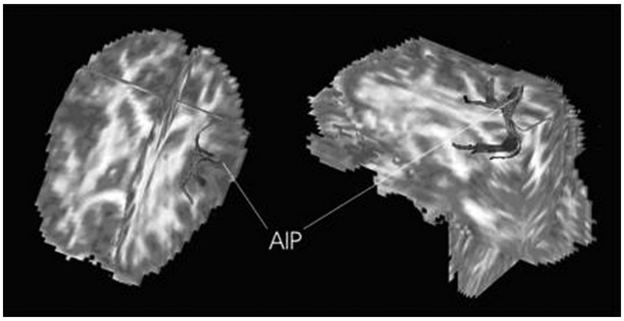

Figure 1 (Binofski et al.). Diffusion-tensor tractography data showing anatomical connections of the anterior intraparietal area (AIP) with primary sensory, ventral premotor, posterior intraparietal, and inferior temporal areas. (Figure from Pisella et al. 2006, with permission)

somatosensory functions (Platz 1996; Reed & Caselli 1994; Reed et al. 1996). In contrast, as mentioned by D&dH, Valenza et al. (2001) described a patient with pure tactile apraxia who had an intact ability to perceive passively applied stimuli, but showed severe impairments when required to use exploratory finger movements for object identification.

However, Delay (1935), while describing tactile apraxia, had already referred to the association between apractic and agnostic deficits. Accordingly, tactile apraxia is often accompanied by deficits in tactile recognition of objects (or astereognosia) (Binkofski et al. 2001; Wernicke 1876). This underpins the tight interaction of the action and the perception systems. Object characteristics trigger appropriate finger movement patterns that serve the perception of object features (action for perception – "feedback"). At the same time, the object properties determine the movement extent – perception in the service of action (perception for action – "feed forward") (Lederman & Klatzky 1997). As shown by Bodegard et al. (2001), the AIP is activated by both passive and active tactile shape discrimination.

Because the AIP receives somatosensory and visual information about objects and is interconnected with the vPMC for planning actions towards the objects and with the inferior temporal cortex for recognising the objects, this area (or its human homologue) seems to constitute one of the most important interfaces between action and perception in the haptic system.

Divide et impera? Towards integrated multisensory perception and action

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Abstract: A visual analogue, two-route model of somatosensory processing is advanced in this commentary. Touch for perception is seen as separate from, although interconnected with, touch for action. Separate modules are additionally proposed for internal (body) and external (object-related) somatosensation. Here we ask whether dissociation (divide) guarantees better efficiency (impera) in terms of the heuristic model within the somatosensory modality and across modalities.

Tracing a parallel to the two visual streams model, Dijkerman & de Haan (D&dH) propose a similar distinction in the somatosensory processing system (SP), whose anatomical and physiological organization would ultimately reflect the action-related use of somatosensory inputs. Their model is built upon multiple evidence showing that different body representations are used for perceptual judgments about the structural relationships among body parts (body image) and for the guidance of action (body schema).

Somatosensation is highly complex, including different submodalities besides discriminative touch, such as proprioception, the information about the relative position of our different body parts in space. It is thus important to describe the possible dissociations, as well as the multiple interconnections, between the different somatosensory streams, as the authors stress. However, one may question the extent to which, nowadays, a dissociation-based approach would help our understanding of SP. For vision, this approach proved to be successful initially, until the need to go beyond dissociations and transcend a dichotomic model for a more interactive one was acknowledged (Rossetti & Revonsuo 2000). The main argument for the dichotomic view was the so-called double dissociation between visual agnosia (patient D.F.'s deficit in visual recognition), and optic ataxia (e.g., patient A.T.'s deficit in visuo-manual guidance), considered as consecutive to ventral and dorsal damage, respectively. However, the empirical foundation of such a dissociation has been largely reconsidered on the basis of both old evidence (Pisella et al. 2006; Rossetti et al. 2003) and recent evidence from the very same patient (Schenk 2006), making the ventral-dorsal dissociation of functions less obvious than previously thought (see also Coello et al. 2007). By showing that not only visuo-motor processing, but also perceptual processing is impaired in optic ataxia, Rossetti et al. (2005) have questioned the perception-action dissociation classically described in optic ataxia. By reporting that D.F.'s performance was impaired on both perceptual and motor tasks in conditions tapping allocentric, but not egocentric, coordinates, Schenk showed that D.F.'s behavior may actually reflect dissociation between different modes of visuospatial processing.

Related evidence against purely encapsulated functional modules in vision comes from studies on normal subjects' grasping at illusory displays (Gentilucci et al. 1996), such as in the Titchener circles illusion. In this size-contrast illusion, two identically sized disks are perceived as being different in size, depending upon the size of the surrounding inducers. It was recently demonstrated that the supposed dorsal stream immunity to visual illusion cannot be advocated to explain the different effects found for perception and action in this and other illusions (Coello et al. 2007). In addition, Pavani and colleagues showed that both perceptual estimation and hand shaping while grasping are similarly influenced by the illusion (Franz 2001; Pavani et al. 1999), challenging the conventional visual perception/action model in the normal brain. So the question arises as to whether action would resist somatosensory illusion (regarding vision, see, Bruno 2001).

Take, as an example, the "fixed-set" method (Uznadze 1966) whereby, for 30 consecutive trials, subjects have to grasp two spheres of different size (one in each hand) simultaneously and report which one is bigger. In the subsequent trials, when two identical spheres are presented to the subjects, an aftereffect emerges: Typically, the sphere held by the hand previously holding the bigger sphere is perceived as being smaller than the sphere in the opposite hand. How would subjects grasp the illusory smaller sphere? Would the proposed two-route model for touch predict that their kinematics reflect the veridical or the illusory somatosensory percept? Besides its empirical interest, the answer to this question might have important theoretical implications for D&dH's model, particularly when considering neuropsychological evidence showing that this method can disclose unconscious residual somatosensory processing of objects' size. A right-brain–damaged patient with left tactile extinction (patient G.R.; see Maravita 1997) was unable to perceive the left sphere, but was deceived by the perceptual aftereffect and reported the size of the right, ipsilesional, sphere incorrectly. As D&dH say, the notion of separation of functional modules has to be taken with caution, and we think this would be the case particularly for SP, which is composed of not only separable, but also functionally and anatomically interconnected submodalities, and integrated at multiple levels with other sensory modalities (Calvert et al. 2004).

Orthogonal to the main dissociation, the proposed model further distinguishes between somatosensory processing occurring in the internal (bodily) space and external (extrapersonal) space. In this respect, an aspect that the model seems to not address fully is the following question: What is the relationship between a touch on the body and the body position in space? In other words, the "tactile where" is not only "where-on-the-body" but also "where-on-the-body-in-the-space." This issue is tightly linked to the multisensory view of somatosensory perception (Brozzoli et al. 2006), because body position information may also be provided by visual input (Rossetti et al. 1995a). Previous work on patients with cross-modal visuotactile extinction (di Pellegrino et al. 1997) provided support for multisensory representations of a third spatial medium, the peri-personal space, linking the body to external space. In this respect, Farnè et al. (2000) found that extinction of tactile stimuli delivered on the contralesional hand is strongest when visual stimuli are presented closest to the ipsilesional hand. A comparable effect was obtained when the visual stimulation was actually presented far from the patients' ipsilesional hand (concealed behind their back), but near a rubber hand that was visible and aligned with the patients' ipsilesional shoulder. Not only visual, but also proprioceptive, information about the distance between hands (body schema) can alter static touch perception, the subjects being faster and more accurate when they perform tactile tasks while keeping their hands far apart (Brozzoli et al. 2006; Driver & Grossenbacher 1996).

In sum, we suggest the model might benefit from a more integrated approach to SP, and incorporating the multisensory peripersonal space representation, to account for the aforementioned phenomena – which are, in addition, tightly related to "acting" in somatosensory terms. Sensorimotor non-conscious maps of the body are plastic, as suggested by the behavioral effects of tool use in human and nonhuman primates (Berti & Frassinetti 2000; Farnè et al. 2005; Iriki et al. 1996), and their adaptive functional role might be better captured within such a wider framework.

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Early development of body representations

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Abstract: The dissociations among body representations that Dijkerman & de Haan (D&dH) describe are also supported by developmental evidence. Developmental dissociations among different types of body-related representations suggest distinct functional systems from the start, rather than progressive differentiation.

Taxonomies of human body representational systems are nearly as numerous as the putative systems themselves. Neuroimaging, neuroclinical, cognitive, and developmental studies over the last 15 years have established that human body knowledge is widely distributed in the adult brain. The most consistently referenced taxonomy of body representations includes at least three partially independent levels (Gallagher 2005; Reed 2002; Sirigu et al. 1991): *Sensori-motor body* representations are primarily responsible for on-line movement and perception of one's own body; *visuo-spatial* body representations specify the structure and physical appearance of the human body; and *lexical-semantic* body representations support conceptual, language-based knowledge about the human body.

Dijkerman & de Haan's (D&dH's) model focuses on sensorimotor body representations. Like Sirigu et al. (1991), the target authors distinguish unconscious, own body representations that control motor activity, from own body representations that underpin conscious perception. These perceptual representations are then further distinguished by D&dH as to whether originating from external stimuli (object exploration and recognition) or from internal stimuli (proprioception). This last level is referred to as "body image" in the target article, which is rather unfortunate because this term is already fraught with multiple confusing meanings and references (Gallagher 2005; Reed 2002; Slaughter & Heron 2004).

D&dH offer convincing evidence for their taxonomy. Given that multiple body-related representations exist in adults, at least two developmental scenarios are possible. One is that, at birth, humans are equipped with a supramodal representational system that subsumes several types of body representations. Meltzoff and colleagues (Gallagher & Meltzoff 1996; Meltzoff & Moore 1995) have proposed this sort of a system, mainly to account for neonatal imitation, which, they suggest, could be accomplished only through coordination of visual perceptual information about others' body movements with proprioceptive information about the infant's own body positions and motor representations that control the imitative act. On this view, development of body representations would involve progressive dissociation, from the supramodal format, into the distinct functional representations evident in adulthood.

Another possibility is that at least some of the distinct body representations described by D&dH are differentiated from the start. Neonatal imitation aside (it should be noted that there is a good deal of debate about whether neonatal imitation exists as a flexible behavioural strategy as opposed to a fixed reflex; see Anisfeld 1996), the developmental evidence suggests that this is the more likely scenario.

Organized motor activity is evident prenatally (Myowa-Yamakoshi & Takeshita 2006) and in the first several months of life. A recent study employed four-dimensional ultrasonography to examine the arm and hand movements that third-trimester foetuses made towards their faces. More than half of the foetal arm movements resulted in the hand touching the mouth, and the majority of reaches to the mouth were preceded by the mouth opening (Myowa-Yamakoshi & Takeshita 2006). Neonates spend approximately 20% of their waking hours touching their own face, and almost one-third of these movements result in the infants touching their mouths (Butterworth & Hopkins 1988; Lew & Butterworth 1995). When infants touch their own face, there is no rooting reflex, which suggests that even at this early age the infants are capable of distinguishing external stimulation from self-stimulation (Butterworth & Hopkins 1988), though this is not yet as complex as the sort of perceptual self-recognition defined by D&dH.

In the target article, perceptual self-recognition is defined as an integration of proprioceptive, kinaesthetic, and visual information. This is not evident until 5 months of age, at the earliest. For instance, when infants were presented with a video playing a contingent view of their own moving legs and a second video playing a non-contingent view of legs (delayed feedback), infants aged 5 months and older preferred to watch the non-contingent view of themselves, as evidenced by longer times spent looking at the unusual display (Bahrick & Watson 1985). Furthermore, infants preferred to watch the non-contingent view of themselves even when they could not also see their own legs, which suggests that they could integrate the visual and proprioceptive information. Thus, body representations supporting self-perception appear to develop later than representations that control motor activity.

D&dH distinguish between perceptual representations for self and for objects. The literature on object exploration in infancy suggests that exploration of the surface features of objects becomes increasingly precise over the first year of life. At birth, motor actions applied to different object sizes, textures, and shapes are largely undifferentiated, which has traditionally been interpreted as a consequence of a general inability to recognize the self as a distinct causal entity (Piaget 1953). However, another interpretation is that the somatosensory representations that guide manual exploration do not develop until after 6 months of age. It is only in the second half of the first year that infants show clear evidence of altering their manual exploration in response to specific object properties (Bourgeois et al. 2005).

Thus, the behavioural evidence from developmental studies is in line with the neuroimaging and neuroclinical evidence presented by D&dH. Whether the distinct processing streams postulated in the target article are evident in infancy and early childhood, is, as yet, unknown, though there is some suggestion that dorsal and ventral streams for object processing are functionally distinct by $8\frac{1}{2}$ months of age (Newman et al. 2001).

Finally, the development of higher-level body representations – visuo-spatial and lexical-semantic – takes place even later. Infants do not recognize the typical human body shape until at least 12 months of age (Slaughter & Heron 2004). Furthermore, a recent study failed to find evidence that the development of representations for recognizing human bodies is related to the maturity or complexity of infants' own sensori-motor representations (Christie & Slaughter, in preparation). Lexical-semantic body knowledge is acquired later still – not until age 15 months at the earliest, when infants first learn names for body parts (Witt et al. 1990).

We know bodies from inside and from without; we know them as objects and as vehicles. It is not surprising that there are numerous varied levels on which the brain represents bodies. Taxonomies of body representations can be useful, but to date there is no comprehensive system for organizing our knowledge about body representations, or for communicating that knowledge. This is an important next step.

How many representations of the body?

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Abstract: Based on functional differences, Dijkerman & de Haan (D&dH) emphasize the duality of somatosensory processing, and therefore of body representations. But how many body representations do we really have? And what kind of criterion can we use to distinguish them? I review here the empirical and conceptual difficulties in drawing such distinctions, and the way to progress.

The way we use information determines the way in which we encode it. Dijkerman & de Haan (D&dH) illustrate this general principle with regard to somatosensory processing. Like vision and audition, proprioception can be either action-oriented or recognition-oriented. However, what characterizes proprioception from other sensory modalities is the role played by body representations. D&dH conclude that the dual somatosensory pathways give rise to two kinds of body representations: the body schema and the body image. But what is the basis of this dualistic distinction? How many body representations do we really have?

One representation that integrates all of the different types of information into a unified neuromatrix (Melzack 1992)? *Two* representations that are either based on functional criteria distinguishing the body image for recognition and the body schema for action (Gallagher 2005; Paillard 1999), or based on temporal criteria distinguishing the actual body from the habitual body (Merleau-Ponty 1945) or short-term and long-term body images (O'Shaughnessy 1995)? *Three* representations that, for a more fine-grained distinction within the body image, take apart visuo-spatial body map and body semantics (Schwoebel & Coslett 2005; Sirigu et al. 1991)?

The evidence provided to support the distinction between different kinds of body representations relies mainly on neuropsychological dissociations: between deafferentation (disruption of body schema) and neglect or numbsense (disruption of body image); or between apraxia (disruption of body schema), autotopagnosia (disruption of structural body description), and body-specific aphasia (disruption of body semantics). However, neuropsychological evidence is open to interpretation. First, there are so many body deficits, and therefore so many possible dissociations, that one may end up with almost an infinite list of body representations. For instance, some patients are unable to identify their own body parts only, whereas others are unable to identify exclusively someone else's body parts (Felician et al. 2003). One would then have to make a further distinction between two types of structural description: for one's own body and for other people's bodies. Second, without a clear definition of what each type of body representation involves, it is hard to find conclusive clinical tests to assess the different levels of body representations in patients. For instance, autotopagnosia has been diagnosed by asking patients to *point* toward body parts, although one could argue that pointing requires not only the body structural description, but also the body schema (Schwoebel & Coslett 2005).

A further problem in validating the distinction between multiple body representations is that there is almost a complete lack of experimentation outside of neuropsychology (except, e.g., Kammers et al. 2006). D&dH emphasize the distinct neuroanatomical bases of somatosensory processing. However, the differences in activations that they describe may depend on the tasks, rather than on the underlying distinct body representations (Holmes & Spence 2006). We have to disentangle two alternatives: (a) one and the same representation used for different functions, or (b) different representations specific to each function. In order to prove the latter hypothesis, one would need to show that what differs is not only the function, but also the content of the representations. The function of body representation, whether it is action-oriented or recognition-oriented, might not provide such a clear criterion, contrary to what D&dH assume.

Action involves many different types of information about the body, which may not be encoded in the same format. On the one hand, one could distinguish the body as a target or as the mean (grouped together in the body schema in Figure 1 of the target article). Whereas the former is encoded in an egocentric frame of reference, like any other goal, this might not be true for the latter (Bermudez 1998). They are both action-oriented, but their spatial perspectives are different. On the other hand, one could distinguish short-term information about body posture and long-term information about bodily constraints, such as the size and the strength of the limbs (de Vignemont 2006). Again, both types of information are necessary to plan a movement, but the dynamics are different.

Recognition covers an even wider scope of bodily information, including body posture and body size. The body image is said to include body percept, body concept, and body affect (Gallagher 2005). The dynamics may vary, from short-term bodily sensations to long-term bodily properties (O'Shaughnessy 1995). A further level of complexity occurs for the body image, as it can be applied both to one's own body and to someone else's body. Why are all of these aspects part of one single category? The unitary function of the body image is far from obvious. It is often described as what is left over after the body schema. Breaking down the body image into pieces is not the optimal solution either. Indeed, the triadic distinction leaves out the emotional component of the body image. Does that mean that there would be four kinds of body representations, or even more?

Shall we then give up on drawing distinctions between bodyrepresentations altogether? No, but one must be careful to avoid three main obstacles: (1) a lack of unity within each kind of body representation, (2) a lack of positive definition, and (3) a risk of infinite multiplication. D&dH have taken the first step by describing in detail the distinction for somatosensory processing. Further work needs to be done for body representations. To establish a taxonomy of body representations, one needs to describe not only the specific functions of body representations, but also their input (e.g., Does the weighting of each sensory modality in multimodal integration depend on the type of body representation?), their content (e.g., Are some body representations self-specific, and others shared between self and other?), their dynamics (e.g., How quickly can body representations adjust to body changes?), and their spatial frame of reference (e.g., Does the body schema/body image distinction overlap with the egocentric/allocentric distinction?). One may then be able to provide a full account of body representations.

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Disentangling functional from structural descriptions, and the coordinating role of attention

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Abstract: The target article fails to disentangle the functional description from the structural description of the two somatosensory streams. Additional evidence and thorough reconsideration of the evidence cited argue for a functional distinction between the *how* processing and the *what* processing of somatosensory information, while questioning the validity and usefulness of the equation of these two types of processing with structural streams. We propose going one step further: to investigate how the distinct functional streams are coordinated via attention.

The target article integrates an impressive amount of the relevant literature into a model on how the brain processes somatosensory information in two distinct streams. However, it fails to disentangle the functional distinction from the structural distinction of the two somatosensory streams.

In vision, two functional streams can be distinguished: One, a visual-spatial processing stream for the control of spatial motor actions (*how*), such as saccading, grasping, or pointing at external target objects. The other, a visual-spatial processing stream for perception, for example, for object and scene recognition (*what*). From a functional and computational perspective, these processing streams have to deal with quite different constraints (e.g., timing, invariance) and produce quite different neurocomputational solutions. For example, consider "how" functions such as keeping the fovea on a moving target, versus "what" functions such as recognizing an object at the basic level from various viewpoints. Milner and Goodale (1995) introduced the functional differentiation between what and how in vision. They also equated this differentiation with a structural distinction between dorsal and ventral processing in the primate brain. Recently, this structural equation has become quite controversial (e.g., see Franz et al. 2001; Glover 2002; Schenk 2006). For example, relevant processing for some actions (e.g., memory-based – not online – saccades) is carried out by both dorsal and ventral brain areas (Özyurt et al. 2006) – there is a heavy interaction between areas from both structural streams for performing a single function!

