From maps to form to space: Touch and the body schema

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ABSTRACT

Evidence from patients has shown that primary somatosensory representations are plastic, dynamically changing in response to central or peripheral alterations, as well as experience. Furthermore, recent research has also demonstrated that altering body posture results in changes in the perceived sensation and localization of tactile stimuli. Using evidence from behavioral studies with brain-damaged and healthy subjects, as well as functional imaging, we propose that the traditional concept of the body schema should be divided into three components. First are *primary somatosensory representations*, which are representations of the skin surface that are typically somatotopically organized, and have been shown to change dynamically due to peripheral (usage, amputation, deafferentation) or central (lesion) modifications. Second, we argue for a mapping from a primary somatosensory representation to a secondary representation of body size and shape (*body form representation*). Finally, we review evidence for a third set of representations that encodes limb position and is used to represent the location of tactile stimuli relative to the subject using external, non-somatotopic reference frames (*postural representations*).

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1. From maps to skin to space—touch and body representations

Information regarding body position in space comes from tactile, proprioceptive, visual, vestibular, auditory and enteroceptive sources. These inputs are integrated to generate representations of the body that are crucial for perception and action. Head and Holmes (1911) introduced the concept of multiple integrated body representations, dividing them into three categories—a *postural schema* that represents the position of the body in space before and after movement, a *superficial schema* used to localize the position of sensation on the body surface (both which form an unconscious *body schema*), and a conscious representation known as the *body image*. Later characterizations of body representations focused primarily on the conscious/unconscious distinction in the *body schema* and *body image* (see Gallagher, 1986, 2005; Paillard, 1999). However, this conscious/unconscious dichotomy is likely to be overly simplistic in characterizing body representations (for a discussion, see de Vignemont, this issue; Gallese & Sinigaglia, this issue). We propose to use evidence from studies of tactile perception to provide a theoretical framework for understanding body rep-

resentations. We argue that representations of the body used in sensory and motor processing (i.e. the body schema as described in Schwoebel & Coslett, 2005) can be divided into three distinct representations used to localize tactile stimuli and interact with the environment.[2]

Advances in neuroscience have provided evidence for the existence of dynamic primary somatosensory representations of the skin surface. These single-cell recording studies in mammals have provided evidence regarding the nature of these representations with respect to the input, that is, the relationship between tactile stimulation and activity in primary somatosensory cortex (SI). However, many of these studies were not designed to address the relationship between primary somatosensory representations and the eventual output—the perception of sensation. Evidence from humans suggests that there is not a perfect one-to-one mapping from input to cortical maps to perceived sensation. Therefore, based on evidence from humans, we propose that a second *body form representation* is necessary. In this representation, information from

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[2] Note that our previous definitions of *body schema* and *body image* have been somewhat different from other characterizations. For example, we have previously defined *body image* as a lexical and semantic representation of information regarding body part names, functions, and associations. We consider *body image* to be dissociable from *body schema*, as demonstrated observing patient performance (see Schwoebel & Coslett, 2005). We also note that our usage of the terms *body schema* and *body image* are not standard; terminologic inconsistencies and confusion has been an enduring problem for the study of body representations.

primary somatosensory representations is mapped to a representation of body form that allows for localization of tactile sensation on the skin surface. We will discuss how deficits due to central and peripheral changes provide evidence regarding the nature of these representations. Furthermore, in representing the location of tactile stimuli, it is not only necessary to characterize location relative to points on the skin surface, but also relative to external space. Therefore, we propose a third set of *postural representations* that are used to localize the body in external space in multiple, egocentric frames of reference. We review the evidence for these distinct, dissociable but highly interactive representations below.

2. From maps to form—primary somatosensory and body form representations

The original mapping studies by Penfield and colleagues (Penfield & Boldrey, 1937; Penfield & Rasmussen, 1950) recording responses after electrical stimulation of primary somatosensory cortex offered two major insights. First, this research demonstrated that representations of the skin surface have a generally somatotopic organization, such that, for example, the hand representation is next to the arm representation. Second, they found that cortical representations of body parts are larger for those that have higher sensitivity and/or are used more often. In keeping with the then prevailing view that brain organization was fixed after childhood, Penfield and colleagues did not explore the manner in which they were altered by time and experience.

In the last 25 years there has been a dramatic increase in interest regarding the manner in which representations of the form and shape of the body are generated and the factors that alter these representations. In single-cell recording studies in mammals, dynamic changes in primary somatosensory cortex have been observed after various alterations. Differential usage of specific skin surfaces (Jenkins, Merzenich, Ochs, Allard, & Guic-Robles, 1990; Recanzone, Merzenich, & Jenkins, 1992) leads to an expansion of the somatosensory representations of the differentially stimulated areas. After tactile impoverishment, somatosensory maps deteriorate (Coq & Xerri, 1999b), while amputation (Rasmusson & Turnbull, 1983) and deafferentation (Merzenich et al., 1983) lead to an expansion of representations of neighboring areas into cortex previously represented by the amputated/deafferented body part. Surgical syndactyly (Clark, Allard, Jenkins, & Merzenich, 1988) in animals results in a blurring of previous boundaries between finger representations in SI. Finally, lesions of the representation of a specific body region in somatosensory cortex result in the reemergence of previously destroyed cortical representations (Jenkins & Merzenich, 1987).

There is abundant evidence for a primary somatosensory representation that may be altered by experience as well as changes in the nervous system. However, multiple lines of evidence argue for additional, higher order representations of the body. One important finding was provided by Taylor-Clarke, Jacobsen, and Haggard (2004). These investigators exploited the fundamental demonstration by Weber (1834/1996) that regions of the skin surface have different levels of tactile acuity, and that the ratio of the size of the body part and the size of the cortical representation reflects these distinctions. The fingertip, for example, has a much larger ratio of cortical representation to skin surface than does the lower back. Taylor-Clarke et al. (2004) presented two tactile stimuli that were identical distances apart to blindfolded subjects at various locations on the skin surface. They found that when comparing localization on regions that had larger cortical representation to skin surface ratios (e.g. the index finger) to localization on areas with lower ratios (e.g. forearm, back), subjects consistently reported that the two stimuli presented to the higher ratio areas were farther apart. When presenting the same task to different skin surfaces with similar cortical representation to skin surface ratios (e.g. index finger vs. face, left forearm vs. right forearm); they found no response bias on these distance judgments. The authors reasoned that, to preserve size constancy, information from primary somatosensory representations must be rescaled to be used by a second representation which contains information on the perceived size and shape of body parts. Furthermore, overestimation biases in distance judgments on higher ratio areas are likely due to systematic errors in the process of scaling from distorted, primary somatosensory representations to this secondary body representation. We will refer to a secondary representation of size and shape of the skin surface, used to map information from primary somatosensory representations, as a *body form representation*.

Advances in neuroimaging have made it possible to examine whether changes in primary somatosensory representations after central and peripheral alterations in humans reflect changes observed in single-cell recording studies with non-human mammals. Importantly, studies of the *sensory consequences* of such changes in humans can inform us regarding the relationships between different body representations. For example, evidence for distinctions between primary somatosensory and body form representations come from the study of the sensory consequences of central (e.g. lesion) and peripheral (e.g. amputation, deafferentation, stimulation) somatosensory alterations. In this section, we will review evidence regarding the behavioral correlates of these changes in order to characterize the relationship between primary somatosensory and body form representations.

2.1. Differential usage

Studies in animals have found that after increased stimulation of an area of skin surface, the cortical representations of the stimulated regions increased substantially (Coq & Xerri, 1998; Jenkins et al., 1990). Expansion of cortical representations has also been observed in studies with humans. Using magnetoencephalography (MEG), Elbert, Pantev, Wienbruch, Rockstroh, and Taub (1995) observed that the SI representations of violinists' digits were significantly larger than those of non-violinist controls, presumably due to increased finger stimulation for violinists. Similar changes have also been reported in sighted Braille readers (Rockstroh et al., 1996). After training normal subjects Braille reading using the second through fourth digits on the left hand, they found a medial shift in the representation of the pinky finger (D5) in SI, away from the representation of the thumb; whereas no such changes were observed in the untrained hand. The authors proposed that this shift in the D5 representation was due to an expansion of the digit 2–4 representations.

The sensory consequences of these use-dependent changes are improved tactile acuity and detection ability. For example, piano players have greater tactile acuity on the fingers (as measured via a two-point discrimination task) compared to non-musician controls, and within piano players there is a direct correlation between hours of piano practice and tactile acuity (Ragert, Schmidt, Altenmuller, & Dinse, 2004). Use-dependent changes have also been studied over shorter periods of stimulation using tactile coactivation paradigms, in which subjects are simultaneously stimulated at two separate locations on the skin surface. Pleger et al. (2001) presented human subjects with a tactile coactivation task for three hours, and found decreased tactile discrimination thresholds on a two-point discrimination task. Using MEG comparing pre- and post-coactivation performance, they also found a lateral dipole shift for the coactivated right index finger compared to the control left index finger. This shift represents an expansion of the index finger representation, consistent with results in non-human single-cell recording studies. Furthermore, the size of the dipole shift was predictive of performance on the two-point discrimina-

tion task, such that larger shifts corresponded to increased tactile acuity (see also Godde, Ehrhardt, & Braun, 2003; Godde, Spengler, & Dinse, 1996; Godde, Stauffenberg, Spengler, & Dinse, 2000). A similar expansion using fMRI was reported in both primary and secondary somatosensory representations of the right index finger and increased spatial acuity in a grating orientation task (Hodzic, Veit, Karim, Erb, & Godde, 2004).

These results demonstrate that differential usage of the skin surface results both in an increase in the size of primary somatosensory representations, and improved tactile acuity. However, a second topic of interest is the sensory consequences of these increases in the size of primary sensory representations after use-dependent changes. When the representation of a region of skin surface expands into a new cortical area that previously represented a different location on the body, what are the effects on tactile perception? Although the long-term effects of use-dependent changes on tactile acuity in musicians have been examined (Ragert et al., 2004), to our knowledge there are no studies of musicians that explore the long-term effects of finger usage on tactile localization. We cautiously assume that, as there are not reports of pianists or violinists frequently mislocalizing tactile stimuli, the mapping from primary somatosensory cortex to a body form representation adjusts over time such that subjects consistently report veridical sensations.