Given that the structural distinction has come under sharp attack with regard to vision, we should beware of a corresponding distinction in the case of somatosensation. The somatosensory system should not be divided into two structural streams – whether dorsal versus ventral or parietal versus insular, whatever – but divided into functional streams of how and what. The evidence provided in the target article speaks the same language – including the patient examples at the very core of the article: Numbsense patients, as "action-without-perception" cases par excellence, suffer from lesions that according to theory belong to structures shared by the streams (and require the postulate of additional connections). Therefore, they convincingly support the functional, but not the structural, distinction. Even more obvious, the "perception-without-action" patient G.L. suffers from lesions that are necessarily shared by both structural streams, namely, peripheral ones. Functionally, however, we can distinguish between G.L. locating cold points within a visual body image (what), but not being able to point to them (how). Note, thereby, that effects of G.L.'s lesions include proprioception, but exclude temperature perception (e.g., see Stenneken et al. 2006). Using temperature perception, G.L. is able to locate targets on the body. Precise pointing, however, requires the integration of the target location on the body with the actual position of the executing and the targeted limb in space. Lacking proprioception, G.L. is not able to perceive the actual position of her limbs in space and, so, G.L. is not able to point to a location on her own body. Thus, G.L.'s dissociation is probably a better example of different processing requirements than of different structures in how and what streams.

Haptic perception, at the very core of somatosensory what-functions, requires strong interactions between structural areas – and, as recognized by Dijkerman & de Haan (D&dH), it cannot even be conceptualized without assuming tight links between sensory processing and control of exploratory movements. The attempt to designate different structural areas as being more responsible for one or the other part is understandable, but this should not mislead us into ignoring that the function, first of all, emerges from structural interplay. In this context, it is also significant that structural networks similar to those observed to be involved in (exploratory) haptic perception (Binkofski et al. 1999a) have recently been seen as responsible for a somatosensory-guided action (how); that is, for adaptive grip-force control during lifting (e.g., Schmitz et al. 2005). Even if, up to now, differences between the structural interplay in haptic perception and in lifting actions might not have been resolved in detail, a great overlap in networks casts additional doubts on the usefulness of a structural distinction between action and perception streams.

Note, besides, that adaptive grip-force control represents a class of actions that is defined but otherwise neglected in the target article: the manipulation of external objects. This includes several actions that require fast and permanent online processing of somatosensory information from the objects – as in throwing or lifting. Differences between the online processing of sensory information for time-constraint somatosensory-guided action in comparison to (probably) more precision-oriented haptic exploration (e.g., in the case of lifting versus weight estimation), are definitely worth future investigations in terms of functional dissociation. In contrast, what the target article does discuss extensively are functional dissociations between perception and cases of action for which we have quite well established models, especially regarding how limits in somatosensory processing are dealt with. Efference copies, well-learned motor programs, and anticipatory parameter control represent ways in which (coarse, as opposed to fine) action control circumvents such limits (e.g., Drewing et al. 2004), and, in functional terms, may partly explain why deafferented patients can perform several spatially oriented movements (such as pointing to a body location) but are not able to sense stimuli with the deafferented limb. For example, the patient cited in section 2 (para. 5) had a complete loss of sensibility, but could still perform a "pincer grip and exploratory movements." Note that this patient's "exploratory movement patterns … of course were never performed in an adequate relation to the explored object" (Pause et al. 1989, p. 1611), and her pincer grip was guided by vision (and was successful in 70%, but not 100%, of trials). The aforementioned well-known "shortcuts" of the how-stream can easily explain this performance because they need not refer to actual somatosensory information. To take another example from the target article, the weaker so-called vibro-tactile illusions (that relate to proprioceptive receptors in the muscle) in pointing, as compared to in perception, and the vanishing of this dissociation after some seconds: these findings agree well with the use of the how-stream–related shortcuts (e.g., fast updating of limb position by efference copy) until sufficient processing time has passed to include actual sensory information (i.e., the illusory information) – but these findings do not agree with dissociated structures.

Taken together, the target article provides convincing evidence of a functional dissociation between "how" and "what" streams while failing to disentangle the functional description from structure. The evidence also raises an urgent question that is only marginally addressed in the article: How is the interplay of the two streams in somatosensory processing coordinated? From experimental work in vision, we know that the two functional processing streams of how and what are coordinated by visual attention. They do not work independently. Evidence for this claim comes from behavioral work on the role of attentional processes in perception and spatial-motor action control (Deubel & Schneider 1996; Schneider & Deubel 2002). Several studies have shown that the selection process of an external target object for spatial movements, such as saccading or grasping (how), is tightly coupled to the selection of the same object for visual (conscious, reportable) perception (what). When humans prepare a movement to an object in space (i.e., select a movement target there), visual perceptual processing resources are focused on that target object. It is plausible to assume that a similar coupling holds for somatosensory processing. Up to now, there are no corresponding studies in somatosensory processing. This holds even more with regard to the more complex, but highly relevant question of coordinating different processing streams from distinct modalities.

Where are somatosensory representations stored and reactivated?

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Abstract: The studies cited by Dijkerman & de Haan (D&dH) stress the distinction between perception and action within the somatosensory system but provide little information about memory functions. Recent findings by our group and by others show that the dorsal stream is also activated during short-term memory maintenance and long-term memory retrieval of haptic information. These data complement and extend the proposed model.

In the visual system, the so-called *what* or ventral stream has been found to be closely related to working memory functions (Haxby et al. 2001; Ishai et al. 2000). Moreover, in a set of fMRI studies, we found that both the dorsal and the ventral visual stream are significantly involved when participants have to reactivate representations from long-term memory that had been visually encoded: Dorsal (parietal) areas light up when participants retrieve spatial information and ventral areas (temporal, inferior frontal cortex) do so when they retrieve object information (Khader et al. 2005; 2007). These findings are in line with the general idea that cortical areas are not only specialized for on-line processing of distinct types of information during perception or action, but that the very same areas are also the locations where information is permanently stored (McClelland et al. 1995; Rösler & Heil 2003). The question, therefore, arises as to whether the areas identified by Dijkerman & de Haan (D&dH) are also involved in haptic working memory and long-term memory tasks. As a matter of fact, recent findings demonstrate that networks within the dorsal action stream are not functionally restricted to immediate guidance of hand actions; rather, they are also recruited for storage and retrieval of action-related spatial information. We briefly summarize the evidence.

Stock et al. (2004; under review) studied blood-oxygen level–dependent (BOLD) responses during long-term memory retrieval of proprioceptive and tactile knowledge (i.e., haptics). They used an association learning paradigm that allows brain activations to be monitored during retrieval of specific types of information without confounding the perceptual and mnemonic processes. To this end, participants learned associations between cues (auditorily presented words) and target stimuli. The targets were either haptically explored three-dimensional objects or haptically explored locations in three-dimensional space. In the retrieval test, participants heard two cue words and had to decide whether or not both were associated with the same target. By manipulating the number of associated targets, the difficulty of the retrieval situation was varied systematically. This procedure enforces memory activation of either object or position knowledge in the retrieval situation, without the necessity of processing different types of stimuli perceptually. The results substantiate the functional distinction proposed by D&dH: Retrieval of haptically encoded objects activated, among other areas, the secondary somatosensory cortex (SII), the insula, and the posterior parietal cortex (PPC), whereas retrieval of haptically encoded spatial positions activated, among others, the SII and the PPC but not the insula. Thus, the functional dissociation proposed by D&dH is not only relevant for perception and action, but it also applies to the retrieval of permanently stored information.

In other studies (Fiehler 2006; in press), we investigated the role of the dorsal action stream in a haptic working memory task. Participants performed a purely haptic version of a delayed-recognition task, in which they encoded, briefly maintained, and finally recognized hand movements without any visual feedback. Task difficulty was systematically manipulated by the number of complex hand-movement sequences per trial. The BOLD response pattern revealed that haptic encoding of hand movements activated the primary somatosensory cortex and secondary somatosensory cortex, the PPC (dorsal stream), premotor areas, and the right occipitotemporal cortex (ventral stream). The majority of these regions responded to task difficulty reflecting increased processing demands. Short-term maintenance of haptic information elicited load-dependent activity in the left anterior intraparietal sulcus and closely adjacent areas (dorsal stream). Consistent with the proposed theory of D&dH, these data confirm that the PPC is recruited for haptic action control, indicating haptic-motor coupling networks within these areas. Moreover, the results demonstrate that the dorsal stream is not only functionally related to online action control but also to working memory maintenance of action-related spatial information. Others (Macaluso & Driver 2003; Ricciardi et al. 2006) observed activation in the PPC for both visual and tactile spatial stimuli, which suggests that this region has multimodal features and may be engaged in short-term maintenance of spatial information irrespective of the input modality.

Evidence for a mnemonic function of the PPC in action processing is also provided by intracranial recordings in monkeys.

Murata et al. (1996) observed neuronal activity in the anterior intraparietal cortex (AIP) during a delayed hand manipulation task in which monkeys had to manipulate the remembered object in the dark. The results indicate that monkey AIP, as part of the dorsal action stream, is involved in working memory maintenance of spatial characteristics that guide hand actions in relation to objects. Studies using delayed saccade tasks also indicate that the human PPC is involved in representing spatial information for prospective guidance of actions. Activity in the PPC was modulated by the length of the delay period, which suggests a critical role of this area for maintaining movement relevant spatial information (Curtis 2006). These findings are supported by brain-imaging studies on delayed pointing movements (Connolly et al. 2003; Lacquaniti et al. 1997).

At first glance, these findings seem to be at variance with clinical studies demonstrating a performance deficit in a patient with visual form-agnosia (ventral stream lesion; Goodale et al. 1994) and performance improvement in a patient with posterior parietal lesions (e.g., Milner et al. 2001) when a delay was inserted in a grasping task. To explain these results, it was assumed that patients used information processed and stored in the ventral stream and that the dorsal stream does not support memory functions. However, the grasping tasks realized in these studies needed visuomotor integration, and the results cannot be immediately generalized to purely haptic memory tasks. The aforementioned studies by Stock et al. and Fiehler et al. employed purely haptic tasks without any visual feedforward or feedback component. Therefore, the results clearly support the conclusion that the areas identified by D&dH are not only recruited for online perception and action control in the somatosensory modality, but that they are also functionally involved in working memory maintenance and long-term memory retrieval of action-related spatial information. Moreover, these findings substantiate the general claim that areas specialized for online processing of specific types of information are recruited for short-term and long-term memory storage and retrieval (McClelland et al. 1995).

Considering general organizational principles for dorsal-ventral systems within an action framework

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Abstract: Support for the proposed dorsal-ventral distinction for the somatosensory system is not yet convincing, nor is the anatomical segregation of its pathways as clearly defined as the visual pathways. Consideration of alternative organizational principles might reveal critical differences across sensory processing systems. The role of attention and manipulations that modulate functional systems might also be worth considering.

The anatomical separation of dorsal and ventral pathways seems clear for the visual system. However, the precise functional roles of these putative pathways are still being debated. My starting point for commenting on the present target article was to consider the possibility that a general distinction between action and perception might turn out not to be the correct organizing principle for other sensory systems.

I see three possible organizational principles that together seem to capture a host of findings cited as evidence in support of functional differences between the dorsal and ventral visual pathways. Briefly, these are, for dorsal versus ventral systems respectively: (1) peripersonal versus extrapersonal, referring to the space immediately surrounding the body versus more distant space; (2) egocentric versus allocentric, referring to representations of body coordinates versus environmental coordinates; and (3) online versus memory-based, referring to real-time versus delayed processing. [Some references that provide more precise definitions include Previc (1998), Rizzolatti et al. (1997), and some of those cited in the target article.] Importantly, I see these not as absolute, but, rather, as relative distinctions that might provide guiding principles for defining the general organization of brain systems.

Based on the careful synthesis of findings provided by Dijkerman & de Haan (D&dH), and related work, it seems that for the visual pathways, all three of these principles are supported. Accordingly, these become candidates for consideration for the other sensory systems, as well.

With respect to the somatosensory system, it seems that on the basis of the neuroanatomical findings elaborated by D&dH, a strict separation of dorsal and ventral pathways is somewhat questionable. It might be just as reasonable to suggest that a mosaic of areas are involved in somatosensory processing, with greater reliance on the insula in the case of recognition (i.e., if recognition turns out to be a defining property). In addition, although some of the neuropsychological findings support the authors' proposal, many seem mixed and open to other interpretations.

In terms of the function of putative somatosensory systems, one might consider a different organizational principle than that proposed by D&dH. Consider, for example, the peripersonal versus extrapersonal space distinction. Most actions performed within peripersonal space involve both visual and somatosensory processes on objects manipulated within that space, although other sensory systems such as auditory and gustatory often are also involved. In contrast, when considering processing of objects some distance from the body (e.g., outside of reaching distance), it seems to be the visual system that does most of the perceiving (e.g., perceiving which object to act on next) – although, of course, audition is used to hear distant objects, and other systems might come into play to a lesser extent. Thus, with respect to peripersonal space, the visual and somatosensory systems are both primary; moreover, the involvement of posterior parietal cortex (PPC) for both types of information (visual and somatosensory) implies its crucial role in sensorimotor transformations on multisensory input. In sum, it seems that the visual and somatosensory systems show a rather nice parallel in terms of proposed functions of the dorsal system(s). For the proposed ventral system(s), however, this brief exercise suggests far less similarity for visual and somatosensory systems. One might ask: Does this lack of a parallel suggest that the proposed organizational principle is the wrong one? Or, does it suggest that general organizational principles might more effectively reveal *differences* rather than similarities across sensory systems? The point is that, perhaps the somatosensory system parallels the visual system in terms of some functions (those related to the dorsal pathways), but for other functions there is no direct analogue.

My second point is basically that a complete discussion of these putative systems might require some reference to the role of attention, particularly given the emphasis on findings in humans. For example, findings from our own neuropsychological studies suggest that the flexible allocation of attention might enable switches between egocentric and allocentric processing systems of the brain (Franz 2003). One might extend this idea to the present context by suggesting that the flexible allocation of attention is likely to influence which pathway(s) is (are) utilized at any particular moment in time. Perhaps more importantly, though, attention might to some extent define the functions of different systems; that is, attention itself might be a guiding principle (Franz 2004).

In relation to the visual and haptic systems, a recent study from our lab demonstrated that visual and non-visual (haptic) attention processes can show similar kinds of effects on motor output (i.e., attention results in measurable changes in output parameters such as the size and shape of a drawn trajectory), although the effects of visual attention were generally greater than the effects of haptic attention (Franz & Packman 2004). These findings could be accounted for by attentional modulations on dorsal system processing (for example). In a different set of studies that required subjects to estimate object sizes on the basis of internal representations, we found that subjects with congenital or acquired blindness tended to be more accurate in their estimations than were sighted subjects. Perhaps even more interesting, the blind subjects most often reported using strategies that relate to the manual grasping of objects (even though they were never asked to grasp the objects), whereas the sighted subjects reported more visual strategies. In addition, a control condition demonstrated that when visual memory processes were not used, the sighted subjects performed similarly to the blind subjects (Smith et al. 2005). These findings again suggest that perhaps the dorsal stream mechanisms might actually be the same (or shared) for visual and somatosensory information, with flexible adaptations occurring based on strategy, attentional influences, and the availability of sensory information.

In sum, it seems that preliminary steps toward elucidating whether general principles apply to different sensory systems are well underway. In my view, the present target article will prove very valuable in generating useful discussion and insightful directions toward this aim.

Revisiting parallel and serial processing in the somatosensory system

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Abstract: The issue of whether information is processed in parallel or in series in the somatosensory system is complicated by a number of factors. Included among these is the failure on the part of the scientific community to reach a consensus as to what actually constitutes the primary somatosensory cortex (SI) in higher primates. A second, related issue is the marked difference in the organization of the cortical areas subserving somatosensation across species.

In 1983, Jon Kaas published a paper titled, in part, "What, if anything, is S-I?" This paper was published at a time when there was a controversy raging about the functional organization of the primary somatosensory cortex (SI). SI had been mapped in a large number of species, as had a second somatosensory map that came to be known as the secondary somatosensory cortex (SII). The numerology denotes the order of the discovery of these fields, and was meant by the founding fathers to convey nothing with respect to whether the areas were organized hierarchically or in parallel. Traditional, and rather crude, recordings suggested that each of these representations contained complete and separate representations of the contralateral body surface, and SI and SII were thought to be homologous across species. Kaas asked the question in 1983 because electrophysiological mapping studies conducted in his laboratory suggested that the four cytoarchitectonic areas of the primate SI (i.e., areas 3a, 3b, 1, and 2) each contains a separate and complete map of the contralateral body. Kaas and colleagues showed that areas 3b and 1 contained complete and separate cutaneous representations of the contralateral body, and, further, that there were patterns of receptive field progression reversals at the border between these two areas that were comparable to the reversals that Allman and Kaas (1971) had found at the borders of separate representations of the visual field in monkey extrastriate cortex. In addition, they suggested that areas 3a and 2 contained maps of deep (e.g., muscle spindle, joint) receptors. These findings and suggestions complicated the issue of homology of SI across species, and raised questions about information processing in anterior parietal cortex. Similarities in somatotopic organization, cytoarchitectural features, location relative to motor cortex, and connections with the ventroposterior nucleus of the thalamus led Kaas and colleagues to suggest that area 3b is the homologue of SI in most other mammals. If one accepts that proposal, the question remains as to how the remaining areas of anterior parietal cortex (3a, 1, and 2) are contributing to somesthetic sensibility.

Some years ago, Garraghty et al. (1990) suggested that area 1 represents a "higher" stage of processing than area 3b because the receptive fields of neurons in area 1 are larger and have more complex response properties than those of area 3b. To test this idea, we recorded in the hand representation of area 1 before and after acute ablations of specific parts of the hand representations in areas 3a and 3b. We found that such ablations immediately deactivated the corresponding part of the hand representation in area 1, and we concluded that area 1 is located at a higher level in a hierarchically arranged processing sequence in anterior parietal cortex. We further noted that this hierarchical view of anterior parietal cortex was not novel, but rather was supported by a number of other observations. First, feed-forward corticocortical projections typically terminate predominantly in layer IV, and this is the pattern displayed by the projections from area 3b to area 1. Second, relay cells in the ventroposterior nucleus project in much larger numbers onto area 3b than onto area 1, and the plexus of thalamic input to area 1 is sparser than in area 3b and largely avoids layer IV. Third, stimuli are represented less isomorphically by neuronal firing patterns and have more complex receptive fields in area 1 than in area 3b, suggesting additional processing in area 1. Fourth, area 1 ablations are followed by less severe behavioral consequences than are area 3 ablations. Finally, in humans, the latencies of evoked potentials attributed to areas 3b and 1 differ by an amount consistent with sequential processing. Despite all of these observations, all too often it is the case that "anterior parietal cortex" and "SI" are used interchangeably as though nothing is transpiring in these four cytoarchitectonic regions (for references, see Garraghty et al. 1990). At least Dijkerman & de Haan (D&dH) devote two boxes to the anterior parietal cortex (APC) in their Figure 1.

The issue of whether sensory information is processed serially or in parallel has proven to be a thorny and complicated one. The complications arise primarily because there is no general consensus about what constitutes the appropriate level of analysis; and because neural interconnections between the putative parallel processing streams, and the temporal patterns of neural responsiveness of neurons at different levels of a putative serial processing stream, can introduce ambiguities. An additional complication is the inclination to view this issue rather myopically by concentrating only on data from "higher" nonhuman primates and humans. This largely eliminates evolutionary considerations – and, clearly, present-day sensory systems are evolved solutions to the problem of detecting and effectively responding to ecologically relevant stimuli. Adopting an evolutionary perspective casts the issue in a different light, and offers the opportunity to ponder the computational implications of somatosensory systems that differ fundamentally in their organization, and what the concepts of "serial" versus "parallel" processing actually mean.

In primates, SII is dependent upon inputs from the fields of anterior parietal cortex for its activation (Pons et al. 1987). If the hand representations in areas 3a, 3b, 1, and 2 are ablated, neurons in the corresponding hand representation in SII can no longer be activated. Such is not the case in all mammals. In cats, for example, ablation of SI does not deactivate the SII cortex. Indeed, in cats, no fewer than five somatosensory cortical fields (SI to SV) have been identified. Although each of these fields may well modulate processing in neighboring areas, no clear hierarchical arrangement exists for any of them. Interestingly, comparable differences exist between the visual cortices of cats and primates, with the lateral geniculate nucleus projecting almost exclusively to area 17 in primates, but to areas 17, 18, and 19 in cats. Thus, sensory processing in general in primates might rely more heavily on hierarchically arranged processing modules, whereas parallel processing strategies might be predominant in cats. While one might presume that some advantage has been conferred on primates by the emergence of serial processing capabilities, one can also note that cats, too, appear to "fit" quite well into their niches. Finally, while we can imagine that the somesthetic world of the higher nonhuman primate is much like our own, we cannot begin to imagine what the cat's solution to the problem would feel like. Perhaps, computational approaches attempting to model these two quite different strategies for processing somatosensory information might reveal how their outcomes differ, as surely these must.

Coming to grips with vision and touch

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Abstract: Dijkerman & de Haan (D&dH) propose a convincing model of somatosensory organization that is inspired by earlier perception-action models of the visual system. In this commentary, we suggest that the dorsal and ventral visual streams both contribute to the control of action, but in different ways. Using the example of grip and load force calibration, we show how the ventral stream can invoke stored information about the material properties of objects originally derived from the somatosensory system.

It is perhaps human nature to think in terms of contrasting dyads: good and evil, left and right, or ying and yang. Cognitive neuroscience has certainly not escaped this kind of dualistic thinking and over the years has generated a number of dyadic concepts such as explicit versus implicit knowledge, declarative versus procedural memory and, of course, perception versus action. Although one has to be careful not to oversimplify things, such distinctions can sometimes serve a useful function in emphasizing important differences in the way in which processing might unfold. The distinction between vision-for-perception and vision-for-action is a good example of this. By examining the differences in the way in which visual information is transformed for perceptual representation, on the one hand, and the control of action, on the other, Goodale and Milner (1992) were able to make sense of an otherwise confusing and apparently contradictory set of observations in human neuropsychology and monkey neurophysiology. In the target article, Dijkerman & de Haan (D&dH) have used this same dialectic method and applied it to the somatosensory system, synthesizing a clear and compelling story from a literature that at first glance seems equally disparate and unconnected. Indeed, the parallels drawn between the organization of the somatosensory system and the visual system are remarkably close, reflecting no doubt the fundamental differences in the nature of the demands that perception and action put on any sensory system.

D&dH provide plenty of evidence that somatosensory information is processed differently for perception than it is for action – and make explicit the idea that this division of labour is similar to that seen in the visual system. But they go on to suggest that the separation in the pathways (and the transformations they perform) may be "less distinct" in the somatosensory system than in the visual system. Although it is true that the visual streams appear to be more anatomically distinct than the somatosensory streams, the dorsal and ventral visual pathways are likely to be just as interactive as those in the somatosensory system. Indeed, in their 1995 monograph, Milner and Goodale made it clear that the two systems were not "hermetically sealed" from each other, but were closely coupled in the production of adaptive behaviour (Milner & Goodale 1995). Certainly, D&dH acknowledge that such interactions occur, but perhaps it is worth emphasizing that the integration between processing in the two visual streams is more intimate than widely believed. A case in point is the way in which high-level visual processing in the ventral stream plays a fundamental role in certain aspects of action control. Moreover, as we shall see, this processing also depends on integrating visual and somatosensory information.

When we reach out to pick up an object, we need to open and orient our hand and fingers appropriately in flight – and when we make contact with the object, we need to apply just the right amount of force so that we do not damage the object and, at the same time, it does not slip out of our hand. The computations underlying the former are largely mediated by mechanisms in the dorsal stream, since information about the size and overall shape of the object, and its disposition with respect to our hand, is readily available from the retinal array (Milner & Goodale 2006). But any calculations about the initial grip and load forces that need to be applied to the object must also reflect the object's mass, density, surface friction, and compliance – characteristics that cannot be derived from the retina directly. For this reason, it is highly unlikely that the dorsal stream by itself could compute this information, and instead the specification of the required forces would have to rely on stored information about the material properties of the particular goal object (or, in the case of novel objects, on predictions derived from stored information about similar objects). The retrieval of this stored information would depend on visual processing in the ventral stream, which would enable us to recognize a goal object and/or its material properties on the basis of a broad range of cues, including both shape and surface properties. Thus, real-time visuomotor control would appear to depend on interactive processing in the dorsal and the ventral streams – in a manner that is not dissimilar to what D&dH have suggested happens in the two functional networks of the somatosensory system.

It is worth emphasizing, too, that the control of the forces required to pick up an object is heavily dependent on the close integration of visual and somatosensory processing. Although visual inspection of an object enables us to program the amount of grip and load forces needed to lift the object, once we have the object in our hand, somatosensory feedback from our fingers enables us to fine-tune the forces, which were initially based on visual processing alone. The result is force output that is more closely matched to the intrinsic properties of the object. Indeed, internal forward models of this kind have been influential in demonstrating the interactions between visual and somatosensory processing in the control of skilled movements (Flanagan & Johansson 2002). A key aspect of these forward models is the initial prediction that the model makes, which is used to program relevant behaviour. In the case of the forces required to grasp and lift an object, this prediction is based on stored information about the material properties of that object derived from the somatosensory system during earlier encounters with the object (or objects made of the same material).

But how does one access this stored knowledge about material properties? One critical route that has been overlooked, at least in the object-recognition literature, is via the visual surface properties of the object (colour, texture, and specularities, for example) that are closely correlated with the object's material properties. In a recent functional brain imaging study, Cant and Goodale (2007) showed that there are distinct pathways within the ventral stream that appear to be specialized for dealing with the surface properties of an object as distinct from its form. Whereas form is processed more laterally in the lateral occipital area (area LO), surface properties (particularly texture) are processed more medially in the collateral sulcus and the lingual and parahippocampal gyri. Presumably, the identification of the surface properties of an object, particularly in the case of novel objects, allows us to calibrate the initial forces required to lift the object by invoking an association between those surface properties and stored information derived from the somatosensory system about previous encounters with the material from which that object is made.

Thus, not only do the ventral and dorsal streams work closely together in the control of skilled movements, but they also have intimate associations with the somatosensory system in both programming and executing this control. Nevertheless, it is important to emphasize that the dorsal stream exercises its control over actions in a direct and largely bottom-up fashion, whereas the ventral stream makes its contributions to this control via indirect and top-down mechanisms. Presumably, such distinctions in the nature of the control will also be evident within the somatosensory system. In any case, the division of labour that D&dH have put forward for the somatosensory system is an important first step in understanding how somatosensation-for-perception and somatosensation-for-action work together in the production of adaptive behaviour.

Close coordination between recognition and action: Really two separate streams?

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Abstract: Somewhat in contrast to their proposal of two separate somatosensory streams, Dijkerman & de Haan (D&dH) propose that tactile recognition involves active manual exploration, and therefore involves parietal cortex. I argue that interactions from perception for action to object recognition can be found also in vision. Furthermore, there is evidence that perception for action and perception for recognition rely on similar processing principles.

In an important attempt to integrate different literatures, Dijkerman & de Haan (D&dH) provide a scholarly review on somatosensory processing. In analogy to the visual system, they propose two distinct cortical somatosensory streams subserving perception and action. They argue convincingly, albeit somewhat in contrast to the notion of separate streams, that tactile object recognition requires the active exploration of the objects with finger and hand movements in order to capture properties like shape and texture. Hence, recognition requires close coordination between action-related and recognition-related processes, as well as temporal and spatial integration of tactile information, and therefore depends on an intricate collaboration of the posterior parietal and the insular system (sect. 3.1). This proposal goes beyond the idea of two strictly separate pathways for perception and action, and raises three related questions which I pursue here: How separate are perception and action in vision? Is the posterior parietal cortex involved in visual recognition and categorization? Do perception and action rely on different processing principles?

First, given their close interrelation in somatosensory processing, are perception and action really separate in vision? In a similar way as in tactile recognition, active exploration strategies are used in visual recognition. For instance, observers systematically explore the visual scene with eye movements (e.g., Yarbus 1967). More generally, seeing has been regarded as a way of acting, of exploring the environment (O'Regan & Noë 2001). Moreover, there is abundant evidence for perception-action couplings in vision (Hommel et al. 2001; Prinz 1990, 1997; Sommerville & Decety 2006). Studies investigating visuomotor priming have demonstrated that observing manipulable objects automatically potentiates actions (e.g., Craighero et al. 1999; Pavese & Buxbaum 2002; Tucker & Ellis 1998; 2001; 2004). In accordance, premotor and parietal areas are active when manipulable objects are perceived that afford motor interactions, like tools (e.g., see Chao & Martin 2000; Grèzes et al. 2003). More direct evidence for interactions from perception for action to the object-recognition system comes from a study showing that knowledge about motor interactions with objects improves recognition performance even in a naming (recognition) task (Helbig et al. 2006). Thus, there seems to be a strong coupling between perception and action not only in tactile, but also in visual recognition.

Second, is the posterior parietal cortex (PPC) involved in visual recognition, as well? The target authors claim that posterior parietal activity is specific for tactile recognition. According to the proposals of two separate visual streams, object recognition and categorization occur in the ventral stream and do not include parietal cortex (Goodale & Milner 2004; Milner & Goodale 1995; Ungerleider & Haxby 1994). However, there is evidence from neuropsychological patients, monkey lesion studies, and neuroimaging studies that the visual recognition of misoriented objects involves the parietal cortex (for a brief review, see Graf 2006). A recent experiment using transcranial magnetic stimulation confirmed that the parietal cortex is involved in object recognition (Harris & Miniussi 2006). The parietal cortex is also active in the visual categorization of motion directions (Freedman & Assad 2006; see also Ferrera & Grinband 2006). Similarly, the categorization of distorted (dot pattern) prototypes involves both lateral occipital and parietal activations (Seger et al. 2000; Vogels et al. 2002).

Third, are processing principles and reference frames in perception and action really so different? The notion of two separate streams is connected with the assumption that the streams are based on different processing principles (Milner & Goodale 1995). Visuomotor control requires coordinate transformations, because receptor surfaces and motor effectors rely on different coordinate systems (e.g., eye centered vs. hand centered). Object recognition, in contrast, is thought to rely on the detection of enduring object properties. Similarly, it is assumed that visuomotor control implies egocentric reference frames, whereas recognition relies on object-centered representations (e.g., Milner & Goodale 1995). Therefore, recognition should be achieved irrespective of viewpoint (sect. 5 of the target article). However, the large majority of findings indicate that visual recognition performance is orientation (viewpoint) and size dependent (for reviews, see Graf 2006; Tarr 2003; Tarr & Bülthoff 1998), suggesting that object representations are coded in viewer-centered (i.e., egocentric) coordinates.

Interestingly, recognition performance is not only orientation and size dependent, but shows orientation and size congruency effects. The ability to identify a misoriented object is facilitated if the object is preceded by a different object shown in the same orientation (e.g., Graf et al. 2005). Therefore, it has been proposed that object recognition is based on an adjustment of a perceptual coordinate system (coordinate transformation) that aligns memory and input representations. Recognition is facilitated if the coordinate system is already adjusted in the correct orientation or size (because of the presentation of the previous object). According to this approach, both object recognition and visuomotor control rely on coordinate transformations (Graf 2006; Graf et al. 2005); coordinate transformations can be regarded as a common processing principle for visuomotor control and object recognition (Graf 2006; Salinas & Abbott 2001; Salinas & Sejnowski 2001).

Similar processes seem to underlie tactile recognition. Tactile recognition, too, is orientation dependent (Newell et al. 2001; Pasqualotto et al. 2005), which suggests viewer-dependent reference frames. Moreover, the representations can be updated with observer movement or scene context, both for visual and for tactile recognition (Pasqualotto et al. 2005). This suggests spatial updating processes with observer movement in tactile and visual recognition, consistent with the notion that recognition relies on transformations of a spatial coordinate system, defined by scene context (Graf 2006).

To summarize, visual and somatosensory processing are even more similar than proposed in the target article by D&dH. Both in somatosensory and visual processing, perception for action and perception for object recognition are not strictly separate, but seem to interact extensively. There is evidence that the PPC is involved not only in tactile recognition, but also in visual recognition and categorization. Moreover, the two streams seem to rely on similar processing principles. Overall, it may be more appropriate to assume two cortical streams that serve complementary purposes and tend to interact to overcome the mutual deficiencies of each stream (Grossberg 2000).

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Dissociating body image and body schema with rubber hands

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Abstract: Dijkerman & de Haan (D&dH) argue that *body image* and *body schema* form parts of different and dissociable somatosensory streams. We agree in general, but believe that more emphasis should be placed on interactions between these two streams. We illustrate this point with evidence from the rubber-hand illusion (RHI) – an illusion of body image, which depends critically upon body schema.

The *rubber-hand illusion* (RHI), which is usually induced when a participant's hidden hand is stroked simultaneously and congruently with visible strokes applied to a rubber hand, is regarded by Dijkerman & de Haan (D&dH) as an illusion of *ownership* over a body part, whereas others have also referred to it in terms of self-attribution (Botvinick & Cohen 1998; Ehrsson et al. 2004; 2005a; Ijsselsteijn et al. 2006; Tastevin 1937; Tsakiris & Haggard 2005; Tsakiris et al. 2006). However, there are several sub-components of the RHI, which may dissociate under the appropriate experimental conditions. Such dissociation provides additional support for the model proposed by D&dH, distinguishing between perception and action streams in the somatosensory system.

The illusion of ownership in the RHI is typically assessed by means of a questionnaire, in which participants express strong agreement, on average, with the statement: "I felt that the rubber hand was my hand." Strong positive responses (i.e., ≥75% of the maximum rating on the scale) to this question have been obtained in a number of studies (Armel & Ramachandran 2003; Botvinick & Cohen 1998; Ehrsson et al. 2004), while weaker positive ratings are given under several "virtual reality" conditions (≥50 and <75%; Ijsselsteijn et al. 2006). Finally, several RHI studies have shown, on average, negative (<50%) responses to the same question (Schaefer et al. 2006a; 2006b).

Accompanying the strong ratings of the "illusion of ownership," participants also tend to respond strongly to "it seemed as if I were feeling the touch in the location where I saw it." Indeed, in the three studies with strong illusions of ownership, and which included both questions, the tactile location illusion (visual capture of touch) was more strongly rated than the ownership illusion (Botvinick & Cohen 1998: approximate values: tactile location = 100%, ownership = 89%; Ehrsson et al. 2004: 89% vs. 83%; Ijsselsteijn et al. 2006: 80% vs. 72%). In addition to, or instead of, these illusion ratings, researchers have also measured "proprioceptive drift," in order to quantify the extent to which the felt position of one's real hand changes during the stimulation and illusion period (Botvinick & Cohen 1998; Ehrsson et al. 2005a; Holmes et al. 2006; Tsakiris & Haggard 2005; Tsakiris et al. 2006).

Most interestingly for present purposes, proprioceptive drift can be dissociated from the illusions of ownership and visual capture. For example, simply viewing a rubber hand in a posturally compatible position (optically superimposed over the real hand by using a mirror) for as little as 10 seconds, can induce significant biases in subsequent reaching and pointing movements made with the exposed hand, but without inducing any illusion of ownership or of visual capture (i.e., ratings were <50%, Holmes et al. 2006; see our Fig. 1 here).

Similarly, questionnaire ratings of the perceived drift of one's felt hand position (i.e., "I felt as if my hand was drifting towards the rubber hand") were consistently lower in the aforementioned studies than ratings of the ownership and capture components (drift ratings were only 6%–30%). Reaching and pointing responses made with the illuded[1] hand (Holmes et al. 2006), or intermanual pointing with the non-illuded hand (Ehrsson et al. 2005a; Tsakiris & Haggard 2005; 2006), result in only a *partial* bias in pointing towards the rubber hand (in all cases, <30%

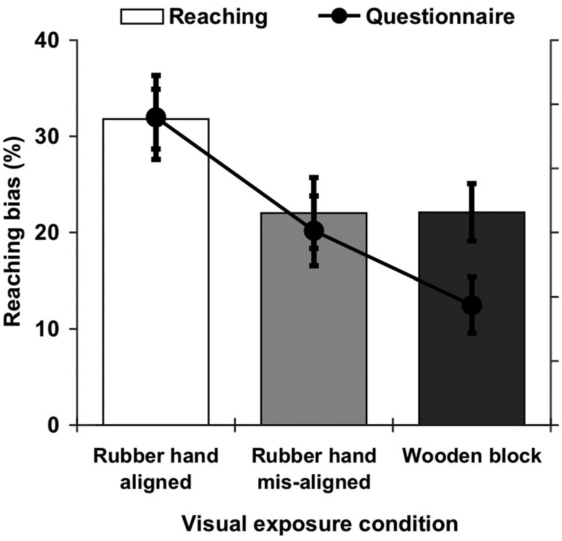

Figure 1 (Holmes & Spence). Dissociation between reaching biases and illusions of body ownership. Illusory "ownership" of the aligned rubber hand was significantly stronger (although, on average still represented denial of the illusion) than the misaligned hand, which was in turn stronger than the wooden block. However, reaching biases in the aligned hand condition were stronger than both the misaligned and wooden block conditions. The latter two conditions did not differ significantly from each other (data show mean ± SEM, redrawn from Holmes et al. 2006).

drift towards the rubber hand). Further, proprioceptive drift increases over time-scales as short as 4 to 12 seconds (Holmes & Spence 2005), and for up to 3 minutes of exposure to a rubber hand (Tsakiris & Haggard 2005). In contrast to these partial and incremental processes, the visual capture of tactile location in the RHI appears to be an all-or-none phenomenon – when participants were asked whether the touch appeared to come from "somewhere between their own hand and the rubber hand," they typically disagreed (Botvinick & Cohen 1998: 28%; Ijsselsteijn et al. 2006: 32%).

In summary, research on the RHI supports the notion that proprioceptive reaching and pointing responses can be dissociated from the visual capture of tactile location, and from higher-order bodily sensations such as ownership. This dissociation parallels, in part, the classical notions of *body schema* and *body image*. Head and Holmes (1911–1912), although they did not use the terms "body image" or "body schema," distinguished three elements of bodily processing which may dissociate from one another following lesions of the spinal cord, brainstem, thalamus, or cortex – a *postural schema* for the appreciation of changes in position and movement of the body (corresponding, perhaps, to the postural and visuo-motor functions of the visual dorsal stream in D&dH's model), a *surface schema* for the localisation of cutaneous stimuli on the body surface (which is not at present separated from postural or proprioceptive information in D&dH's model), and more conscious *visual images* of the body (which may correspond to the *body image* in D&dH's model).

We do not see at present how the model proposed by D&dH accounts in detail for two consistent findings in the RHI literature: (1) that proprioceptive and tactile aspects of the illusion are dissociable, though often correlated; and (2) that postural compatibility of the visible rubber hand is a *necessary* component for induction of the RHI and related phenomena. At present, the model does not appear to provide a direct link between postural, proprioceptive, or visuomotor processing (related to the body schema) and the conscious recognition and ownership of one's body (related to the body image). The RHI demonstrates that we cannot *incorporate* rubber hands into our conscious body image unless they are compatible with our unconscious body schema.