However, subjects who have experienced synchronous stimulation of different fingers in a tactile coactivation task have demonstrated tactile mislocalizations. Pilz, Veit, Braun, and Godde (2004) coactivated the middle three digits of one hand (D2–D4) either synchronously or asynchronously for three hours. Synchronous activation resulted in increased finger mislocalizations along with closer representations of each digit in SI, whereas asynchronous activation resulted in fewer mislocalizations and finger representations that were shifted apart (see also Kalisch, Tegenthoff, & Dinse, 2007; Schweizer, Braun, Fromm, Wilms, & Birbaumer, 2001). Furthermore, blind Braille readers who coactivate multiple fingers in reading also demonstrate a similar pattern of performance. Sterr et al. (1998a,b) used magnetic source imaging to characterize the nature of digit representations in primary somatosensory cortex in sighted controls, blind one-finger, and blind three-finger Braille readers. They found that three-finger Braille readers had larger and topographically disordered finger representations when compared to one-finger Braille readers and sighted controls. Furthermore, they found that three-finger Braille readers were significantly more likely to mislocalize tactile stimuli compared to the other two groups. In fact, there was a significant correlation between finger mislocalization and topographic disorder in primary somatosensory cortex. In a later study, they found that error rates over all fingers were lowest for those used in Braille reading, and that errors on non-reading fingers tended to be localized onto Braille reading fingers (Sterr, Green, & Elbert, 2003).

However, tactile mislocalizations after use-dependent changes have only been examined when skin surfaces on *separate* body parts were synchronously stimulated. Associative pairing from synchronous stimulation of multiple fingers leads to the emergence of neurons with receptive fields that encompass multiple fingers (Godde et al., 1996). For example, subjects with syndactyly have more neurons with receptive fields that encompass multiple fingers compared to controls, due to the increase in paired stimulation of skin surfaces on different digit pads (Allard, Clark, Jenkins, & Merzenich, 1991; Mogilner et al., 1993). To our knowledge, there are no studies that have examined tactile mislocalization after coactivation of multiple points on a single digit, which would presumably result in the expansion of only that digit's cortical representation without an increase in the number of multi-finger receptive fields. In such an experiment, it would be possible to examine whether short-term, use-dependent changes in primary

somatosensory representations that result in mislocalization are due to mismappings with body form representations.

2.2. Lesion

Studies of cortical lesions in mammals have also provided evidence regarding the dynamic properties of primary somatosensory representations. Jenkins and Merzenich (1987) selectively lesioned the entire cortical representation of the third digit in owl monkeys, and found a reemergence of the third digit representation in areas that were previously active for stimulation of the second or fourth digit. This and other related studies provide evidence that even after complete elimination of a cortical representation of a skin area, a new representation of that surface can develop in the cortex (see also Brown, Aminoltejari, Erb, Winship, & Murphy, 2009; Coq & Xerri, 1999a; Jain, Qi, Collins, & Kaas, 2008; Xerri, Merzenich, Peterson, & Jenkins, 1998).

Although a variety of studies have examined changes in the characteristics of somatosensory evoked potentials subsequent to stroke in humans (Rossini & Dal Forno, 2004; Tsumoto, Hirose, & Nonaka, 1973; Wikstrom et al., 1999), as well as topographic changes in primary motor cortex after stroke (e.g. Cramer & Crafton, 2006), relatively few studies have examined changes in the topographic organization of SI after stroke. Using MEG, Rossini et al. (1998) localized the cerebral sources of somatosensory evoked fields for stimulation of the first and fifth fingers. In every case, subjects still demonstrated "classical" homuncular somatotopy, such that D5 was always represented medially to D1. Furthermore, in 25% of subjects, all but one with a subcortical lesion, they found an extension of the distance between the representations of the first and fifth fingers in the lesioned hemisphere. Other studies have found interhemispheric differences in the location of the somatosensory hand representation after stroke, also suggesting the capacity for cortical reorganization (Altamura et al., 2007; Tecchio et al., 2007). However, in these studies, the majority of subjects did not have somatosensory lesions, and in others studies, subjects with primary somatosensory damage were excluded (Schaechter, Moore, Connell, Rosen, & Dijkhuizen, 2006). To our knowledge, there is only one imaging study of SI after damage to that area. Using fMRI, Cramer, Moore, Finklestein, and Rosen (2000) reported a single subject with damage to the postcentral gyrus (primary somatosensory cortex) and found a large area of activation in precentral gyrus (usually primary motor cortex) during tactile stimulation, demonstrating basic representational plasticity in sensorimotor cortex.

These studies provide some general evidence regarding changes in somatosensory cortex after stroke throughout the brain. However, these studies do not address how changes after lesions to somatosensory regions affect the percept of tactile stimulation. There have been a handful of studies examining changes in somatosensory processing after stroke. Damage to somatosensory cortex usually results in an inability to detect touch (hemianaesthesia) and/or correctly localize tactile stimuli. Halligan, Hunt, Marshall, and Wade (1995) described a subject with a large SI lesion who could accurately report being stimulated on the contralesional arm, but was highly inaccurate (or completely unable) to report the location of the stimulus. These results provide evidence that damage to the primary somatosensory cortex does not necessarily result in the inability to detect tactile stimuli, but can result in massive impairments in tactile localization. Turton and Butler (2001) examined localization of tactile stimuli in a subject with damage to the posterior limb of the right internal capsule and right thalamus, testing localization of stimuli over the entire body. Stimuli presented to his hand and feet were perceived more proximally, stimuli presented to the upper arm were perceived more distally, and stimuli presented to the feet were mislocalized to the hand. Furthermore,

testing over time revealed a decrease in the number of mislocalized sensations, suggesting possible reorganization over time.