NOTE

1. Patrick Haggard uses the word "illuded" for the "hand subject to the illusion."

Skin stimulation, objects of perception, and the blind

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Abstract: The model developed in the target article is not as comprehensive as might be desired on two counts: (1) in that how the transition from proximal stimulation at the skin gives rise to the perception of external objects is taken for granted; and (2) in that another population of participants, the blind, constitute an important group from which we can understand somatosensory processing and neural plasticity.

Dijkerman & de Haan (D&dH) synthesize a diverse literature in the development of their two-stream model of somatosensory neural processing. I have few concerns regarding the value or utility of their model, and I appreciate the synthesis. However, I raise questions that have long lurked in the literature in which investigations of perception by touch, blindness, and neuroscience overlap, and which may be pertinent in judging the comprehensiveness of D&dH's model.

D&dH state in their introduction that tactile exploration "informs us about the characteristics of external objects" (sect. 1, para. 1), which, while true, glosses over an important achievement: making an ontological transition from patterns of proximal stimulation to objects and environment, making a *distal attribution*. The basis by which perceivers come to attribute patterns of proximal stimulation to objects and events with which they are in contact, directly or indirectly, is fundamental to perception in all modalities. How it arises in the somatosensory system is important because (among other things) the sentient skin serves as the boundary between the self and the environment. Perhaps it could be argued that any contact at the skin surface, by definition, must be caused by a distal object. But, as I illustrate further on, this is not the case. Moreover, as D&dH explain, somatosensation has multiple roles: to inform of the body's internal states, as well as to inform of the external world; and to yield descriptions of the environmental objects, as well to contribute information for guided movements with them. If the somatosensory system reliably and accurately assigns causes to stimulation, an important issue is by virtue of what operations, in what neural complexes, these different functions take place.

What psychological or neural operations give rise to the perception that the proximal stimulation is caused by a distal object in the environment making contact with the skin? To cite an everyday example: A pencil held by the contact with five fingerpads of one hand produces five distinct patterns of stimulation but is perceived as an external, single object (Gibson 1962). Moreover, it can be perceived as an object of certain size, held at a certain location with respect to its length (e.g., see Carello & Turvey 2000). Does the model give clues as to how or where these important perceptual achievements occur? Might the model explain how unusual grips (such as crossed fingers) can give rise to the illusory perception of multiple objects when only one is present (e.g., Benedetti 1985; 1986)? It is not clear how these questions can be answered by the data marshalled by D&dH in developing their model.

It seems not to be the case that distal attributions arise because such stimulation can only have been caused by an external object literally contacting the skin. For example, the tactile-vision substitution system (TVSS) developed by Bach-y-Rita and his colleagues (e.g., Bach-y-Rita 1972; White et al. 1970) revealed that digital camera images converted into isomorphic vibrotactile patterns on the skin are perceived by congenitally blind perceivers qualitatively differently, depending on whether or not the perceiver has active control of the camera. Proximal, skin-based attributions (e.g., "sharp" and "ticklish") predominate when the camera is still or passively moved, but distal attributions (objects perceived "out there") are rapidly made once sensorimotor control of the camera is established. However, in these instances, the distal attributions may well have been based on the users' intellectual understanding of the system that they were operating: someone told them how it all worked. Would a naïve perceiver ever be able to make distal attributions without some independent knowledge of the cause of stimulation at the skin; that is, by being told how it works or by bringing other sensory modalities into play (vision or audition) (e.g., Epstein et al. 1986)? What conditions would be necessary for this to arise? Epstein et al. (1986) suggested that although conscious awareness of the sensorimotor contingencies takes place and may be necessary for distal attribution, it does not appear be sufficient. Perceivers tend to understand that self-movements cause proximal changes in stimulation without necessarily attributing the proximal changes to distal objects. There appears to be some other factor(s) that are required for the transition to occur.

Systems such as the TVSS raise important questions about the nature and ontogenesis of perception in the somatosensory system of the blind. The philosophically inclined may ask whether such perception through the skin counts as "seeing" (e.g., Morgan 1977; O'Regan & Noë 2001). Experimental psychologists seek the informational bases for the qualitative shift from proximal to distal attributions. In terms of the neuroscience of the somatosensory system, what neural structures would support any long-term changes in perception via systems such as the TVSS? It is conceivable that areas of cortex beyond those identified by D&dH as part of the somatosensory processing network are recruited for perceptual purposes in the blind. There is already considerable evidence that extensive areas of occipital cortex (e.g., Amedi et al. 2003; Sadato et al. 1998) and cerebellum (Gizewski et al. 2004) are active in Braille-related tasks by the blind. Hence, although D&dH show how useful neural lesion data are to our understanding, the blind (both congenital and adventitious) constitute a research population whose increased reliance on somatosensation indicates another crucial source of data for testing models of somatosensory processing.

Do intention and exploration modulate the pathways to haptic object identification?

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Abstract: Our model of haptic object recognition points to the importance of material, as well as geometric properties of objects. Collectively, these can elicit a recognition response after an initial contact, without sequential exploration. This model suggests a revision of the authors' proposals, which takes into account an individual's intention – whether it is for perception or action – and the extent of exploratory movement.

In referring to tactile object recognition as "one major function of the somatosensory system" (sect. 3.1, para. 1), Dijkerman & de Haan (D&dH) echo a theme that has guided our research for over 20 years. However, we would substitute the term *haptic* for *tactile*: Whereas the latter refers primarily to skin sensation (Loomis & Lederman 1986), object recognition by touch is fully active, affording valuable kinesthetic, as well as cutaneous information. That very activity is difficult for the present authors to handle, because it points to an essential link between perception and action that they seek to decouple.

D&dH's arguments are weakened, we claim, for two reasons. First, they confuse object primitives at proximal and distal levels, as evidenced, for example, by the target article's combining vibration, pressure, and roughness under the rubric of "simple stimulus features" (sect. 3.1, para. 2). Second, they underestimate the role that material properties play in haptic object recognition. The first error leads to over-emphasizing the role of spatiotemporal integration (via the posterior parietal cortex [PPC]). The second error leads to discounting the richness of material properties.

We have developed a model for haptic object recognition that makes certain fundamental points. As a preliminary, it is important to distinguish among distal and proximal descriptions of objects accessed by the sense of touch. We differentiate between proximal object primitives that arise at the receptor level (e.g., heat flow, vibration) and distal properties of external objects (e.g., apparent warmth, roughness) (Klatzky & Lederman 1999). Transitioning from proximal to distal representations requires computation by neural systems. Further, we have made a critical distinction between two broad categories of distal object properties available to the sense of touch. There are geometric properties, including size and shape features (e.g., curvature) and material properties (e.g., roughness, compliance, apparent warmth).

Given this partitioning, we can move to the first point our model raises, which concerns how properties contribute to object recognition. Generally, *recognition* refers to the assignment of an instance to a category with a common name. It has been demonstrated that there is a basic level of categorization, corresponding to high-frequency names, which hierarchically dominates subordinate categories (Rosch et al. 1976). Members of a basic-level category tend to look alike; however, object categories at both basic and subordinate levels share non-shape features as well, and these are effectively perceived by the sense of touch. Lederman and Klatzky (1990) asked subjects to rate the diagnostic features of objects that were to be categorized haptically at basic and subordinate levels. We found that, at the basic level, shape was deemed important for touch, like vision, but texture was also highly diagnostic; moreover, at subordinate levels, categories were often defined by material properties. An important implication of this work is that haptic object recognition relies on material properties as well as, and in some cases instead of, geometric ones.

Our second point is that when an object is recognized by touch, correlations among object properties can be exploited. A china plate is not only round and thin, but also cool, smooth, and hard. The conjunctions of these properties diminish the diagnostic value of shape and can lead to a rapid identification response *without overt exploration*. Although sequential manual exploratory movements can be linked to perceived object properties, they are not necessary for object recognition by touch.

We have observed (Lederman & Klatzky 1990) a common two-stage process for haptic object recognition. In Stage 1, people begin by grasping and, where feasible, lifting the object. This encompasses the exploratory procedures we call enclosure and unsupported holding, which are sufficient to provide coarse information about many geometric and material object properties (Lederman & Klatzky 1987). For objects being named at the basic level, the grasp–lift movement is often sufficient. Indeed, brief fingertip contact, without grasping, can suffice for recognizing many objects (Klatzky & Lederman 1995). Stage 2, which comprises extensive exploration, occurs when initial contact, grasp, or a grasp-lift combination is insufficient. Particularly when object categories are designated below the basic level (a *dull* pencil), one observes exploratory procedures being used that are optimal (most precise) for obtaining the desired diagnostic information.

Our model casts a new light on the present proposal that the anterior parietal cortex (APC)–PPC route guides action, including exploratory procedures, whereas the APC–insula (+ right PPC) route provides perceptual descriptions leading to recognition. The model suggests that we need to further consider two aspects of an object-recognition task. One is whether the individual intends to perceive or to act; the other is whether he or she performs purposive exploration, or merely Stage-1 contact.

With respect to whether the performer's intention is to perceive or to act, we note that similar actions can arise from different motivations. When we close our fingers around an apple, we may want to feel it to see whether it is ripe, or grasp it in order to eat. Although these intentions are distinct, both have perceptual consequences. Contact with an object has the consequence of feeling, just as breathing has the consequence of smelling. Importantly, the perceptual consequences may not be the same, given equivalent patterns of action. Just as the brain has been found to gate the processing of odorants according to whether the intent was to breathe or to smell (Zelano et al. 2005), it might gate the processing of touch sensations arising from a grasp, depending on whether the actor's goal was to sense or to act.

Considering the second task feature, namely, whether the performer uses Stage-1 contact or, alternatively, extended purposive exploration as the mode of touch, our model suggests that sequential exploratory procedures will be observed only in the case where there is an intention to perceive that is not satisfied by grasping and lifting. Because the exploratory action is invoked by the perceptual system, the ensuing processing will then be gated toward object identification.

Our analysis suggests, ultimately, that two aspects of the performer's action – intention and extent of exploration – define three distinct cases that are likely to modulate the balance between the two pathways identified by D&dH. When there is an intention to act, not perceive, extended purposive exploration will generally not be observed, and the APC–PPC pathway will predominate. When purposive exploration is directed toward perceptual consequences, the APC–insula pathway would predominate, although the PPC would be invoked for purposes of guiding action. Finally, if perceptual consequences were intended but achieved through minimal exploration, a more equal balance between these two pathways would be found.

A call to arms: Somatosensory perception and action

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Abstract: Somatosensory processing for action guidance can be dissociated from perception and memory processing. The dorsal system has a global bias and the ventral system has a local processing bias. Autistics illustrate the point, showing a bias for part over wholes. Lateralized differences have also been noted in these modalities. The multi-modal dysfunction observed may suggest more an issue of interhemispheric communication.

Dijkerman & de Haan (D&dH) propose that somatosensory processing for the guidance of action can be dissociated from the processing leading to perception and memory. Leisman (1989a; 1989b) showed that voluntary movement, like all other movements, consists of operations in time and space specified by physical parameters. When, for example, a person lifts a cup to his or her lips, the trajectory of the teacup, force vectors, acceleration, velocity at every point, total length of the path, locus of origin, and the time of onset specify the voluntary movement. Neurologically normal adults usually perform voluntary movements of this kind quickly, precisely, and without information concerning the total mass or its contents.

There are two types of explanations for the surprising precision with which we move our limbs. One is, that the motor system calculates in advance the values of movement parameters sufficiently accurately to assure successful performance. The other explanation is based on the fact that every muscular contraction changes the state of receptors in muscles and tendons. These receptors measure parameters of voluntary contraction and transmit this information to the motor system. The motor system is then thought to control voluntary contraction under the guidance of sensory feedback from these receptors. Although there is no contradiction between these two explanations, there is disagreement as to the relative importance of specific motor versus sensory feedback.

Other equally important dimension in the understanding of the organisation of voluntary motor control include the question of: (1) what are the levels of the central nervous system at which the desired values of voluntary contraction parameters are calculated? (2) what is the extent to which voluntary contractions are automatic, given that humans are able to consciously vary the parameters of voluntary contractions in an infinite number of ways?

D&dH suggest that the posterior parietal cortex (PPC) subserves both perception and action, whereas the insula subserves perceptual recognition and learning. The authors infer a close relationship between the auditory system and the dorsal and ventral visual systems. D&dH have provided an intellectual genealogical extension of the work by Milner and Goodale, who reinterpreted Ungerleider and Mishkin's (1982) distinction between the "what" and "where" visual systems (Goodale & Milner 1992; Milner & Goodale 1995). Ungerleider and Mishkin (1982) suggested that the *ventral* visual stream (geniculostriate pathway projecting to the inferotemporal cortex) subserves object identification, whereas the *dorsal* stream (projections from the striate cortex and colliculi to the posterior parietal cortex) subserves object localization. This suggests that the function of the dorsal stream is better described as mediating visually guided actions. Therefore, D&dH replace Ungerleider and Mishkin's *what* versus *where* distinction with a distinction between *what* and *how*.

In the visual system, we see the dorsal and ventral stream process different types of visual information. Specifically, the dorsal system has a global bias focusing on lower spatial frequency information, whereas the ventral system focus has a local processing bias utilizing higher spatial frequency information. The dorsal system tends to focus on global form, whereas the ventral system focuses on details or parts of wholes.

Autism is an excellent example where there exists a weighting of one system and diminished processing of the other. Frith (1996) proposed a theory of weak central coherence in autism spectrum disorder (ASD). Additionally, her theory of *enhanced perceptual discrimination* (Shah & Frith 1993) attempted to explain the uneven profile of abilities and difficulties in ASD. *Central coherence* refers to the ability to put information together to extract meaning, to remember the gist of a story rather than its details. Individuals with ASD show a bias for part over wholes – often excelling at noticing and recalling detailed information. Perception and processing features are believed to be superior, possibly at the expense of processing global information. Mottron et al. (2000) showed this same type of bias in the auditory system of autistic individuals, along with sensory motor deficits, explained partly by a more ventrally based sensory motor system focusing more on action and less on perception. Autistics are believed to have poor body schema and spatial localization of body parts. Many autistics cannot identify their body parts in a mirror (Mitchell 1997). Even if they know the word "nose," they may still identify the wrong body part. They have poor proprioception and are generally clumsy (Minshew et al. 2004; Schmitz et al. 2003). These examples emphasize increased action and decreased perception. This parallels what we see in vision and audition with the emphasis on the ventral system and decrease in the dorsal system. The mirror neuron system is dysfunctional in autistics (Hadjikhani et al. 2006). This system also seems to utilize similar processes to recognize movements in an implicit manner for the extraction of meaning of intent, and for emotion.

In normal individuals, motor activity suppresses *mu* wave activity in the sensory motor cortex, but it is also suppressed in normals when they observe someone else performing a motor act (Oberman et al. 2005). In autistics, we see that the *mu* wave is suppressed only with their own actions but not when they observe others. This again would seem to show unevenness in sensory motor modalities with an emphasis on action and diminished perception.

Lateralized differences have also been noted in these modalities. It has been well established that, in vision, the right hemisphere processes information primarily with the more globally focused dorsal system (Melillo & Leisman 2004). The left hemisphere tends to focus on detail similarly to the ventral visual system. The same right/left hemisphere differences exist in the auditory system. The right hemisphere is more spatially oriented toward the dorsal *where*, whereas the left hemisphere is focused on the ventral *what*. This is also believed to exist within the somatosensory system, where the right hemisphere is more focused on dorsal perceptual/sensory systems and proprioception, as well as implicit knowledge of egocentric relationships, and the left hemisphere is more focused on action or motor activity and conscious awareness of body parts.

The multi-modal dysfunction observed in ASD may suggest an issue of the adequacy of hemispheric function in the argument presented by D&dH.

The perception-action interaction comes first

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Abstract: Dijkerman & de Haan (D&dH) study perception and action as two independent processes. However, in all daily activities the processes are completely intertwined, so it is difficult to separate one from the other. Humans perceive in order to move and also move in order to perceive. Understanding first how perception and action are coordinated, leads us then to determine how each component works independently.

In the target article, Dijkerman & de Haan (D&dH) argue "in normal circumstances, . . . perceptual and action-based processes must operate in a coordinated fashion" (sect. 7, para. 1). According to their account, healthy participants coordinate their perceptions and actions more than disabled participants do. However, the authors do not explain *how* perception and action are coordinated. They mostly focus their arguments on how these two processes are separated from each other in the somatosensory modality. We want to focus, instead, on the coupling between perception and action. We argue that to begin any discussion on perception and action, it is necessary to start from how perception and action are linked before knowing how these two systems are subdivided. We attempt to illustrate our argument with two major points.

First, two decades of research have shown that inter-limb relationships and environment-movement relationships can be thoroughly understood if one first considers the so-called macroscopic level of coordination (Kelso 1995; Turvey 2004). In multiple experiments (Kelso et al. 1990; Stins & Michaels 1999; Wimmers et al. 1992), experimenters showed that when one oscillating limb is coordinated with an external stimulus, the coordination is more stable when the phase difference between these two components is in phase (*synchronization*) rather than in anti-phase (*syncopation*). For instance, if the two components are in anti-phase, then an abrupt phase transition to in-phase, through a loss of stability, is provoked when the control parameter of frequency (rate) is increased; if the initial phase relation is in-phase, then the pattern of phase difference is maintained over the same range of parameter change. Moreover, at a neurophysiological level, the spontaneous changes from syncopation to synchronization provoked by the variation of the rate of the periodic stimulus is accompanied by a drastic reorganization of the large-scale cortical activity (Fuchs et al. 1992; 2000; Mayville et al. 1999). These results are observable because one is looking at the macroscopic level. To do so, one needs a measure that affords a direct quantification of the relation between the components, which corresponds, for instance, to the relative phase between the actor and the environment. If we were to try to study each component separately, we would not have access to the crucial information about the actual stability of the behavior. In the first place, stability indicates the particular relations between movement and environment that can be maintained and, therefore, that are spontaneously selected. Secondly, through stability changes one may address transitions between coordination patterns that occur under variations of environmental or internal parameters (e.g., rate of stimuli, attention load).

Other experiments in interpersonal coordination using a dual EEG set-up bring evidence for neural correlates specific to the actual state of the coordination between the participants, quantified by the variability of the phase difference between participants' movements, not by the variability of the phase for each participant's movements considered in isolation (Tognoli et al. 2007). In the case of multisensory integration, it was also recently found that this macroscopic level is the relevant level of study to understand the binding of movement and multiple senses. For example, Lagarde and Kelso (2006) found with a basic paradigm that the particular relationships between action (such as flexion and extension of an oscillating finger) and periodic sensory modalities (such as sound and touch) were determinants of the stability of multisensory integration and its breakdown. Together, this empirical evidence proves that one should not consider lightly the impact that the dynamic link between perception and action has on the adaptive behavior of humans or animals, and the non-trivial qualitative consequences of this link on the functioning of both perception and action.

The second reason that we believe the link between action and perception is a fundamental discussion point, is demonstrated by Pagano and Cabe (2003; see also Pagano et al. 1993) in a study where blindfolded participants had to recognize the shape and length of simple rods. Results showed that participants accurately judged the shape and the length of the rod by moving it with one hand. In this case, it is the *action* that permits the *perception* recognition process. This illustration shows that not only is perception needed for an action, but also an action is needed for perception. When considering the *what* (perception for recognition) and *how* (perception for the guidance of action) of somatosensory processes as proposed by D&dH, it is coordination that prevails: some object's properties are perceived via movement. Following from Gibson's perception view (Gibson 1979), this very relevant example illustrates how movement creates the information required to recognize the object's properties. Going further, Bardy and Laurent (1998) demonstrated that, to control a somersault, gymnasts use peripheral optical flow information. But the optical flow is produced by the somersault itself. This example perfectly illustrates the inextricability of the "what" and "how" and, by extension, perception and action as well. Dissociating the two processes should not come first, and is clearly applying a very restricted understanding of goal-directed behavior's adaptive properties – perception and action are inseparable.

In understanding perception and action, the dynamic relationship between the two components must be considered. From our point of view, it is necessary to start from the coupling among components in order to understand the macroscopic *state* of the behavior, its stability, and hence its efficiency in a given context. Understanding how perception and action are linked will help us understand how each component works, because coordination is the hallmark of what people do every day in any given movement and is the level at which the stability of behavior ultimately lies.

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Taking a conscious look at the body schema

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Abstract: Dijkerman & de Haan (D&dH) propose a somatosensory perceptual pathway that informs a consciously accessible body image, and an action pathway that provides information to a body schema, which is not consciously accessible. We argue that the body schema may become accessible to consciousness in some circumstances, possibly resulting from cross talk, but that this may be detrimental to skilled movement production.

Following Paillard (1999) and consistent with the conceptualization of visual pathways for perception and action (e.g., Milner & Goodale 1995), Dijkerman & de Haan (D&dH) claim that the perceptual somatosensory pathway informs a body image that is conscious, but that information in the action pathway is interpreted within a body schema that is not consciously accessible. Paillard described the body image as an internal representation of body features. The body schema, on the other hand, describes the position of body parts relative to one another as represented by an internal sensorimotor body map. These definitions would suggest that the position of one limb, relative to another, is not normally represented in consciousness, presuming that vision of the limbs is unavailable.

D&dH present ample evidence from patients (e.g., see Rossetti et al. 1995b; 2001) and healthy subjects (e.g., see Westwood & Goodale 2003) to support their claims. However, a growing literature within the movement sciences suggests that we can become acutely aware of the position of our limbs and their movement relative to each other (e.g., Beilock & Carr 2001; Gray 2004; Masters & Maxwell 2004; Wulf et al. 2001), particularly when required to perform under adverse psychological conditions (e.g., competitive pressure; Masters 1992) or in degraded sensory environments (e.g., Maxwell et al. 2003). Maxwell et al. (2003) demonstrated that withholding visual feedback about the outcome of a golf-putting task caused subjects to focus their attention on the mechanics of their movements. Also, Gray (2004) found that expert baseball players are acutely aware of their batting action, particularly when playing poorly – an observation supported by Maxwell and colleagues' contention that performance errors tend to increase conscious awareness of movement parameters (Maxwell et al. 2001; Poolton et al. 2005; in press). Masters et al. (2004) also found that Parkinson's patients report being more aware of their movements than healthy age-matched controls, which suggests conscious monitoring of their actions.

Furthermore, it is traditionally recognized that as expertise is acquired, athletes become increasingly reliant on the availability of proprioceptive information and less reliant on visual information to control their movements and posture (Bardy & Laurent 1998; Fleishman & Rich 1963; Robertson et al. 1994; Robertson & Elliot 1996). Athletes, particularly those with aesthetic aspects to their sport, also often practice with their eyes closed, presumably in an attempt to enhance awareness of proprioceptive feedback generated by their movements.

More controversial is evidence that newborn infants are aware of their movements. Rochat and Morgan (1995) simultaneously presented 3-month-old infants with two online video images of their own kicking legs. The infants looked longer and generated more leg activity while looking at the video image displaying their leg movements in a direction different than they were producing (i.e., the legs were displayed with a left-right inversion). Thus, even preverbal infants may be aware of how they move body parts relative to one another.

These observations suggest that both the body image and the body schema may be consciously accessible in some circumstances or that the information normally contained within the body schema is somehow represented by the body image. However, Masters and colleagues also contend that conscious access to this information may be detrimental to the production of fluent, accurate movements (e.g., see Baumeister 1984; Masters 1992; Masters & Maxwell 2004). Masters and Maxwell (2004) argue that movement control should remain implicit (automatic and unconscious), rather than explicit (controlled and conscious), if optimal performance is desired. They reason that conscious processing of movement parameters places a heavy load on working memory resources (Baddeley 1986). When working memory must process secondary information (e.g., tactical decisions; Poolton et al. 2006), movements are susceptible to disruption. Implicit or unconscious processing does not tax working memory and is, therefore, less susceptible to disruption from secondary tasks. Hence, Masters and Maxwell suggest that the learner should not attempt to focus on the mechanics of their movements.

The detrimental effects of focusing internally, on the mechanics of movement, have also been repeatedly demonstrated by Wulf and colleagues (for a review, see Wulf & Prinz 2001). They argue that focusing internally constrains movement parameters, interfering with their normally automatic execution (McNevin et al. 2003). In contrast, focusing externally, on the outcome of movement, has been shown to maximize performance and promote automaticity. It could be argued that focusing internally promotes conscious processing of the body schema.

Masters and Maxwell (2004) have couched their implicit motor learning theory within an evolutionary context, claiming that implicit motor processes are more stable than explicit processes because the former evolved first (Reber 1992). It is plausible that the neurological structures that support the action pathway evolved before structures supporting the perceptual pathway. Evolutionarily older processes tend to be less susceptible to disruption from psychological stress, disorders, and dysfunctions; are relatively independent of developmental stage, age, or general intelligence (IQ); and should demonstrate lower inter-individual variability than younger processes (Reber 1992). If this is true, then several dissociating characteristics should be observable for D&dH's somatosensory pathways. For example, incidents of neurological disruption to the more explicit perceptual pathway should be more numerous than to the more implicit action pathway. If we assume that conscious information is processed in working memory, then we would also expect disruption to the processing of information from the perceptual pathway when working memory is occupied with a demanding secondary task. Disruption to information from the action pathway should be seen only when it has been made conscious.

In conclusion, the idea that the internal representation of a body schema is always unconscious may be flawed. It is possible that in certain circumstances the information becomes directly or indirectly accessible to consciousness. Given the high degree of interaction between the two pathways and the possibility of cross talk, noted by D&dH, this seems a plausible suggestion. However, current evidence suggests that elevating body schema information to the level of conscious awareness will be detrimental to the performance of skilled movement.

Central role of somatosensory processes in sexual arousal as identified by neuroimaging techniques

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Abstract: Research on the neural correlates of sexual arousal is a growing field of research in affective neuroscience. A new approach studying the correlation between the hemodynamic cerebral response and autonomic genital response has enabled distinct brain areas to be identified according to their role in inducing penile erection, on the one hand, and in representing penile sensation, on the other.

In their target article, Dijkerman & de Haan (D&dH) review results suggesting that cortical somatosensory processing is organised into distinct functional streams, and distinguish between (a) processing for action versus perception, on one hand, and between (b) processing for external target versus stimuli related to the body itself, on the other hand. These distinctions are related to different neural pathways and neuroanatomical correlates.

According to numerous ethologists, sexual behaviour is one of the most important goal-directed behaviours, and the brain plays a key role at each step of its development (Pfaus 1999). Ignored during a long period, the main results regarding this question have come from animal studies, which often remain difficult to extrapolate to humans. However, research on the neural correlates of human male sexual arousal has been developing in recent years thanks to the use of modern neuroimaging tools such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). Until recently, a classic approach used for the statistical analysis of data followed a *subtractive* approach that contrasted brain activations recorded during a period of sexual stimuli presentation with those recorded during a control condition. Such an approach has produced many interesting results (for reviews, see Mouras & Stoleru 2007; Stoleru & Mouras, in press). The presentation of sexual stimuli induces a great number of behavioural responses, ranging from emotional to autonomic reactions. However, neuroimaging regression models often contain hypothetical temporal functions (block-type functions, for example, to describe periods of different experimental conditions). Because of the large set of neural responses involved, one can argue that models that include more specific and objective functions would be more suited to identifying the brain circuits involved.

Penile plethysmography, an objective method of measuring genital response, was used successfully within an fMRI scanner (Arnow et al. 2002; Ferretti et al. 2005; Moulier et al. 2006). Pertinent to the purpose of this commentary, Arnow et al. (2002) did not identify many brain areas by performing subtractive analyses, whereas in many areas the blood-oxygen level–dependent (BOLD) signal was correlated with the penile response as measured by circumferential plethysmography. In this study, the highest correlation was reported in the right insular/subinsular region, in accordance with the role of insula in somatosensory processes (Augustine 1996). In a recent study (Moulier et al. 2006), we used the higher sensitivity of volumetric plethysmography (Kuban et al. 1999) to distinguish brain areas more involved in penile-response command from those involved in genital response cortical representation, by manipulating the time window separating erectile and cerebral responses. Interesting results have been found pertaining to the distinctions made by D&dH.

Whereas the correlational analyses clearly identified insulae bilaterally, our data suggested a role of the *anterior* portion of the insula in mediating the erectile response (i.e., the genital response, a cross-correlation led by the cerebral signal). This was in accordance with the report of diastolic blood pressure and heart rate variations after electrical stimulation of the anterior insula (Oppenheimer et al. 1992). Conversely, a role of the *posterior* portion of the insula in sensory integration was suggested by a cross-correlation led by the plethysmographic signal (for a voxel located in $x = 36$, $y = -23$, $z = 15$ mm). Accordingly, sexual stimulation of the penis has been shown to strongly activate the right posterior insula (Georgiadis & Holstege 2005), especially for a very close location ($x = 36$, $y = -24$, $z = 14$ mm).

Different areas were also distinguished with regard to penile cortical representation. A positive correlation was found in the paracentral lobules, which are located on the medial surface of the hemisphere and correspond to the first localization of the penile cortical representation of the homunculus (Penfield & Rasmussen 1950). However, in the same correlational analysis a second location was found more on the lateral surface of the somatosensory cortices; this location became larger and had a higher correlation coefficient when the plethysmographic signal preceded the BOLD signal by 10 seconds. This result was in accordance with previous recordings of evoked cortical potentials by stimulation of the dorsal nerve of the penis (Bradley et al. 1998). Following these results, we then proposed a distinction between two distinct penile representations: (a) one on the medial surface of somatosensory cortices, corresponding to the original one and related to the perception of genital response proper; and (b) one on the lateral surface of the cortices, which would be more related to superficial skin stimulation (Kell et al. 2005).

Finally, our correlational approach allowed us to identify high correlations between the cerebral and genital responses in regions related to motor preparation and imagery processes, such as left inferior parietal lobule, frontal opercula, ventral premotor area, and supplementary motor areas.

Thus, many of the target article's main arguments are largely supported by studies of the neural correlates of human penile response using, in particular, correlational analyses between autonomic genital response and hemodynamic cerebral response. Overall, the results of such studies support the central role of the insula in penile sensation awareness – that is, in higher-order somatosensory processing. Consistent with D&dH's viewpoint (see sect. 3.2 of the target article), the insula could be involved in the emotional component of sexual arousal (Redoute et al. 2000). Another striking point of convergence between data reviewed by D&dH and our results in the Moulier et al. (2006) study is that we found that the magnitude of penile tumescence drives, with a lag of about 10 seconds, the BOLD signal recorded from the paracentral lobule (part of the posterior parietal cortex). This suggests that this area is involved in the command of the penile response – which is again clearly consistent with the role of Brodmann 5 in goal-directed actions as reported by D&dH.

In conclusion, the recent application of penile plethysmography within the neuroimaging setting allows the study of the correlation between the cerebral and autonomic responses. Moreover, the high sensitivity of volumetric plethysmography enables brain areas more related to the conduction of the erectile response to be distinguished from those areas more related to the encoding of penile sensation, once the autonomic reactions appear. The high correlations found for areas related to motor imagery underline the central role of physiological reactions in goal directed behaviours.

Divisions within the posterior parietal cortex help touch meet vision

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Abstract: The parietal cortex is divided into two major functional regions: the anterior parietal cortex that includes primary somatosensory cortex, and the posterior parietal cortex (PPC) that includes the rest of the parietal lobe. The PPC contains multiple representations of space. In Dijkerman & de Haan's (D&dH's) model, higher spatial representations are separate from PPC functions. This model should be developed further so that the functions of the somatosensory system are integrated with specific functions within the PPC and higher spatial representations. Through this further specification of the model, one can make better predictions regarding functional interactions between somatosensory and visual systems.

In external space, both somatosensory and visual systems perform the critical functions of object localization and recognition. In touch, the hand is a flexible exploring effector that combines motor capabilities with sensory capabilities to actively find objects in personal (on the body) and in peripersonal (within reaching distance) space (Lederman & Klatzky 1987; Previc 1998). Once an object is located, the hand then executes a series of exploratory procedures to extract information about the material and geometric properties of the object (Klatzky et al. 1989; Lederman & Klatzky 1987). Thus, in haptics, action is inextricably part of perception. Most real, common objects can be recognized in less than 2 seconds (Klatzky et al. 1985). Nonetheless, haptic perception is best suited to extract local, material properties from objects (Klatzky et al. 1987). Information regarding the complex contours and part relations of objects, especially for large objects that exceed the size of the hand, is more difficult to apprehend. Although touch physically interacts with portions of the outside world, it needs information about objects located in extrapersonal space, outside of reach.

In contrast, perception is separate from action in the visual system. Vision is well suited to obtain the information that touch lacks and vice versa. In vision, the spatial layout of objects in extrapersonal space is easily obtained, as are the spatial relations of one object to another and the spatial relations of object features. However, physical object properties need to be inferred. By itself, vision cannot perform actions in the world.

Although touch and vision can find objects in peripersonal and personal space and recognize them independently, they typically function together. The motor/somatosensory system uses spatial information from vision to help move the body through space in order to help bring objects in extrapersonal space into peripersonal space, in which the haptic system can be effective. This system also uses information regarding frames of reference and spatial relations to help construct representations of object-shape and object-part relations. In turn, the somatosensory system provides the visual system with the means to perform actions. The interaction of the systems expands the object localization and recognition capabilities of both. Thus, neuroanatomical divisions within the posterior parietal cortex (PPC) should aid this interaction by providing the lacking information to each.

First, consider known divisions of labors within the visual stream of processing. Creem and Proffitt (2001) proposed that visual information processing can be divided into "what," "where," and "how" pathways. The "what" pathway is involved in object identification and follows a ventral route from primary visual cortex to inferior temporal cortex. The "where" pathway is involved in the coordination of spatial maps and spatial frames of reference and follows a more dorsal route to the inferior PPC. Finally, the "how" pathway is involved in coordinating visual information with action on objects and follows the most dorsal route to the superior PPC.

Of interest is how these divisions of labor for vision within the PPC relate to divisions of labor within touch. For tactile object recognition, converging evidence from primate, patient, and neuroimaging literatures points to a somatosensory "what" processing stream: A modality-specific ventro-lateral stream moves from the sensorimotor cortex to the secondary somatosensory cortex (SII), the insula, and the inferior PPC before connecting with modality-general portions of the ventral object processing stream (Reed et al. 2004). A patient with unilateral tactile agnosia (impaired tactile object recognition) had left hemisphere inferior parietal damage (Reed & Caselli 1994). Her object-recognition impairment did not influence other forms of spatial processing, but her specific errors indicated a problem in integrating the different parts of objects (Reed et al. 1996). For tactile object localization, data from fMRI studies suggest a somatosensory "where" processing stream that differentially involves bilateral superior PPC (Reed et al. 2005).

At first glance, the somatosensory "what" and "where" systems appear to be connected to the wrong parts of the visual system: The somatosensory "what" system appears most closely related neuroanatomically to the visual "where" system, and the somatosensory "where" system appears most closely related to the visual "how" system. However, when one considers what information each system needs most to perform specific functions, the divisions of labors may make sense. The somatosensory recognition system includes inferior PPC but requires information regarding spatial relations among objects and their parts. The "where" system for vision, also associated with the inferior PPC, contains this information. Thus, when somatosensory "what" meets visual "where," more precise multimodal object recognition can occur. Similarly, the somatosensory "where" system, associated with superior PPC, contains information regarding sensorimotor information in relation to body space. The visual "how" system, also associated with the superior PPC, connects with visual properties for object interaction with sensorimotor information for more precise object-related actions. These processing streams in touch and vision allow for better transmission of information for multimodal functioning.

In summary, Dijkerman & de Haan's (D&dH's) model is underspecified with regard to the integration of the higher spatial information with the PPC and how the PPC might be functionally divided for the somatosensory system. These divisions have implications for how the somatosensory system interacts with the visual system for the important functions of object localization, recognition, and interaction. Nonetheless, the model has achieved what the authors intended – it has provided a model from which predictions can be made.

Pathways of tactile-visual crossmodal interaction for perception

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Abstract: There is a task-specificity in the visual-tactile interaction for perception: The polymodal posterior parietal cortex is related to the comparison of the shapes coded by different sensory modalities, whereas the lateral occipital complex is the part of the network for multimodal shape identification. These interactions may be mediated by some latent pathways potentiated by sensory deprivation or learning.

In the target article, Dijkerman & de Haan (D&dH) propose that the visual-tactile modalities interact closely through the polymodal higher-order cortical areas such as the posterior parietal cortex (PPC) and the lateral occipital complex (LOC), whose functions may differ. They suggest that the PPC is involved in multimodal coding of body-related configuration for the guidance of action, whereas the LOC is a multimodal area involved in perceptual representation of object form features. Here we argue that these polymodal areas also show some specificity of the cross-modal interaction for perception.

Mah-Jong is a Chinese game similar to card games, involving two-dimensional plastic tiles with various marks carved on one side; therefore, shape can be identified by both visual and tactile inspection. Visual-tactile cross-modal shape comparison with Mah-Jong tile activated the caudal part of the intraparietal sulcus more prominently than did intramodal comparison (Saito et al. 2003). This is consistent with the notion that the two processing streams in both modalities project to the same higher-order cortical areas that are involved in multimodal sensory integration. Therefore, this finding may suggest that the PPC is related to the comparison of shapes coded by different sensory modalities.

Intramodal tactile shape comparison does not usually recruit the visual cortex in activation (Harada et al. 2004). In contrast, during three-dimensional object naming, Amedi et al. (2001) first demonstrated consistent somatosensory activation in the LOC. They suggested that cortical neurons in the LOC in humans may function as a part of the multimodal object-selective network (Amedi et al. 2001). The activation in the LOC reflects stored object-related visual information that can be accessed via cues from somatosensory modalities, and possibly from other modalities as well (Amedi et al. 2001). This argument suggests that direct interactions among modality-specific sensory pathways underlie the multimodal representation of objects (Amedi et al. 2001). According to this view, bimodal activation occurs in the visual cortex rather than in the somatosensory areas because object recognition relies primarily on vision. Hence, the LOC is related to the multimodal shape identification.

The involvement of the multimodal LOC in tactile processing appears to be modified by learning (Saito et al. 2006) or sensory deprivation (Sadato et al. 2004). Some well-trained Mah-Jong players can identify the carved patterns of the tiles by touch. The subjects who were well trained in the tactile comparison of Mah-Jong patterns showed more prominent activation in the visual cortex, including the LOC and V1, when performing this task than did the naïve subjects, who showed activation in the LOC but not in V1 (Saito et al. 2006). Both the LOC and the V1 of the well-trained subjects were activated during Braille tactile comparison tasks to which they are naïve. This is probably due to cross-modal plastic changes produced by the effects of long-term training on one set of cards (Mah-Jong) that generalizes to an untrained set of cards (Braille) (Saito et al. 2006). During tactile shape comparison with Braille characters, lately blind subjects (i.e., those with late onset of blindness) who had never learned Braille showed the activation of the association visual cortex, including the LOC (Sadato et al. 2004). This may be interpreted as that the visual deafferentation caused less demand on bottom-up visual processing, which may in turn introduce an opportunity for the expansion of tactile representations in the visual association cortex.