Rapp, Hendel, and Medina (2002) examined localization of tactile stimuli presented at various sites on the contralesional hand of a subject with a left hemisphere lesion that included the hand region of both SI and SII. We found that this subject (RSB) consistently mislocalized stimuli in a compressed manner, such that localization judgments of stimuli presented to the distal segment of a digit were often made on the medial segment of that finger; medial stimulation often resulted in proximal segment localization, etc. The relative topography of the hand, however, was intact, such that subjects tended to make judgments on the correct finger. Since RSB does not have intact cortex in the location of the typical SI hand representation, we assume that other cortical areas now represent the hand. This suggests that, as observed in primate single-cell recording studies, other cortical regions can take over the function of representing tactile stimuli presented to the hand. Second, this study provides novel evidence regarding the relationship between primary somatosensory representations and the mapping to higher order body form representations. Along with reorganization of the hand representation in SI, one possibility is that there would also be reorganization of the body form representation used to localize tactile stimuli. If parallel reorganization of both primary somatosensory representations and body form representations was successful, then one would expect no change in localization perception. However, subjects with primary somatosensory lesions often demonstrate consistent mislocalizations of tactile stimuli, suggesting that the relationship between primary somatosensory maps and body form representations used to localize tactile stimuli are altered after brain damage. Since we know little about the neural correlates of body form representations, this mismapping could be due to damage of both primary somatosensory and higher order body form representations, or is a consequence of an inability of body form representations to rescale successfully after extensive cortical reorganization. Future work examining the relationship between primary somatosensory damage and the perception of touch is necessary to examine this further.

Finally, Aglioti, Beltramello, Peru, Smania, and Tinazzi (1999b) reported a peculiar patient with a small lesion to the traditional hand representation of primary somatosensory cortex. When stimulated on the hand two months post-stroke, she did not report stimuli on the hand, but instead reported consistent double sensations on the contralesional scalp and the back of the neck. However, these anomalous double sensations ceased one year after stroke. Furthermore, double sensations have also been reported in normal subjects who were presented with constant vibrotactile stimulation on the forearm for over two months (Craig, 1993). Both cases likely reflect reorganization of primary somatosensory and/or body form representations, though the exact nature of the changes necessary to induce double sensation is unclear. Double sensations after single stimulation have also been reported by amputees that experience phantom limbs.

2.3. Amputation and acute deafferentation

A third manner in which the sensory consequences of changes in somatosensory maps have been explored is by studying subjects who have lost a limb (amputation) or have temporarily lost limb sensation (acute deafferentation). Merzenich et al. (1984) first found evidence for changes in primary somatosensory representations after digit amputation. After amputating D3 in owl monkeys, they found that neurons previously active for D3 stimulation were now active for fingers that were represented adjacent to D3 in the somatosensory map (D2, D4). Merzenich's seminal paper, along with other studies demonstrating plasticity in primary somatosen-

sory cortex, sparked an interest in reexamining the perceptual correlates of amputation in adults. For example, if human brains exhibited the same remodeling after peripheral injury reported by Merzenich et al. (1984), one might expect that after hand amputations, both the face and arm representations would extend into the region that formerly represented the amputated hand.

The functional correlates of these changes were famously explored by Ramachandran (Ramachandran, 1993; Ramachandran & Hirstein, 1998; Ramachandran, Rogers-Ramachandran, & Cobb, 1995; Ramachandran, Rogers-Ramachandran, & Stewart, 1992). Earlier reports of phantom limb phenomena focused on spontaneous phantom sensations, whereas Ramachandran was the first to study the relationship between actual tactile stimulation and the perceptual characteristics of these sensations on phantom limbs. In Ramachandran's case reports, amputated subjects were stimulated on either the face or the amputated stump. In some amputees, stimulation of the face resulted in a localizable sensation at a specific location on a phantom limb. Further testing revealed that stimulation of specific regions on the skin surface resulted in a repeatable, localizable report of sensation on the phantom limb. Furthermore, the relationship between tactile stimulation and the location of phantom sensation often reflected a general somatotopic organization (see also Aglioti, Bonazzi, & Cortese, 1994; Aglioti, Smania, Atzei, & Berlucchi, 1997; Borsook et al., 1998; Halligan, Marshall, Wade, Davey, & Morrison, 1993).

Based on these results, Ramachandran introduced the remapping hypothesis. In a subject with an amputated hand and lower arm, Ramachandran hypothesized that due to the extension of the face representation, stimulation of the face would result in activation of the "face area" regions that represented the hand before amputation. This explanation likely assumes the existence of a body form representation that takes information from primary somatosensory areas as input and results in the conscious perception of a tactile stimulus at a specific location on the "phantom" skin surface. Importantly, in cases of phantom referred sensations, it is assumed that the relationship between activation in the primary somatosensory representation and a phantom representation of body form does not change after amputation. In this case, stimulation of the face would result in activation of neurons that were formerly active for stimulation of the hand and are currently active for stimulation of the face. This would then result in both a veridical tactile sensation on the face, and a phantom tactile sensation on the non-existent hand. Supporting this hypothesis, Kew et al. (1997) reported two subjects who experienced consistently referred vibrotactile sensations on the phantom limb after stimulation of the ipsilateral trunk. Using positron emission tomography, vibrotactile stimulation of the trunk region contralateral to the amputated limb resulted in activation in the traditional trunk area in contralateral SI. However, stimulation of the trunk ipsilateral to the amputated arm resulted in a much larger pattern of SI activation compared to controls, extending from the traditional trunk region ventrally into traditional hand and arm areas. If the mapping from primary somatosensory representation to a phantom body form representation remains relatively fixed based on the pre-amputation state, then the observed activation should (and does) result in the sensation of tactile stimuli both on the trunk and the phantom limb (see also Elbert et al., 1997; Weiss et al., 2000; Yang et al., 1994).