Burton et al. (2004) showed that simple vibrotactile stimulation activates both lower-tier visuotopic (e.g., V1, V2, VP, and V3) and several higher-tier visual areas (e.g., V4v, V8, and BA 37). Early blind participants showed the most extensive distribution of activity. Lately blind participants exhibited activity in mostly similar regions, but the response magnitudes declined with the age of onset of blindness. Three sighted individuals had supra-threshold activity in V1. These results suggest that vibrotactile inputs probably activate the visual cortex through some latent pathway common to both blind and sighted subjects (Burton et al. 2006). Burton et al. (2006) speculated that visual deprivation alone induces reorganization of the visual cortex, particularly in regions with already strong multisensory properties, where a competitive shift to non-visual inputs may readily follow visual deprivation (Sadato et al. 2004). In contrast, cross-modal reorganization of the lower-tier visual areas, which are not cross-modally responsive in sighted people, may be activated particularly through regular attention to selected non-visual inputs. Such learning might be needed to strengthen the more remote connections with multisensory cortical areas (Saito et al. 2006). Cross-modal reorganization of lower-tier visual areas may thus be triggered in sighted subjects by learning such skills as Mah-Jong pattern identification by touch.

In conclusion, visual–tactile interaction for perception is mediated by task-specific pathways which are dynamically modified by sensory deprivation or learning.

Multifaceted functional specialization of somatosensory information processing

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Abstract: We review evidence for multifaceted functional specialization of somatosensory information processing, both within and outside classical somatosensory cortex. We argue that the nature of such specialization has not yet been clarified adequately to regard the proposed action/perception dichotomy as being established. However, we believe this is a good working hypothesis that can motivate further work.

Although most investigators would agree on the existence of functional specialization for processing somatosensory information, we argue here that the nature of such specialization, both within and outside classical somatosensory cortex, is far from clear. In monkey primary somatosensory cortex (SI), focal ablation of Brodmann's areas 1 or 2 has been found to specifically impair perception of texture or form, respectively (Randolph & Semmes 1974); whereas, lesions of Brodmann's area 3b (Randolph & Semmes 1974) and of secondary somatosensory cortex (SII) (Murray & Mishkin 1984) non-selectively impair perception of both texture and form. Partly consistent with these findings are neurophysiological observations in monkeys that neuronal responses in SI and SII encode texture changes (Jiang et al. 1997; Pruett et al. 2000; Sinclair et al. 1996) and that neurons in Brodmann's area 2 are shape-selective (Koch & Fuster 1989).

These functional differences described in monkeys do not map neatly onto humans. Somatosensory cortical lesions were formerly thought to produce complex discriminative deficits, as opposed to thalamic lesions resulting in simpler problems with detection of touch or pain, but this clinical dogma has fallen by the wayside in the era of neuroimaging (Sathian 2007). Whereas SI lesions affect both texture and form discrimination (Roland 1987), parietal opercular lesions seem to specifically compromise form perception (Roland 1987; Caselli 1993; Reed et al. 1996). However, another report indicates that SI lesions cause deficits in kinesthesis and discriminative tactile perception, whereas parietal opercular-insular lesions result in thermo-nociceptive deficits and poststroke pain (Kim 2007). Thus, the findings from studies of patients with somatosensory cortical lesions have not yet led to a coherent picture.

Functional neuroimaging studies of somatosensory cortex have led to similarly heterogeneous results. Some studies have noted common regions of activation in the postcentral sulcus (PCS) (O'Sullivan et al. 1994; Servos et al. 2001) or parietal operculum (Ledberg et al. 1995) during perception of both texture and form. We reported PCS activity selective for form relative to texture in two independent studies (Peltier et al. 2007; Zhang et al. 2004). Since the PCS corresponds to Brodmann's area 2 (Grefkes et al. 2001), form-selectivity in this region is consistent with the aforementioned neurophysiological and lesion studies in monkeys that implicate area 2 in form perception (Koch & Fuster 1989; Randolph & Semmes 1974). Despite the implication of parietal opercular activity in form perception (Reed et al. 2004), such activity has not been shown to be form-selective. On the contrary, parietal opercular activity is stronger during texture than form perception (Roland et al. 1998; Stilla et al. 2006). It should be noted that parietal opercular cortex, which was initially equated with SII (for a review, see Burton 1986), actually contains multiple somatosensory areas, with evidence now for three areas in monkeys (Fitzgerald et al. 2004) and four in humans (Eickhoff et al. 2006a; 2006b).

There is, surprisingly, greater consensus on findings outside classical somatosensory cortex, in regions now identified as multisensory. Conjoint tactile and visual form-selectivity characterize the visual cortical region known as the lateral occipital complex (LOC) (Amedi et al. 2001; Peltier et al. 2007; Zhang et al. 2004), the anterior intraparietal sulcus (aIPS) (Grefkes et al. 2002; Peltier et al. 2007; Zhang et al. 2004), and foci located more caudally in the IPS (Peltier et al. 2007; Saito et al. 2003; Zhang et al. 2004). Tactile texture-selectivity outside somatosensory cortex appears to be confined to medial occipital cortex at the border between visual areas V1 and V2, where it overlaps with visual texture-selectivity (Stilla et al. 2006). Task-specific, modality-independent engagement of particular cerebral cortical regions during perception seems to be a general rule; that is, regions known to be specialized for processing particular aspects of vision are also recruited during performance of corresponding tactile tasks (for a review, see Sathian 2005).

So, what about the proposed dichotomy of processing? One study (Reed et al. 2005) suggested distinct processing streams for form and extrapersonal spatial processing, although selectivity was found only outside somatosensory cortex, involving fronto-cingulate cortex and superior parietal cortex, respectively. Another study (van Boven et al. 2005) described hemispheric specialization within posterior parietal cortex, rather than a dorso–ventral dichotomy, the left aIPS being preferentially active during discrimination of grating orientation, and the right temporo-parietal junction, during discrimination of small differences in grating location on the fingerpad. We have reported somewhat similar specializations, involving left aIPS and left parieto-occipital cortex for tactile discrimination of grating orientation, and the right angular gyrus for tactile discrimination of grating groove width (Sathian et al. 1997; Zangaladze et al. 1999; Zhang et al. 2005). Our findings of selectivity for form in PPC foci and for texture in parietal opercular cortex (Stilla et al. 2006) could be interpreted as consistent with the proposed action/perception dichotomy of somatosensory processing: The dorsally directed pathway into PPC can be considered as specialized for grasping, which fits with findings for the aIPS region in monkeys (Murata et al. 2000) and humans (Frey et al. 2005) – grasping is an action closely linked to haptic form perception. The ventral pathway via the parietal operculum into the insula, in contrast, might be particularly concerned with material object properties, such as texture, which are especially the province of touch (Klatzky et al. 1987). Even the activity of the left aIPS during mental rotation of tactile (Prather et al. 2004) and visual (Alivisatos & Petrides 1997) forms, which we suggested represents activation of the dorsal visual pathway on account of spatial processing (Prather et al. 2004), could be viewed in terms of manipulation of images, a kind of internal action. However, given the multifaceted nature of somatosensory specialization, we think the proposed action/perception dichotomy should be considered a working hypothesis of somatosensory processing to motivate further research, rather than being regarded as established.

The multiple relations between vision and touch: Neonatal behavioral evidence and adult neuroimaging data

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Abstract: Neonatal behavioral data support the argument that multiple relations exist between vision and touch. Looking at an object triggers the motion of a neonate's arm and hand towards it. A textured surface that is seen can be recognized tactilely, but not a volumetric shaped object in cross-modal transfer tasks. These data are supported by adult neuroimaging data.

The relations between vision and touch in infancy have been studied according to two paradigms: (1) Fine descriptions of the visuo-prehensile coordination when infants attempt to reach and grasp objects near them. (2) Looking or holding times obtained in cross-modal transfer tasks between touch and vision. The analysis of evidence obtained from the separate bodies of literature (see Streri 1993) supports Dijkerman & de Haan's (D&dH's) argument regarding dissociation between somatosensory processing for perception and for action. On one hand, cross-modal transfer of shape is not bi-directional from birth. In these tasks, newborns were familiarized with an object in one modality (touch or vision) and then, in the test phase, they received the familiarized object and the novel one in the other modality. A longer holding or looking time for the novel object is taken as evidence of cross-modal recognition. Newborns visually recognize a shape held previously (Streri & Gentaz 2003; 2004), but they fail to recognize tactilely a shape seen previously (Sann & Streri 2007). On the other hand, visuo-prehensile coordination is also present at birth. The newborns, firmly seated on a chair inclined at 50° (with the chair supporting their head and trunk) are able to move their arms towards a target. The direction of movement is always correct, and this gesture is considered as visually triggered. However, contact with the object is rarely achieved (von Hofsten 1982). Neonatal visuo-prehensile coordination is also uni-directional. When newborns hold an object, they never move it towards the eyes (Streri & Gentaz 2003; 2004).

In short, when newborns hold an object, they do not attempt to look at it, but are able to recognize it visually in a cross-modal transfer task. When newborns look at an object, they do not recognize it tactilely, but attempt to reach and grasp it. This neonatal reaching is visually triggered, whereas perceptual recognition is tactilely supported. During the course of development, this scenario remains unchanged. Concerning cross-modal transfer, the failure from vision to touch has been demonstrated in 2-month-old infants (Streri 1987) and in 1-year-old infants (Rose and Orlian 1991). Also, adults' performances are worse in the visual-tactile (V-T) modality than in the tactile-visual (T-V) modality (Connolly & Jones 1970; Jones & Connolly 1970; Juurmaa & Lehtinen-Railo 1988; Newham & McKenzie 1993; cf. Hatwell 1994). Thus, from birth and throughout life, the T-V modality appears to be performed better than the V-T modality. Regarding visuo-prehensile coordination, by the age of about 4–5 months, a child's hand approaching an object is guided visually and the focus of gaze switches back and forth from the hand to the object to be grasped. Infants are able to anticipate the trajectory of a moving target, and the hand is prepared to receive visually gained information. This action has several characteristics of the adult system (Jeannerod 1986; von Hofsten & Rönnqvist 1988).

We suggest that visuo-prehensile coordination is devoted mainly to spatial process (*Where*). Because cross-modal transfers require memory and recognition processes, they are mainly devoted to the identification of the shape of objects (*What*). This dissociation is supported by the neuroimaging data obtained from studies on adults (Reed et al. 2005). Reed et al.'s data provide direct evidence that neural regions for somatosensory "what" are different from "where."

Another dissociation in the somatosensory system can be evoked by the processing of the characteristics of objects. The somatosensory processing of microgeometric properties (such as texture) has to be distinguished from the somatosensory processing of macrogeometric properties (such as shape). Support for this idea is based on two lines of evidence: (1) our studies on newborns' perception of both properties of an object in bidirectional cross-modal transfer tasks between vision and touch (Sann & Streri 2007), and (2) neuroimaging data obtained in adults. The results of the former revealed that cross-modal transfer of shape is not bidirectional. In contrast, cross-modal transfer of texture is bidirectional. Vision and touch appear to be equivalent for gathering, exchanging, and processing information about texture, but not about shape. Regarding neuroimaging data obtained in adults, Roland et al. (1998) suggest that a functional separation may exist in the cortical processing of microgeometric and macrogeometric cues: Shape and length discrimination activate the anterior part of intraparietal sulcus more than does roughness discrimination. Merabet et al. (2004), using repetitive transcranial magnetic stimulation (rTMS), showed that a transient disruption in the somatosensory cortex impairs microgeometric (texture) judgment, while a transient disruption in the visual cortex impairs macrogeometric (distance) judgment. More recently, a functional magnetic resonance imaging (fMRI) study investigated the activity and the connectivity of parietal and occipital cortical areas during haptic, and (in separate runs) visual, shape or texture perception (Peltier et al. 2007). The results revealed that a network of cortical regions is selectively activated during haptic shape perception compared to haptic texture perception. The intraparietal sulcus and the lateral occipital complex appear to be shape-selective in the tactile modality, as well in the visual modality.

Taken together, these data suggest that, from birth, somatosensory processing is organized into several functional streams, and its evolution appears stable. Neonate behavioral data and adult neuroimaging data provide an answer to the major question concerning the visual influences on somatosensory processing. These influences differ for action and for perceptual recognition. They also differ according to the perceptual processing of object properties.

Body image and body schema: The shared representation of body image and the role of dynamic body schema in perspective and imitation

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Abstract: Our commentary addresses two issues that are not developed enough in the target article. First, the model does not clearly address the distinction among external objects, external body parts, and internal bodies. Second, the authors could have discussed further the role of body schema with regard to its dynamic character, and its role in perspective and in imitation.

Dijkerman & de Haan (D&dH) propose a model that takes into account the role of the somatosensory system in perception and action, in analogy with the dual-route model of the visual cortical system. In our commentary, we address two issues that are not developed enough in the target article.

One of the core aspects of D&dH's model is that, differently from the dual-route model of the visual system, it distinguishes between internal and external stimuli, that is, between somatosensory processing of one's own body and of external objects. First, despite the target article's wide review of literature on body image, we believe the model does not clearly address the distinctions among external objects and external body parts, and internal bodies as regards body image. Second, the target article should have discussed further the role played by body schema. The authors do not sufficiently underline the dynamic character of body schema. In addition, even though they admit that the neural correlates of visual representation of the observers' own body has received scarce attention, they do not address the behavioral and neural literature focusing on the role of one's own as well as others' perspective in body schema. Finally, we think that D&dH should take into account the role of the body schema in the imitation of action. Here, we consider these two aspects in turn.

D&dH do not clearly discuss how the bodies of others are processed: Are they considered as external objects or as external bodies? For example, their model is not fully able to explain how tactile recognition of others' body parts takes place. This is an important issue, because both neuropsychological and experimental studies on body image suggest that a common supramodal representation is used for representing the bodies of others, as well as one's own body (Bosbach et al. 2006; Buxbaum & Coslett 2001). This is suggested, for example, by the inability of autotopagnosic patients to locate body parts on their own body, on another's body, or on a mannequins' body (Buxbaum & Coslett 2001; Ogden 1985; Semenza 1988; Sirigu et al. 1991), and by the results of a test with healthy participants by Reed and Farah (1995). A possible way for explaining how this recognition takes place might be to assume that an external hand is tactilely recognized and activates its corresponding representation in semantics (as suggested by the link between the tactile object-recognition module and the semantics module, which also includes the semantic knowledge about the body). However, because of the lack of a direct link between semantics and the internal body image, it is difficult to understand how another body's hand can, for example, be recognized as being a right or a left hand. D&dH should at least add a link between the internal body image and semantics. In this regard, a clarification is needed concerning terminology. The authors distinguish between body schema, body image, and some form of semantic and conceptual representation of the body. However, in the recent literature a more clear terminology is proposed. For example, Schwoebel et al. (2004) distinguish between body schema, body image, *or* body semantics, and body structural description. In sum, even though D&dH discuss the existence of a semantic and conceptual representation of the body, they do not relate body image to semantics in their model.

The authors do not discuss enough the role of body schema as far as three aspects are concerned: its dynamic character, the role of perspective, and the role of body schema in imitation. The dynamicity of body schema is clearly demonstrated by the neural and behavioral literature focusing on the enlargement of the body schema on account of tool use (for a review, see Maravita & Iriki 2004). We believe that this interaction between the body and objects conceived of as extensions of the body should be at least briefly considered.

Moreover, the target article does not develop enough the role played by perspective-taking. The authors dismiss the literature in this field by arguing that there is ample evidence for egocentric coding of external targets, and that the neural correlates of visual representation of the observers' own body have received less attention. However, the role of perspective is an important issue: Perspective is one of the visual characteristics that enables us to distinguish our own body from the body of someone else. According to the in-use terminology, "egocentric" refers to the perspective consistent with looking at one's own body, whereas "allocentric" refers to the perspective that is consistent only with looking at someone else's body (Saxe et al. 2006). Both neural and behavioral studies have provided evidence for distinct representations for self and others with respect to visuo-spatial perspective taking. Much neural evidence confirms our sensitivity to action perspective (Carey et al. 1997; David et al. 2006; Jackson et al. 2006; Knoblich 2002; Ruby & Decety 2001). On the behavioral side, evidence of the role of perspective is more scarce. However, Vogt et al. (2003) suggest the existence of two different priming effects: a visuomotor priming effect, driven by a visual stimulus (a hand) that automatically evokes a motor response, and a motor visual priming, driven by planning, which enhances the visual processing of body parts in the egocentric perspective.

Finally, we think that the authors should at least briefly consider the role of dynamic body schema in action imitation, as shown by recent neuropsychological and brain-imaging studies (Buxbaum et al. 2000; Chaminade et al. 2005; Goldenberg 1996). Indeed, there is a common code linking different body parts and their spatial configuration that is independent of different modalities and perspective (Goldenberg & Karnath 2006).

Haptic perception is a dynamic system of cutaneous, proprioceptive, and motor components

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Abstract: A general shortcoming of the localist, decompositional, approach to neuroscientific explanation that the target article exemplifies, is that it is incomplete unless supplemented with an account of how the hypothesized subsystems integrate in the normal case. Besides, a number of studies that show that object recognition is proprioception dependent and that cutaneous information affects motor performance make the existence of the proposed subsystems doubtful.

Dijkerman & de Haan's (D&dH's) target article can be seen as an effort to apply the kind of dissociative organization proposed by Milner and Goodale for the visual system (see Goodale & Milner 1992; Milner & Goodale 1995), to somatosensory processes. Such a strategy is an example of a decompositional approach to neuroscientific explanation: It starts with a functional analysis of a cognitive process and decomposes it into different subsystems (each one supposedly responsible for processing different kinds of information); and then tries to determine the neural bases of each subsystem. The proposal is considered successful if these subsystems can be differentially correlated with different neural paths and regions, either by neuroimaging studies or by neuropsychological (double) dissociations.

However, a common problem of such explanations is that they are not complete until they can show how these different subsystems integrate and work together in normal, healthy subjects. The idea that the brain processes different information in different places at different speeds is fine, but the model must also offer an account of the time course of the different processing paths, how these different paths may conflict and integrate, how the internal activity evolves in interaction with the specific kinds of information available in the environment, and how the brain is able to organize its resources, so that on a given occasion, a given informational pathway may take over (Gomila & Calvo, forthcoming).

In this case, however, we think there are grounds for doubting D&dH's functional analysis in the first place. Their article proposes that tactile object recognition and body image constitute a different system from the one involved in proprioception. This implies that somatosensory processes involved in perception are different from somatosensory processes involved in action. Unfortunately, this distinction does not take into account results, like those obtained in the field of dynamic touch (Turvey 1996), that support a more comprehensive view on touch. In fact, it only focuses on what, following Jones and Lederman (2006), may be called tactile sensing, as opposed to haptic sensing (which involves *exploratory procedures*, that is, hand movements for haptic object perception (Lederman & Klatzky 1990). There is plenty of evidence obtained from these more comprehensive approaches that shows, on the one hand, that proprioceptive information is relevant to object recognition (Blanco & Travieso 2003; Pagano & Turvey 1998; Pagano et al. 1996), and, on the other hand, that cutaneous stimulation may contribute to motor control through the body schema (Travieso & Lederman, under revision; Westling & Johansson 1984).

To illustrate the relevance of proprioceptive information in object recognition, we will focus on a concise length and weight perception task. In such a task (Amazeen & Turvey 1996), a subject is asked to estimate the length and weight of a non-visible object which cannot be grasped completely (it can only be handled). What Turvey's group has been able to prove is that, in order to perform this task, the subject needs to extract the rotational inertial properties of the object. These are obtained from the antigravitational force required by the muscles to hold the object (their rotational dynamics). The invariant tensor of inertia, which according to Turvey (1996) is the physical quantity we extract, can be obtained only from the muscular effort required to move the object. Hence, this example clearly shows that intentional movement is necessary for haptic length or weight object perception. Furthermore, the same information is used to perceive both our own body and the external object (Pagano & Turvey 1998; Pagano et al. 1996), which contradicts D&dH's functional separation.