Mislocalizations have also been observed after acute deafferentation via anaesthetization. Weiss, Miltner, Liepert, Meissner, and Taub (2004) injected ropivacaine to block the radial and medial nerves, resulting in anaesthesia of D1–D3 and the radial side of D4. Within an hour of anaesthesia, magnetic source imaging revealed shifts in D5 and lip representations that reflected an expansion across the deafferented area. Furthermore, subjects were stimulated with von Frey hairs and asked to report if and where they

were stimulated, in order to test both tactile intensity thresholds and localization ability. Examining stimuli presented to the ulnar side of D4 and all of D5, they found that subjects made significantly more errors during nerve blockade than controls, with subjects frequently reporting stimulation on the ulnar portion of D4 as sensation on D3.

These studies account for referred sensations as a mismapping between primary somatosensory representations and a representation of body form that is based on the pre-amputation state and inaccurately assumes the continued existence of a phantom limb. Interestingly, reports of changes in referred phantom sensations over time may reveal evidence regarding the lability of the mapping from primary somatosensory representations to body form representations. Two separate case studies describe subjects who at first reported consistent, repeatable localization of phantom sensations after tactile stimulation (Halligan, Marshall, & Wade, 1994; Knecht et al., 1998). In both cases, the subject returned (either one month or one year later), and the mapping between tactile stimulation and phantom sensation had completely changed. Knecht et al. (1998) reported that stimulation at only 13% of locations which had evoked phantom sensation on the first visit led to phantom sensations on the second visit. These results suggest that after amputation, primary somatosensory representations and/or body form representations are still labile over time, resulting in consistent referred phantom sensations within a testing session, but inconsistent phantom sensations as these representations continue to change.

2.4. Body form representations and tactile perception

The studies reviewed above provide evidence regarding the sensory consequences of cortical reorganization in primary somatosensory representations, and the relationship between primary somatosensory and body form representations. Differential usage of a skin surface results in clear changes in tactile acuity. Reorganization after damage to primary cortical representations results in either systematic mislocalizations of tactile stimuli, or the emergence of double sensations; both reflect an errant mapping between primary somatosensory and higher order body form representations. Finally, evidence from amputees suggests that vestiges of the mapping between primary somatosensory areas and higher order body form representations may remain after amputation, leading to referred sensations on phantom limbs. Furthermore, primary somatosensory and/or body form representations may still be labile well after amputation.

The relationship between primary somatosensory and higher order body form representations can also be examined by observing the sensory consequences of visual and proprioceptive illusions that alter perceived body shape. Earlier, we reported the results of Taylor-Clarke et al. (2004), in which two stimuli presented at the same distance apart on different skin surfaces were misjudged relative to the ratio of cortical representation to skin surface size, likely reflecting an imperfect transformation from primary somatosensory to body form representations. In further investigation of this rescaling process, the authors instructed subjects to gaze at their arm for one hour, with the view of their hand distorted to half its normal size, and the forearm to double its normal size. They surmise that changing the perceived shape of the body would also alter the scaling from primary somatosensory representations to an external, body shape representation. They found the bias for responding "longer" for stimuli presented on the finger versus the forearm was eliminated after viewing both the enlarged forearm and shrunken hand. These results provide evidence for a body form representation used to transform information from primary sensory maps to a representation of the skin surface. Furthermore, this demonstrates that the rescaling process can be altered by changes in the visual perception of body form.

These changes also result in differences in tactile acuity. Non-informative vision of the skin surface (without seeing the presented tactile stimulus) results in enhanced tactile acuity, a phenomenon known as "visual enhancement of touch" (Halligan, Marshall, Hunt, & Wade, 1997; Press, Taylor-Clarke, Kennett, & Haggard, 2004; Taylor-Clarke, Kennett, & Haggard, 2002; Whiteley, Kennett, Taylor-Clarke, & Haggard, 2004). Kennett, Taylor-Clarke, and Haggard (2001) found that when viewing their own arm magnified 2.5 times larger than normal size, tactile acuity was significantly greater than when viewing their arm without magnification. It has been suggested that this enhancement of touch via magnified vision is also modulated by primary somatosensory cortex, as changes have been observed in SI after viewing a magnified hand (Schaefer, Heinze, & Rotte, 2008). These results may reflect a dynamic relationship between primary somatosensory and higher order body form representations.

Changes in perception of tactile stimuli have also been observed after proprioceptive illusions. Perception of body form can be altered using what is known as the Pinocchio illusion (Lackner, 1988). Vibration of the biceps results in the illusory sensation of forearm movement. Furthermore, when touching the nose with the vibrated arm, subjects will often report an illusory extension of the nose. de Vignemont, Ehrsson, and Haggard (2005) used the Pinocchio illusion to create an illusory elongation of the finger, and found that during the illusion stimuli on the finger were perceived as farther apart than compared to a no illusion condition. These results also provide evidence that perception of the location of tactile stimuli is strongly influenced by representations of body form.

These studies have provided evidence regarding the effects of changes in perceived body form on tactile perception. However, there have been fewer studies of the characteristics of body form representations themselves. This may be due to the rarity of reports of subjects with chronic deficits in body form perception after lesion. Changes in body size have been reported in subjects with microsomatognosia or macrosomatognosia, in which the entire body or body parts are perceived as abnormally large or small (Podoll, Muhlbauer, Houben, & Ebel, 1998; Podoll & Robinson, 2000, 2002). Most reports of micro- or macrosomatognosia are transient, subsequent to migraine headache and not brain injury. Other reports of changes in body size occur during and after anaesthesia (Gandevia & Phegan, 1999; Paqueron et al., 2003). Therefore, evidence for the neural underpinnings of body form representations is limited. However, in one fMRI study, Ehrsson, Kito, Sadato, Passingham, and Naito (2005) recorded neural activity during an illusory shrinking of the waist using a variant of the Pinocchio illusion. They found activity in two distinct activation peaks: a more inferior peak near the junction of the intraparietal and postcentral sulcus (iPCS) and the anterior intraparietal sulcus (aIPS), areas involved in tactile-proprioceptive integration (Iwamura, 1998). Importantly, different regions were active for illusory arm movements without illusory shrinking of the waist, suggesting that this activation is specifically related to changes in body form perception. However, to our knowledge, there are no other studies that have attempted to examine the neural correlates of body form representations. Future studies on the nature of body form representations and the sensory consequences of changes in perceived body form on tactile perception will likely aid our understanding of body representations.

3. From Form to space—touch and postural representations

In the previous section, we discussed the relationship between primary somatosensory representations and body form representations in leading to a percept of tactile stimulation on the skin surface. However, localizing relative to the skin surface is not sufficient. One must also know the location of one's body in order to

localize tactile stimuli relative to objects in the environment and external space. One case study provides evidence for a dissociation between representations for localizing tactile stimuli on the skin versus external space. Paillard (1999) reported a subject with a peripheral deafferentation who could, with verbal response, accurately report the location of a stimulus presented to her skin surface with her eyes closed. This indicates a relatively preserved mapping from primary somatosensory representations to a body form representation. However, she was highly impaired at identifying the position of these stimuli in external space. These results suggest a dissociation between the mapping of primary somatosensory representations to body form (intact) and a representation of body posture (impaired) necessary for localizing the body and tactile stimuli in external space. We will refer to the latter as *postural representations*, and review how changes in body posture affect perception of tactile stimuli in both normal and brain-damaged subjects.

3.1. Somatotopic versus external frames of reference

The location of tactile stimulation can be encoded both relative to the skin surface (somatotopic frame of reference) and relative to the position of the stimulus in external space (what we will call "external" frames of reference). For example, a neuron in a strictly somatotopic representation with a receptive field on the left index finger would be active whenever a tactile stimulus is presented to that finger, regardless of finger position in external space. However, the location of a point on the skin surface can change with respect to other reference points as the organism moves, and necessitates encoding locations in external reference frames.

Early research providing evidence for somatotopic and external tactile representations was studies of patients with tactile extinction. Bartolomeo, Perri, and Gainotti (2004) described 24 right brain-damaged subjects who had bilateral stimuli presented to their hands or knees with their limbs crossed or in the anatomical position (i.e. uncrossed). They found three subjects who performed substantially worse in detecting stimuli when a hand was in contralesional space relative to the subject's trunk, regardless of whether it was the left or right hand. Since this pattern of performance affected both hands based on their position in external space, it is consistent with an impairment to a external tactile representation. The authors also reported multiple subjects whose deficit was limited to reporting left hand stimuli and was not modulated based on hand position in space, consistent with damage to a somatotopic representation (see also Berti et al., 1999; Moro, Zampini, & Aglioti, 2004; Peru, Moro, Sattibaldi, Morgant, & Aglioti, 2006; Smania & Aglioti, 1995; Valenza, Seghier, Schwartz, Lazeyras, & Vuilleumier, 2004).

Studies of performance on tactile temporal order judgment tasks manipulating hand position have provided evidence for separate somatotopic and external stages in representing tactile location. In a tactile temporal order judgment task, subjects are presented with two tactile stimuli, one to each hand, and are instructed to report which tactile stimulus was presented first. Yamamoto and Kitazawa (2001) presented this task to subjects with their hands crossed or uncrossed. In the uncrossed condition, subjects were accurate at assessing the location of the first stimulus, with the just noticeable difference for the two stimuli as short as 70 ms on manual and saccadic responses. However, in the crossed condition, subjects were significantly less accurate, with some subjects consistently inverting their responses when interstimulus intervals were between 100 and 200 ms. The experimenters also presented subjects with the same task using visual stimuli attached to the hands, and did not find any difference in performance between the crossed and uncrossed conditions, suggesting that this system of spatial encoding is limited to the somatosensory domain. The

authors conclude that initial processing of hand location assumes that the hand is not crossed, and that the actual position of the hand is subsequently represented (see also Shore, Spry, & Spence, 2002). Furthermore, this effect is not limited solely to crossing the hands. Schicke and Roder (2006) observed a similar hand crossing foot over foot, and even foot over hand, suggesting that this postural representation encompasses the whole body.