With respect to the contribution of cutaneous information to motor control, several studies have shown that cutaneous information contributes to proprioception. It is well known that the perception of hand position and orientation is mediated by cutaneous information, but recent studies show, as well, that the contribution of cutaneous information also extends to the perception of other body parts (Collins et al. 2005). On the other hand, cutaneous deficits also affect motor dexterity (Moberg 1983; 1991). For example, Travieso and Lederman (under revision) have found inverse correlations between the spatial resolution thresholds at the fingertips and the time needed to perform motor-dexterity tests and to recognize three-dimensional objects, together with deficits in texture perception (Travieso & Lederman, under revision; Travieso et al. 2001). These results also contradict the separation of different somatosensory processes for perception and action proposed by D&dH.

As a last point, we want to highlight that the authors themselves implicitly acknowledge in the target article that their proposed functional decomposition does not really fit with the neuroanatomical data, given that the posterior parietal cortex plays a role both in recognition and in action, which rather suggests common processing. That their functional analysis is problematic can also be seen, for example, in how they interpret the performance of patient G.L. in a pointing task (Fig. 3). In section 3.2, paragraph 3, D&dH review different studies that claim that different representations of the body are used for the guidance of movements and for perceptual judgments. In this context, they interpret the results obtained by Paillard (1999) when studying patient G.L. as showing a dissociation between a normal "perceptual" representation (because she is able to recognize objects and point to a picture of her hand) and an impaired "sensorimotor" representation (because she has problems when pointing towards haptic stimuli). However, what we think the results show is that G.L. was simply poor at pointing without vision: she was equally good at pointing with vision towards her hand or towards a picture. Her problem was not with the action itself, but with the use of haptic information alone (without vision). This example shows a problem shared by all those models which try to establish strict functional separations between perception and action: When looking for experimental support for the dissociation, it is never clear whether a task is really a "perceptual task" or an "action task" (for an example, see Franz 2003), or whether the tasks chosen are really equivalent and comparable (for a discussion of this issue in the case of vision, see, e.g., Franz 2001; Franz et al. 2001). This is so because perception and action are closely intertwined in our interaction with the world, as our example of haptic length and weight perception shows.

In summary, we think that a comprehensive view on touch cannot be reduced to a twofold perception-action system with corresponding independent neural pathways. In particular, the dynamic properties of perception-action loops must be taken into account to provide a satisfactory explanation of the haptic system.

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A hemispheric asymmetry in somatosensory processing

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Abstract: The model presented in the target article includes feature processing and higher representations. I argue, based on neuropsychological evidence, that spatial representations are also involved in perceptual awareness of somatosensory events. Second, there is an asymmetry, with a right-hemisphere–based bilateral representation of the body. Third, the specific aspect of bodily awareness concerning motor function monitoring involves a network that includes the premotor cortex.

The somatosensory processes supporting perception and action discussed by Dijkerman & de Haan (D&dH) do not involve major hemispheric asymmetries, as illustrated by their Figure 1. These are briefly mentioned with reference to tactile object recognition and tactile agnosia. The role of spatial processing and of the right hemisphere, and the effects of unilateral spatial neglect after damage to the right posterior parietal cortex (PPC), are considered. D&dH's conclusion is that tactile agnosia may be caused by – and possibly through different underlying pathological mechanisms – both left- and right-sided brain damage.

A hemispheric asymmetry exists, however, at the much more basic level of pain sensation and proprioception. In a study of a large, unselected series of left- and right-brain-damaged patients, Sterzi et al. (1993) reported that these somatosensory deficits, as assessed by a clinical, standardized neurological exam, are more frequent after right-brain damage than after left-brain damage. This result contrasts with the time-honored view, which still informs clinical neurology (Ropper & Brown 2005), that there is no hemispheric asymmetry in the more "elementary," non-cognitive stages of sensation. The asymmetry is not confined to the somatosensory domain and extends to the visual and motor systems: Both visual half-field and motor deficits (hemianopia and hemiplegia), contralateral to the side of a hemispheric lesion, are more frequent after right-hemispheric damage (Sterzi et al. 1993).

One interpretation relates the higher incidence of left somatosensory deficits to disorders of spatial processing and, more specifically, to unilateral spatial neglect, which also are more frequent and severe after right-brain damage (Bisiach & Vallar 2000). In line with this view, in right-brain–damaged patients the detection of left single and simple somatosensory stimuli (touches) is definitely, though temporarily (for about 30 min), improved by the physiological maneuvers, such as caloric vestibular stimulation, that also ameliorate other aspects of the neglect syndrome, in both extra-personal and personal space (for reviews, see Rossetti & Rode 2002; Vallar et al. 1997). Although the empirical data are definite, the precise nature of the relationships between somatosensory awareness and spatial processing is open to interpretation.

I take the view that in the somatosensory, as well as in the visual domain, perceptual awareness of a sensory event – that necessarily occurs in space – involves not only the more peripheral stages of sensory analysis, but also its localization in the sector of extra-personal (as in the case of visual stimuli), or personal, bodily (as in the case of somatosensory stimuli) space where the event takes place. Accordingly, in patients with right-brain damage, visual and somatosensory (left-sided in retinotopical and somatotopical reference frames) deficits improve, when the stimuli are presented in the right, preserved, side of space, with regard to spatial egocentric coordinate frames (Kooistra & Heilman 1989; Smania & Aglioti 1995). A partially preserved spatial processing may give rise, in the tactile modality, to the phenomenon of "blind touch" (analogous to "blind sight"), whereby patients can localize by pointing – possibly by using more automatic and implicit sensorimotor loops – stimuli of which they are not explicitly perceptually aware (i.e., unable to detect and identify) (see also the review by Gallace & Spence 2007).

The hemispheric asymmetry of the neural underpinnings of these spatial reference frames, that support perceptual awareness in the somatosensory domain, is further elucidated by a recent study: Bottini et al. (2005) showed that right hemianesthesia in left-brain–damaged patients is also temporarily improved by caloric vestibular stimulation, provided, however, that the type (cold water) and the side (left ear) of stimulation are those which activate the right cerebral hemisphere, and have proved to be able to ameliorate left hemianesthesia in right-brain–damaged patients (Vallar et al. 1993). Interestingly, in two brain-damaged patients the brain regions activated by vestibular stimulation during the temporary recovery of contralesional somatosensory deficits included the insula (right-brain–damaged patient R.F.; Bottini et al. 1995), the right temporoparietal junction, the secondary somatosensory cortex (SII), and the supramarginal gyrus (left-brain–damaged patient L6; Bottini et al. 2005) (See Figure 1 here.)

The observation that a caloric vestibular stimulation (cold water in the left ear canal), activating mainly the right hemisphere, temporarily improves both left hemianesthesia in right-brain–damaged patients and right hemianesthesia in left-brain–damaged patients, suggests that a right-hemisphere–based neural network supports a representation of both sides of the body (Bisiach & Vallar 2000; Mesulam 2002). Specifically, there is some evidence that in the right hemisphere the somatosensory representation of the ipsilateral right side may be based on non-crossed afferent projections to SII (Bottini et al. 2005).

The hypothesis of a right-hemisphere–based network supporting a bilateral representation of the body is also consistent with the well-known hemispheric asymmetry of disorders involving delusional beliefs about the ownership of body parts (somatoparaphrenia) (Bisiach & Geminiani 1991), and of anosognosia for hemiplegia (Pia et al. 2004; Vallar & Ronchi 2006). As to the relevant brain regions, there is neuropsychological evidence in brain-damaged patients that associates lesions of the right insula with disownership of contralesional body parts (patient F.B. reported by Bottini et al. [2002] and patient 4 reported by Cereda et al. [2002]; see also the two patients reported by Moro et al. [2004]). These impairments may be listed under the rubric of *body image* disorders, separate from the mainly proprioceptive-motor, and largely unconscious, *body schema* (Vallar & Papagno 2003). Within bodily awareness, and the "body image," a distinction should be drawn, however, between the sense of ownership of body parts (the deficit being somatoparaphrenia) and the monitoring of motor function (the deficit being anosognosia for hemiplegia) (Vallar & Ronchi 2006). In the latter disorder, the main lesion correlate may be the right frontal premotor cortex (Berti et al. 2005), rather than the right insula (Karnath et al. 2005). The close association of these higher-order disorders of different aspects of the internal representation of the body (somatoparaphrenia and anosognosia) with unilateral spatial neglect may reflect the damage to common components of a network, specifically related to the integration in spatial reference frames of somatosensory and motor representations. Relevant components may include SII, the PPC, the insula, and, as regards the monitoring of the motor function of the body, the frontal premotor cortex. Damage to single components of this network may gives rise to selective, and spatially constrained, disorders of bodily awareness, ranging from the inability to report single somatosensory stimuli to the higher-order deficits of somatoparaphrenia and anosognosia for hemiplegia.

In sum, D&dH's flow chart (target article, Fig. 1) may be enriched by three additions: (1) What is termed "higher spatial representations," and is based on the activity of networks comprising the PPC and the insula, is involved not only in "tactile object recognition," but also in the more basic ability of detecting somatosensory stimuli, and, more generally, in perceptual and motor bodily awareness. (2) Bodily awareness, as far as the monitoring of motor function is concerned, involves the premotor cortex. (3) There is a hemispheric asymmetry, with the right side of the brain supporting a bilateral representation of the body.

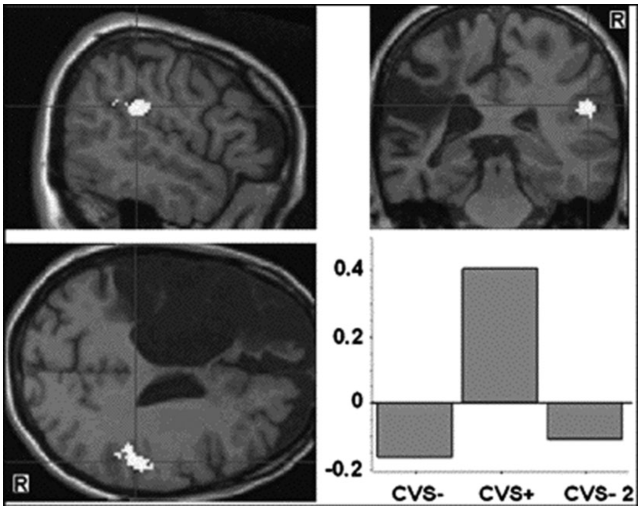

Figure 1 (Vallar). Physiological effect of left caloric vestibular stimulation (CVS) on touch in a left-brain–damaged patient (L6). The area of significant interaction of left CVS with right-sided touches in Patient L6 (left) is displayed on her magnetic resonance imaging (MRI) scan. The bar plot shows the average fMRI blood oxygenation level–dependent signal change (compared with rest in that brain region) before CVS (−), after CVS (+), and at a 30-minute delay (CVS-2). The values of signal change are mean-centered. Images are displayed with the anatomical right (R) on the right side. (Reprinted from Bottini et al. 2005, figure 2, with permission of *Neurology*.)

Authors' Response

Somatosensory processing subserving perception and action: Dissociations, interactions, and integration

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Abstract: The commentaries have raised important points regarding different aspects of our model. Some have queried the nature of the proposed dissociations, whereas others have requested and provided further details regarding aspects we had glossed over. Here we suggest that our approach to identify major processing streams based on the processing goal does not preclude interactions between them. We further specify details regarding body representations, haptic object recognition, and crossmodal processing, but are also aware that several features of the model require further filling in.

R1. Introduction

We were pleased to receive comments on a wide range of aspects of our proposed model. Some commentaries provided supportive evidence from areas we had not touched upon in our review (e.g., development of body representation, **Christie & Slaughter**), others had important comments on the nature of the proposed dissociations between functional and neural entities and possible interactions between them (e.g., **Brozzoli, Farnè, & Rossetti** [**Brozzoli et al.**]; **Drewing & Schneider**; **Holmes & Spence**), and some found fault with general idea of separate processing pathways for action and perception in the somatosensory system (e.g., **Graf**; **Marin & Lagarde**; **Travieso, Aivar, & Gomilla** [**Travieso et al.**]). Finally, several comments were related to detailed aspects of the model, which we had not filled in sufficiently (**de Vignemont**; **Hughes**; **Klatzky & Lederman**; **Tessari & Borghi**; **Vallar**). As a first response, we feel encouraged by the overall positive reactions to our ambition to summarize the existing literature into a comprehensive and testable model of somatosensory processing. We hope that it will serve as a platform for generating new research, and the comments we have received suggest that we have already succeeded to some degree.

. We have organized our detailed response in separate sections, each dealing with commentaries on specific parts of our target article. The following aspects are discussed: (1) the nature of the anatomical and functional dissociations and comparison with the visual system; (2) body representations; (3) haptic object recognition; and (4) crossmodal interactions (see Table R1).

Table 1. *An overview of the commentaries for each section of this response*

Topic	Commentaries
The nature of functional and anatomical dissociations and comparison with the visual system	Graf
	Travieso et al.
	Marin & Lagarde
	Drewing & Schneider
	Franz
	Goodale & Cant
	Garraghty
	Sathian et al.
	Mouras
	Brozzoli et al.
	Vallar
	Fiehler et al.
Body representations	Christie & Slaughter
	De Vignemont,
	Holmes & Spence,
	Maxwell et al.
	Tessari & Borghi
	Leishman & Melilo
Tactile object recognition	Binkofski et al.
	Hughes
	Klatsky & Lederman
Crossmodal interactions	Goodale & Cant
	Brozzoli et al.
	Sadato, et al.
	Sathian et al.
	Reed
	Streri & Sann

R2. The nature of functional and anatomical dissociations and comparison with the visual system

One of the starting points of our review was the analogy with the visual system in which two separate processing streams have been identified by Milner and Goodale (1995) for visuomotor control and object recognition. Several commentators question the strict distinction between processing for perception and action for the somatosensory, as well as for the visual system (**Graf**; **Marin & Lagarde**; **Travieso et al.**). All three commentaries cite evidence in favour of close interactions between perception-related and action-related processes, but from different angles. With respect to the commentaries of Marin & Lagarde and Travieso et al., part of the differences in opinion seems to be related to differences in definition of what perception constitutes. Both commentaries implicitly seem to equal *perception* to "processing of sensory signals." In contrast, within the context of the perception-action dichotomy, we use the term *perception* in a more strict sense. Here, "perception" is conceptualized as a goal for processing, in this case, recognition and conscious experience. This may cause confusion as visual sensory processes, such colour or texture extraction, are in this view *not* perception. These are the primitives that may be used to achieve perception.

Another confusion concerns the erroneous interpretation of our model that there is a strict division between the two pathways from different types of peripheral sensory input up to high-level processes (i.e., conscious perception or action). For instance, **Travieso et al.** suggest that proprioceptive input aids object recognition, and, on the other hand, cutaneous input is involved in motor control, which would contradict our model. However, we entirely agree with this idea and have never meant to suggest that tactile input is solely related to object recognition and proprioception to action. In section 2 of the target article, we state the following:

> Indeed, certain types of input may be more important for certain tasks, with proprioceptive input contributing more to action-related processes, and the skin receptors providing more information for perceptual purposes. However, this mapping of different somatosensory submodalities to output is by no means absolute. (sect. 2, para. 4)

As we suggested before, it is not the input characteristics rather than the purpose of sensory processing that determines the processing routes. Therefore, several examples provided by **Marin & Lagarde** and Travieso et al. do not, in our opinion, contradict our model (e.g., haptic involvement in object recognition [mentioned earlier here]; cutaneous involvement in motor control; phase synchronization).

A central issue is raised by **Graf**, who questions the validity of this distinction in vision. He suggests that – as we proposed for the somatosensory modality – that there are substantial interactions between the two visual pathways, as well. He discusses three lines of evidence, which are mainly concerned with the idea that the ventral object recognition stream uses visuospatial information and invokes parietal activation. First, perception and action operate conjunctively when eye movements actively explore a visual scene. Second, regions within the parietal cortex are recruited in certain recognition tasks, such as misoriented or distorted images of objects. Finally, Graf argues that the processing principles in the "what" and the "how" streams might be more comparable than Milner and Goodale have put forward. These comments are important as they concern our *conceptualisation* of two separate processing steams. **Drewing & Schneider** express similar concerns. They suggest that we have put forward a convincing case for a functional dissociation between "how" and "what" streams but have failed to disentangle the functional description from structure. They point to the act of manipulating external objects as the most poignant example of a situation that requires heavy interactions between structural areas. We are grateful to **Graf** and to Drewing & Schneider for raising this issue in such an eloquent manner as this provides us with an opportunity to clarify our position on this matter (which has been commented on by others, too, e.g., **Brozzoli et al.**; **Franz**; **Goodale & Cant**).

We envisage a cumulative approach in which it is useful to delineate the major processing steams first. The work of Milner and Goodale was exemplary here as they proposed one of the first models of vision that focussed on the objective, to which end information was being processed – that is, vision for action versus vision for recognition. The distinction between these pathways was further corroborated by the finding of parallel processing. Neuropsychological double dissociations (Milner & Goodale 1995), differential activations in imaging studies (Culham et al. 2003; James et al. 2003) and distinct differences in behavioural tasks (Pelisson et al. 1986) have all supported the idea that one stream can function independently of the other. However, these observations do not preclude the possibility of cross-talk between the processing streams. It was always likely that this was the case in vision, given the anatomical connections between the ventral route and the dorsal route, and it is logically necessary in somatosensory processing. Milner and Goodale (1995) already stated that the two streams are not "hermetically sealed" (see also **Goodale & Cant**). In sum, we agree with **Graf** that there is evidence for cross-talk in the visual system, but in our view this strengthens the idea of separate pathways. This probably applies to vision, audition, and somatosensory processing. In order to prevent circularity of arguments and to allow the model to be falsifiable, clear, a priori descriptions are required of the type of tasks in which interactions between the pathways occur, and the putative neural mechanisms. These descriptions should allow testable hypotheses to be developed.

The suggestion by **Drewing & Schneider** that it is "attention" that forms the "glue" between the two systems is interesting and requires further study. It appears to us, however, that a substantial amount of processing that depends on both pathways does not require conscious attention. The issue of attention is also discussed by **Franz**. She suggests that it is the *allocation* of attention that determines which pathway is engaged. Again, we have no problem with this suggestion, although we would like to see a more tangible definition of attention and especially of the concept of allocation. There is a risk here of reverting back to the idea of a homunculus in charge of an army of talents. Franz's suggestion that attention might to some extent "define the functions of different systems . . . attention itself might be a guiding principle" (para. 6) is beyond the scope of our model. Our proposal is less ambitious and merely tries to define the function of somatosensory subcomponents in terms of goal-specific processing.

Another issue that is brought up in several commentaries concerns the nature of the processing characteristics within the two visual streams. In particular, it has been suggested that other distinctions or dichotomies (than perceptual and action) may be more appropriate to describe the ventral and dorsal stream functions (**Brozzoli et al.**). As previously described by Milner and Goodale (1995), and summarized in our target article, a distinction based on what the sensory input is used for, does have consequences for the processing characteristics in each stream. That is, accurate performance of a goal-directed grasping movement may require different visual parameters than, for example, successful recognition of an object. As a consequence, the characteristics of visual processing in the dorsal stream (real-time egocentric) differ in a number of aspects from ventral stream processing (viewpoint-independent and storage over a longer period). Milner and Goodale further suggest, as we mentioned, that ventral stream processing may be required for several aspects of visuomotor action, for example, when a delay is introduced between the stimulus display and the motor action (see also Goodale et al. 1994; Milner et al. 2003). This is also true during the visual control of grip force (as **Goodale & Cant** describe in their commentary) or, indeed, when the motor response depends on an allocentric spatial representation. The recent observation of a dissociation between ego and allocentric task performance of patient D.F. (Schenk 2006), therefore, does not seem inconsistent with the original proposal put forward by Milner and Goodale and indeed has been reported previously (Carey et al. 2006; Dijkerman et al. 1998; Murphy et al. 1998). We suggest that action-related processing and perception-related processing in the somatosensory system differ with respect to a number of characteristics. For example, several authors have suggested that the somatosensory characteristics contributing to different body representations differ, with the action-related body schema representation being mainly fed by bottom-up signals from the entire body and being less enduring than the perceptual body image that can also be prone to local inconsistencies (Tsakiris et al. 2006) (see also section R3 on "Body representations").