This two-stage hypothesis, with an initial somatotopic representation of tactile stimulus position followed by a representation of the limb in external space, has been supported by behavioral and somatosensory event related potential (ERP) studies. Groh and Sparks (1996) observed saccades to somatosensory targets by humans with their hands uncrossed and crossed. Saccades were fairly direct towards the target when hands were uncrossed. However, when the hands were crossed, subjects would often saccade first in the direction opposite of the stimulus, and then change path and saccade towards the actual target. Azanon and Soto-Faraco (2008) presented subjects with a task, arms crossed, in which they were to judge the vertical location of a visual stimulus cued by a tactile stimulus at various cue latencies. They found a congruency effect such that subjects were faster when the tactile cue and visual stimulus were presented over *opposite* hands when the cue-target interval was less than 100 ms. However, this cueing effect reversed with cue-target intervals over 200 ms, such that the tactile cue facilitated vertical location judgments when they were over the same hand. We (Medina et al., submitted for publication) employed the Simon effect, a phenomenon in which subjects respond more slowly in a non-spatial task when the stimulus and response are on different sides of space (incongruent) compared to the same side of space (congruent), to examine tactile processing in somatotopic and external reference frames. In the uncrossed conditions, we found a robust tactile Simon effect, as subject responded faster when stimuli were presented to the same hand as the response foot. With crossed hands, we found two interesting results: First, with hands crossed we found a significant Simon effect based on a somatotopic representation, and no evidence of an externally based Simon effect. Second, subjects were significantly faster at identifying stimulus intensity in the crossed hands position compared to the uncrossed hands condition. These results are also consistent with a two-stage model of encoding tactile location, with faster responses using a somatotopic reference frame with the arms crossed, and slower responses likely incorporating somatotopic and external information with the arms uncrossed.

There is also evidence for dissociable external and somatotopic ERP components for orienting to tactile stimuli. Eimer, Forster, and Van Velzen (2003) presented subjects with a task in which they were asked to respond verbally whenever a tactile target was presented on the cued side of space. The experiment was presented with the subject's arms uncrossed and crossed, and the experimenters examined lateralized ERP components (anterior directing attention negativity, ADAN; and late directing attention positivity, or LDAP) that are usually associated with the preparation of orientation of attention. When the arms were uncrossed, both the ADAN and LDAP components were contralateral to the direction of the attentional shift. When the arms were crossed, the LDAP was contralateral to the *side of space* where attention was oriented. However, the ADAN is instead contralateral *to the hand* where attention was oriented. The authors suggest that the LDAP component is generated by an external tactile representation, whereas the ADAN component is generated by a somatotopic representation (see also Eimer, Forster, Fieger, & Harbich, 2004).

3.2. Reference frames of external postural representations

These results all provide evidence for an initial, somatotopic representation that is used to encode location without informa-

tion regarding the position of the limbs in external space, what we refer to a body form representation. Then, a second stage of processing takes into account limb position in external space, and may refer to our proposed postural representations. One interesting topic is the identification of the reference frame(s) used to localize tactile stimuli in postural representations. Evidence suggests that tactile stimuli are represented in trunk- and head-centered reference frames, as may also be represented based on the position of the other hand or stimulus.

Ho and Spence (2007) presented vibrotactile stimuli along the waist with the subject's head positioned straight ahead, or to either side, and found that the perceived location of stimulation was shifted opposite the direction of head turn, suggesting the involvement of head-centered representations in localizing tactile stimuli. We reported a case study (JDY) of an individual with left fronto-parietal damage who experienced bilateral sensations in response to unilateral tactile stimulation—a condition known as synchiria (Drinkwater, 1913; Janet, 1898; Sathian, 2000). These phantom sensations likely result from the failure of inhibitory mechanisms to prevent ipsilateral neural activity (Hlushchuk & Hari, 2006; Lipton, Fu, Branch, & Schroeder, 2006). Manipulating the subject's hand and body position, we found that synchiria was modulated by hand position relative to multiple reference frames. Specifically, synchiria decreased as the subject's hands moved from contralesional to ipsilesional space in a trunk- and head-centered reference frame (Medina & Rapp, 2008). These findings provide evidence that there are mechanisms for representing (and inhibiting) tactile stimuli that operate in multiple egocentric reference frames. Furthermore, the subject was tested with the hands crossed in both ipsilesional and contralesional space, and reported no phantom synchiric sensations on these trials. These and other similar results to be reviewed suggest evidence for representations based on the *relative position* of the other hand and/or stimulus.

This concept was first introduced by Aglioti, Smania, and Peru (1999a) in a study of 24 subjects with right hemisphere brain damage and extinction. The authors presented unilateral and bilateral tactile stimuli in the crossed and uncrossed positions with their hands positioned centrally, in ipsilesional or in contralesional space relative to the subject's head and trunk. In each trunk field condition, subjects demonstrated decreased extinction of left hand stimuli in the crossed condition compared to the anatomical condition, generally consistent with an externally based trunk-centered deficit. This improved performance could be due to the contralesional hand being in more ipsilesional space when the hands are crossed versus uncrossed. However, these subjects showed little difference in performance in contralesional versus ipsilesional space when comparing trials within the crossed or uncrossed conditions. These results are therefore, not consistent with a simple egocentric, external tactile impairment. Aglioti and colleagues suggested that there may be a representation that encodes the position of the hands relative to each other. In such a representation, when the hands are crossed the (assuming right brain damage) right hand is always positioned to the left (i.e. contralesional to) the left hand. Being that the left hand is always represented contralesionally in such a representation, subjects would likely demonstrate more extinction with the arms crossed versus uncrossed. Furthermore, assuming no other deficits, there would not be any change in performance in contralesional compared to ipsilesional space relative to the trunk, head, etc. A limb-relative representation of body posture is conceivable, as it may be useful to efficiently represent limb location relative to other limbs in tasks involving bimanual coordination.