Brozzoli et al. wondered whether action is less susceptible to somatosensory illusions. There now is evidence from at least four different somatosensory illusions that suggest task-dependent differences of these illusions. The effects of a haptic size contrast illusion on grasping and perceptual size matching responses were described by Westwood and Goodale (2003). Differential effects of the vibrotactile illusion have been reported by Marcel (2003) and Kammers et al. (2006), and the rubber-hand illusion is discussed in section R3. In addition, we have recently obtained opposite patterns for size matching and grasping responses involving Weber's illusion (Anema et al., submitted b). We are therefore confident that differential effects of somatosensory illusions on perception-related and action-related responses do exist, although we do not claim that motor responses are always more veridical. Whether they are also present for the after-effect described by Brozzoli et al. remains to be tested.

The discussion by **Garraghty** regarding the physiological data on somatosensory processing across species is crucial. The suggestion that cats and primates may have a different architecture is important to the degree that we should not over-generalise data from other species (see also **Sathian, Lacey, Gibson, & Stilla** [**Sathian et al.**]). More important are the suggestions concerning the role of the different modality-specific processing areas. Garraghty and others will have noticed that we have omitted the use of the term *primary somatosensory area* (SI) in our target article, because we were aware of the ongoing debate about the specific role of these primary somatosensory areas. More research is needed to define the precise distribution of labour here. Furthermore, Sathian et al. comment on differences in cortical areas involved in processing of different somatosensory submodalities, with the anterior parietal cortex (APC) being associated with kinaesthesis and tactile input and the parietal opercular-insula region being involved in thermo-nociceptive processing. We are, of course, aware of input from touch thermal and pain receptors to the insula, bypassing the APC (Craig 2002; Olausson et al. 2002). Indeed, the work of Craig described in our article has been particularly relevant, and this input may be especially important for the affective aspects of body representations as mentioned in section 3.2. The data presented by **Mouras** in his commentary are also consistent with the idea of involvement of the posterior insula in sensory processing for affective body representations. However, the context in which he defines goal-directed behaviour is somewhat different from ours.

The neural basis of somatosensory processes is also discussed by **Vallar**. His insightful commentary provides several important additions and specifications to our proposed model. He is correct when he observes that we have not always been very specific about laterality differences regarding somatosensory processing. His suggestion that higher spatial representations related to the right hemisphere not only play a role in tactile object recognition and higher-order perceptual body representations, but also in the more basic ability to detect somatosensory stimuli, is convincing. Indeed, in addition to temporary improvement of tactile detection after left caloric stimulation, we have also observed a long-term improvement in tactile pressure sensitivity and proprioceptive finger-position sense after adaptation to rightward-displacing prisms in a patient with a right hemisphere lesion (Dijkerman et al. 2004). A second suggestion made by Vallar concerns the role of the premotor cortex. Our model has mainly been concerned with posterior cortical areas, but we agree that the premotor cortex is also important for bodily awareness and ownership. Evidence for this comes from patient studies (e.g., see Arzy et al. 2006a) and functional imaging studies using the rubber-hand illusion (Ehrsson et al. 2004; 2005a).

A further comment regarding the neural basis of somatosensory processes was made by **Fiehler, Engel, & Rösler** (**Fiehler et al.**). The neural areas involved in memory for haptically explored objects (secondary somatosensory cortex [SII], insula, and posterior parietal cortex [PPC]) and haptically encoded spatial positions (SII and PPC) are similar to the areas we proposed to be involved in haptic object recognition and spatiotemporal integration. The idea of storage of somatosensory representations for actions is in our opinion more controversial. Fiehler et al. cite evidence from a hand-movement recognition task, showing activation of APC, SII, and PPC. Although not described in detail, the hand-movement sequences made in this task were probably not goal directed and may involve different somatosensory processes, compared with goal-directed grasping movements (this distinction is similar to that made between optic ataxia and apraxia in the visual modality). Again, the maintenance of hand-movement sequences which increase in length may require greater temporal-spatial integration, resulting in activation of the PPC. In contrast, the numbsense patient studied by Rossetti et al. (2001) reverted to chance-level performance when reaching movements were made after a delay of only a few seconds. This finding suggests little, if any, memory capacity when somatosensory target input is processed for guidance of a goal-directed action.

R3. Body representations

The commentaries raised several important points regarding the functional characteristics of different body representations. Interesting supportive evidence for different body representations for perceptual and action-related responses comes from developmental studies. **Christie & Slaughter** suggest different developmental trajectories for sensorimotor representations (present before birth) and recognition of one's own body (present at 5 months of age). This is followed by manual exploration of objects at about 6 months of age, while higher-level visuospatial and higher-level body representations appear even later. These findings are consistent with the idea of multiple body representations, although they by no means rule out a certain interdependence between the development of the different representations.

The commentaries by **Holmes & Spence** and by **Maxwell, Masters, & van der Kamp** (**Maxwell et al.**) both relate to possible interactions between action-related and perception-related representations. Holmes & Spence describe the effect of the rubber-hand illusion on different measures of limb displacement. They suggest that the visual capture effect and the feeling of ownership result in a larger displacement as compared to proprioceptive drift (as measured by pointing movements). This is consistent with a differential effect of the illusion on action-related responses as compared to perceived position and body ownership. Recent work from our lab also confirms that the rubber-hand illusion has a stronger effect on perceived position of the hand as compared to motor localisation responses (Kammers et al., submitted). Holmes & Spence, however, argue that a link is required between the body image and the body schema representations, as the illusion is significantly stronger when the rubber hand is placed in an anatomically compatible position. This suggests that input from a *postural schema* is used during the rubber-hand illusion. In our view, this finding is also compatible with the idea that structural knowledge about the body is important for inducing the arm displacement in the rubber-hand illusion. Structural knowledge about the body would be related more to perceptual body representations as compared with sensorimotor representations (see also, Buxbaum & Coslett 2001; Schwoebel & Coslett 2005). Note that this does not mean that we consider the body image and body schema as entirely separate representations without any scope for one to influence the other. There are probably many instances in which perceptual representations influence sensorimotor representations (see sect. R2). Here of course the danger of a non-falsifiable model resurfaces, and one of the current challenges is to define the specific conditions and circumstances in which such interactions occur.

Maxwell et al. suggest that the body image may not always be unconscious. They describe several instances in which performers are aware of how their body moves during their actions, and they describe how this usually has a detrimental effect on the performance of the movements. Although it feels intuitively plausible to consider that the input one is aware of is the same that is used to guide one's actions, this may not necessarily be the case. Studies with somatosensory illusions, such as the vibrotactile illusion (Marcel 2003; Kammers et al. 2006), but also the rubber-hand illusion (as discussed earlier), suggest that the position of where one consciously perceives one's arm to be is not necessarily the position one's motor system "considers" the arm to be at. Rather, the effects described by Maxwell et al. suggest that the perceptual body image may be able to influence the motor system, but is less proficient in doing so.

Holmes & Spence's comments regarding the effect of a postural schema on the rubber-hand illusion also relate to the precise definition of the different body representations. Uniformity in definitions unfortunately is rather lacking, as **de Vignemont** and **Christie & Slaughter** point out. We have tried to be clear in our definition by linking it to some of the most well-known descriptions of body image and body schema made by Paillard (1999) and Gallagher (2005). But a detailed description is wanting. De Vignemont and Christie & Slaughter are, therefore, right to suggest that further specification and more precise definitions are an important next step. De Vignemont provides some useful suggestions about which criteria to use and which pitfalls to avoid, and she also suggests that a distinction between action-oriented and recognition-oriented body representations may not be such a clear criterion as we assume.

Of course, these are very broad categories which can easily be further subdivided, and we agree that this may be necessary. Nevertheless, we suggest that a basic organisation principle of sensory systems, including the somatosensory system, is that processing depends on task requirements; and considering that these are different for action-related and perception-related responses, we assume different processing characteristics. Indeed, body representations may be dynamic in nature, in that they draw upon different input sources (visual, proprioceptive, tactile, semantic, and structural knowledge) to different extents, depending on task requirements. The basic difference between body representations may be their access to certain input sources. For example, the action-related body representations may not be influenced by semantic and other cognitive knowledge about the body, whereas the body image is. **Tessari & Borghi** also comment on the definitions of different body representations and suggest we did not relate the body image to semantics in our model. Indeed, we have not been very explicit, in either the target article text or in its Figure 1, about the link between body image and semantics, although we do mention this in the text. As described earlier in this response, we do consider this link to be important and a characteristic that distinguishes body image from body schema. Other aspects that are mentioned by Tessari & Borghi and by **Brozzoli et al.** are the dynamic nature of the body schema (in that it can be modified during tool use) and perspective taking. We agree that the dynamic nature of the body schema is an important characteristic and one that may be less applicable to the body image (Gallagher 2005).

Regarding perspective taking, this has been an issue mainly with respect to *visual* representations of body parts. As somatosensory input is inherently egocentric, this topic has received considerably less attention (but see Newell et al. [2001] for the role of perspective taking for haptic object recognition). Nevertheless, it would be of interest to assess whether haptic input can lead to representations from a third person's perspective, and we are currently planning such experiments. With respect to imitation, an accurate representation of one's own body no doubt plays an important role as suggested by **Tessari & Borghi**; however, this is not only fed by somatosensory input, but also by visual input. Indeed, the studies mentioned by Tessari & Borghi – Buxbaum et al. (2000), Chaminade et al. (2005), Goldenberg (1996) – mainly deal with visual imitation and do not specifically assess the role of somatosensory input pertaining to the body. We would hypothesize that if the somatosensory body schema, as defined in our target article, is impaired, this may affect visual imitation. However, to our knowledge this has so far not been tested.

One interesting aspect touched upon by **Leishman & Meillo** is the difference between global and local processing. They suggest that, for visual input, global processing is generally related to dorsal stream processing, whereas local processing is related to the ventral stream. A similar suggestion has been put forward with respect to body representations. Gallagher (2005) suggested that the body schema functions in a holistic and more integrated way, in contrast to the body image, which may involve partial or local representations of the body (and therefore also be more susceptible to inconsistencies such as those evoked by the rubber-hand and vibrotactile illusions). We, therefore, view this as another example of similarities in functional organisational principles between different modalities.

R4. Haptic object recognition

Across the commentaries, comments regarding the tactile object recognition emphasize the interaction between somatosensory processing for perception and for action (**Binkofski, Reetz, & Blangero** [**Binkofski et al.**]; **Graf**; **Marin & Lagarde**; **Reed**; **Travieso et al.**). As several commentaries deal with visual, as well somatosensory, processing, they are discussed in different sections. Binkofski et al. focus their commentary on the role of area intraparietal sulcus (AIP) in object recognition. They suggest that this area appears to be involved in haptic object recognition, as well as exploratory finger movements. They proposed that AIP may be a crucial interface between perceptual and action-related processes. This is entirely consistent with our ideas and indeed has been mentioned in section 3.1 of the target article.

Klatzky & Lederman suggest that *haptic* rather than tactile object recognition is a more accurate description, because recognition of objects does not only involve tactile but also proprioceptive input. This is, of course, correct, and we do agree that haptic may be a more accurate description. However, especially in the neuropsychological and functional imaging literature, the term *tactile object recognition* is commonly used, which is why we adopted it. More importantly, Klatzky & Lederman further specified different stages during object recognition, based on their model (Lederman & Klatzky 1990). We agree that haptic object recognition does not necessarily always involve extensive exploratory finger movements and that Stage 1 (grasping, and where appropriate, lifting) may be sufficient. Again, considering the wide scope of the target article, we were unable to discuss different strategies to achieve object recognition in detail, and we are grateful to these authors for stressing this point in their commentary. Klatzky & Lederman's proposal of variations in the involvement of the APC-PPC and APC-SII-insula routes, depending on the extent and purpose of exploration, is interesting and warrants further investigation. We would like to add that different components of the APC-PPC route may be involved in the movements made during Stage 1 (grasping and lifting) and Stage 2 (extensive exploration). For example, neurons in area 5 in monkeys have been related to grasping (Stage 1) (Debowy et al. 2001; Gardner et al. 1999; Ro et al. 2000), whereas AIP is involved in exploratory finger movements, as mentioned by **Binkofski et al.**, and in grasping (Culham et al. 2003). Whether right hemisphere dominance for haptic object recognition may also be particularly related to Stage 2, or is involved in other aspects of somatosensory processing as suggested by **Vallar**, remains to be tested.

Klatzky & Lederman and **Hughes** further mention the difference between distal and proximal levels. The main point raised by Hughes relates to the mechanism that produces a transition of proximal stimulation of the skin to an object representation through distal attribution. He describes the example from Gibson (1962) which illustrates how, when holding a pencil, contact with five-finger pads can result in the percept of one object. Hughes wonders how the question of distal attribution can be answered by the data used for developing our model. We have glossed over this important issue, and we are grateful to Hughes for raising it. Although the mechanisms through which distal attribution is achieved are far from clear, we hypothesize that the APC-SII-insula route would be particularly important. This would involve a combination of increasingly complex feature processing within this route, crossmodal interactions, and top-down influences from higher-order perceptual and semantic systems situated within the infero-temporal cortex. Interestingly, the examples provided by Gibson (1962) and Benedetti (1985; 1986) suggest that the spatial configuration of the hand influences perceptual processing of external stimuli. Recent experiments on finger agnosia in a patient with Gerstmann's syndrome also support this point. This patient was impaired when asked to state verbally, or point to a line drawing of a hand, which finger had been touched (Anema et al. 2006). Nevertheless, she performed normally when asked to point directly to the touched location, suggesting a perceptual "finger image" impairment with intact "finger schema" (cf. Paillard 1999). She additionally showed an impairment in perceptual integration of tactile stimuli in external space across fingers, suggesting that internal perceptual body representations can influence perception of external tactile stimuli (Anema et al., submitted a) This suggests that representations of the body influence representations of external stimuli, similar to interactions between perceptual and sensorimotor processes. An important challenge for future research is to establish when and how these interactions occur.

R5. Crossmodal interactions

There is now abundant evidence for a close collaboration between the sensory modalities. This means that any model concerned with sensory processing should take these interactions into account. In our target article, we have addressed a number of issues in this realm, but we have not covered all possible crossmodal phenomena. One such omission is commented on by **Goodale & Cant**, who remind us that calculating the grip force and load force during reaching movements requires adequate knowledge about the material properties. More importantly, they emphasize the close collaboration that is required between the visual and somatosensory systems for the act of manipulating external objects. Vision guides us towards objects, whereas somatosensory feedback informs us in detail about the weight and size. This information is used to fine-tune the forces applied to the object. Functional imaging studies have discerned dedicated areas within the ventral system that encode objects' surface characteristics, such as texture, that help to define the material properties. We completely agree with the suggestion that this information, in addition to stored knowledge about objects, is used in modulating reaching movements. In fact, it is reminiscent of our proposals regarding the interactions between the two somatosensory streams. **Streri & Sann**'s commentary concerning the developmental trajectories of visuo-tactile interactions also supports the idea of a separate crossmodal system for sensory processing for perception and action because the influence of vision differs. In addition, a further distinction can be made between macro- and micro-geometric properties with respect to perceptual crossmodal interaction. Perhaps this may also be the case when contrasting the development of the relation between grip force and size and texture cues in the action system.

Brozzoli et al. also point to recent data that question a strict division between the two pathways in vision. By implication, it is suggested that such a division cannot be absolute in somatosensory processing either. Again, we want to stress that we feel that the interactions between the different pathways that we identified are a central feature of the model, and, second, that the model is postulated in order to refine the descriptions of these interactions. In addition, Brozzoli et al. point to an important aspect of visual-tactile interaction, which is, that perceived (visually or somatosensory) variations of limb positions in *peri-personal* space modulate localisation performance in the other modality. We agree that the model should incorporate a multisensory peri-personal space representation to deal with these findings.

The interaction between the visual modality and the somatosensory modality for object recognition in peri-personal space is critically reviewed by **Reed**, who argues that close scrutiny of the intermodal connections suggests that the visual "what" system connects to the somatosensory "where" system, and vice versa. Although the evidence presented is in our view preliminary, we concur that this is an interesting idea that deserves further exploration, and we agree that this kind of detailed filling in of the model is required.

In their commentary, **Sathian et al.** point to the complex structure of the somatosensory cortex, and, in general terms, we agree with their observation that important details are missing in the model we have proposed. It was intended to be, as they phrase it, a working hypothesis. In addition, they point to the observation that particular cerebral cortical regions are activated in functional imaging studies in a "task-specific, modality-independent" manner, suggesting that crossmodal processing is a general rule in perception (Sathian 2005). Regions known to be specialized for processing particular aspects of vision are often also recruited during performance of corresponding tactile tasks. In our review, we focussed on the question of whether there is specificity in the crossmodal interactions with somatosensory processing. More specifically, do processes in other modalities influence somatosensory processing for action differently, compared with perceptual recognition? The additional data reported by Sathian et al. suggesting that regions that are specialized for processing particular aspects of vision may also be recruited during performance of corresponding tactile tasks, do not contradict our proposal.

Sadato, Nakashita, & Saito (**Sadato et al.**) provide further evidence from functional imaging for specificity in visual-tactile interactions. Their studies suggest that the PPC is involved in the comparison of shapes presented in the two modalities. Perhaps more relevant, their data support our notion that the lateral occipital complex is important for object recognition whether the object is presented visually or through touch. Interestingly, their results suggest substantial plasticity in crossmodal effects in the lateral occipital complex, as subjects with a large amount of visual and tactile experience with the objects showed significantly more activation.

R6. Epilogue

The target article on somatosensory processing was intended to bring together different strands of research in order to postulate a model that would enable the formulation of testable hypotheses. We feel that we have touched upon an emerging area within the cognitive neurosciences. This exercise was instructive for more than one reason: Among others, it showed us that there is so much work going on in different scientific realms that do not communicate on a regular basis. There is already gratification in the idea that we might have promoted further interdisciplinary discourse.

The replies have been very instructive and have brought a number of central issues to the fore. First, the *perception-action* dichotomy, whether in vision, audition, or haptics, appears to be – at the same time – both a viable organisational principle of the functional neuroarchitecture and a simplification that impedes a true understanding of the brain. It depends who you talk to. We are convinced that the idea of the *purpose* of processing as an important guiding principle when describing the organisational structure of cortical somatosensory processing (which has led to the formulation of the perception-action dichotomy) remains valid. Second, despite the similarities between modalities, somatosensory processing has unique properties. The intricate relationship between perception and action, as exemplified by the exploratory movements of the fingers and the hand during tactile recognition, is, perhaps more than in any other sensory systems, a defining feature of haptic processing. Third, the monomodular exploration of individual sensory systems is a methodological shortcut, but we are acutely aware that these systems are intertwined. For a more complete understanding, future research will need to expand in order to incorporate these crossmodal interactions. Fourth, the commentaries have raised several important points regarding the functional characteristics of different body representations. In this context, we sense a great allegiance to the late Jacques Paillard, who first suggested many of the ideas we incorporated in our model. His distinction between *body schema* and *body image* remains a guiding principle. But of course more work is needed.

The exploration of the processes and brain structures involved in somatosensory processing is now gaining momentum, but it will require more and more multidisciplinary investigation. Only from this synergy will evolve a better understanding, or, as Seneca would have put it: "One hand washes the other."

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[Letters "a" and "r" appearing before authors' initials refer to target article and response references, respectively.]

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