However, a second possibility is that the two tactile stimuli are being represented in an allocentric reference frame based on the stimulus, and not hand, position. A subject with left tactile extinction was presented with bilateral stimuli to both sides of the hand

or both sides of the finger, with the hand positioned either palm up or palm down (Tinazzi, Ferrari, Zampini, & Aglioti, 2000). The subject extinguished the more contralesional stimulus relative to the subject in every manipulation. For example, with stimuli presented to the thumb and pinky of the right hand, the subject would extinguish stimuli presented to the thumb with the palm down and the pinky with the palm up. The authors suggest that tactile stimuli can be encoded based on reference frames that dynamically scale from a trunk-centered midline to other body-part centered midlines (hand-centered, finger-centered, etc.). However, these results are also consistent with an impairment affecting a representation that encodes location based on the relative position of the two stimuli (see also Moscovitch & Behrmann, 1994). Future studies are necessary to examine whether there is a distinction between limb-relative and allocentric tactile representations.

3.3. Postural representations—neural substrates and visual contributions

Studies of tactile sensation after manipulations of body position have revealed the following. First, subjects with tactile detection deficits provide evidence for both somatotopic and external representations of tactile stimuli. Furthermore, localizing tactile stimuli likely occurs in two distinct stages: an initial somatotopic stage in which stimulus location is identified relative to its position on the skin surface, and a second stage that takes into account limb position in external space. In these egocentric, external representations, there is evidence for encoding tactile location based on trunk-centered, head-centered, and limb-relative and/or allocentric frame of reference.

Postural representations likely involve inputs from both proprioception and vision in order to construct an accurate representation of limb position in external space. One possible substrate for postural representations is the superior parietal lobe. Wolpert, Goodbody, and Husain (1998) reported a subject with a large superior parietal cyst in which the perception of her arm drifted significantly over time until it seemed to disappear completely, suggesting its involvement in maintaining a representation of body posture. In non-human primate studies, neurons in Brodmann area 5 represent the location of the hand in a trunk-centered reference frame. Lacquianiti, Guigon, Bianchi, Ferraina, and Caminiti (1995) instructed macaque monkeys to use their hands to touch a stationary target, and then move to a second stationary target in three-dimensional space. Before a reach, neuronal populations in area 5 were active depending on the position of the hand along the three axes in a trunk-centered reference frame. Sakata, Takaoka, Kawarasaki, and Shibutani (1973) found neurons in area 5 of the rhesus monkey that responded preferentially to cutaneous stimulation only when the stimulated body part was in a specific location in space. For example, one neuron in area 5 responded preferentially when the forearm was stimulated while the arm was drawn towards the body, but did not respond to the same forearm stimulation when the arm was positioned away from the body. A second candidate region is ventral intraparietal sulcus, which has been implicated for representing limb position in humans (Lloyd, Shore, Spence, & Calvert, 2003) and non-human primates (Avillac, Deneve, Olivier, Pouget, & Duhamel, 2005; Rizzolatti, Fogassi, & Gallese, 2002).

Finally, vision likely contributes to the maintenance and development of representations of body posture. This has been examined extensively using manipulations of perceived body posture using tactile temporal order judgment experiments. Azanon and Soto-Faraco (2007) presented subjects with a tactile temporal order judgment task with the arms crossed or uncrossed. However, they added a manipulation in which rubber hands were placed, either in the crossed or uncrossed positions, directly above the

subject's actual, unseen hands. As reported before (Yamamoto & Kitazawa, 2001), the just noticeable difference was longer with crossed compared to uncrossed real hands, suggesting the influence of proprioceptive information regardless of visual input. But within crossed real hand trials, performance was significantly better with uncrossed fake hands compared to crossed fake hands, providing evidence for the influence of a visual representation of body posture on performance in a tactile temporal order judgment task. Shore, Gray, Spry, and Spence (2005) found that just noticeable differences were shorter when the hands were positioned far away (1 m apart) compared to when they were positioned close together (adjacent). Gallace and Spence (2005) found this effect also held when hands were in the same position, but were visually perceived as being farther apart versus close together (see also Kobor, Furedi, Kovacs, Spence, & Vidnyanszky, 2006; Rorden, Greene, Sasine, & Baylis, 2002). These studies all suggest that the contributions of visual information to body posture affect perception of tactile stimuli.

4. Conclusions

Representing the location of tactile stimuli in space requires that multiple complementary types of information be integrated. In this paper, we propose a preliminary model in which the traditional body schema is partitioned into three distinct but interactive representations. First, we suggest that primary somatosensory representations provide a depiction of the nature of stimuli on the body surface; this representation is altered by use as well as peripheral and central nervous system disruption. The body form representation, in contrast, takes information from a "distorted" primary somatosensory representation, incorporating knowledge of body size and shape in order to represent sensation on the skin surface. Finally, postural representations incorporate visual, proprioceptive, vestibular and spatial information to achieve a representation of the position and configuration of the body in space. Action requires that the body form and postural representations be bound together to generate a representation that specifies the size and shape of the body as well as its configuration and location in space.

Although there have been substantial advances in understanding the nature of body representations, this area of inquiry is still in its infancy. Future investigations will be required to explore the interactions between the putative body representations and to determine if the plasticity noted by numerous investigators can be exploited.

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