Published in final edited form as:

Neuropsychologia. 2010 February ; 48(3): 645. doi:10.1016/j.neuropsychologia.2009.08.017.

From Maps to Form to Space: Touch and the Body Schema

Jared Medina and H. Branch Coslett

Department of Neurology, University of Pennsylvania

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*).

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; Gallagher, 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 representations. 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 environment¹.

© 2009 Elsevier Ltd. All rights reserved.

Corresponding address: Jared Medina, 3 West Gates, 3400 Spruce Street, University of Pennsylvania, Philadelphia, PA 19104, Phone: 215-614-0274, Fax: 215-349-8260, jared.medina@uphs.upenn.edu or H. Branch Coslett, 3 West Gates, 3400 Spruce Street, University of Pennsylvania, Philadelphia, PA 19104, Phone: 215-349-5696, Fax: 215-349-8260, hbc@mail.med.upenn.edu.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

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 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.

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 (SI) 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 *et al.*, 1990; Recanzone *et al.*, 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 *et al.*, 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

¹Note 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.

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, Jacobsen, & Haggard (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 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.

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 and colleagues (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 *et al.*, 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 and colleagues (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 discrimination task, such that larger shifts corresponded to increased tactile acuity (see also Godde *et al.*, 2003; Godde *et al.*, 1996; Godde *et al.*, 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 *et al.*, 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 using musicians to study 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 and colleagues (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 *et al.*, 2007; Schweizer *et al.*, 2001). Furthermore, blind Braille readers who coactivate multiple fingers in reading also demonstrate a similar pattern of performance. Sterr and colleagues (1998a 1998b) 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 *et al.*, 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 *et al.*, 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.

Lesion

Studies of cortical lesions in mammals have also provided evidence regarding the dynamic properties of primary somatosensory representations. Jenkins & 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 *et al.*, 2009; Coq & Xerri, 1999a; Jain *et al.*, 2008; Xerri *et al.*, 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 *et al.*, 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 and colleagues (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 *et al.*, 2006). To our knowledge, there is only one imaging study of SI after damage to that area. Using fMRI, Cramer and colleagues (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 and colleagues (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 & 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 and colleagues (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.

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 and colleagues (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 somatosensory 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 and colleagues (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 *et al.*, 1995; Ramachandran *et al.*, 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 *et al.*, 1994; Aglioti *et al.*, 1997; Borsook *et al.*, 1998; Halligan *et al.*, 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 and colleagues (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 and colleagues (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 mismatching 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 *et al.*, 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 and colleagues (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.

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 reflecting an errant mapping between primary somatosensory and higher-order body form representations. Finally, evidence from amputees suggest 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 and colleagues (2004), in which two stimuli presented at the same distance apart on different skin surfaces were misjudged based on 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 *et al.*, 1997; Press *et al.*, 2004; Taylor-Clarke *et al.*, 2002; Whiteley *et al.*, 2004). Kennett, Taylor-Clarke & 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 *et al.*, 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, Taylor-Clarke & 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 *et al.*, 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 anesthesia (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 and colleagues (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.

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.

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 and colleagues (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 *et al.*, 2004; Peru *et al.*, 2006; Smania & Aglioti, 1995; Valenza *et al.*, 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 milliseconds 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 milliseconds. 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 *et al.*, 2002). Furthermore, this effect is not limited solely to crossing the hands. Schicke & 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 & 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 milliseconds. However, this cueing effect reversed with cue-target intervals over 200 milliseconds, such that

the tactile cue facilitated vertical location judgments when they were over the same hand. We (Medina *et al.*, submitted) employed the Simon effect (Simon & Small, 1969), defined as when 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 and colleagues (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 *et al.*, 2004).

Reference frames of external postural representations

These results all provide evidence for an initial, somatotopic representation that is used to encode location without information 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 & 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 *et al.*, 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 *et al.*, 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 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.

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 & 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. Lacquaniti and colleagues (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 and colleagues (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 *et al.*, 2003) and non-human primates (Avillac *et al.*, 2005; Rizzolatti *et al.*, 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 and colleagues (2005) found that just noticeable differences were shorter when the hands were positioned far away (1 meter apart) compared to when they were positioned close together (adjacent). Gallace & 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 *et al.*, 2006; Rorden *et al.*, 2002). These studies all suggest that the contributions of visual information to body posture affect perception of tactile stimuli.

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.

REFERENCES

- Aglioti S, Bonazzi A, Cortese F. Phantom lower-limb as a perceptual marker of neural plasticity in the mature human brain. *Proceedings of the Royal Society of London Series B-Biological Sciences* 1994;255(1344):273–278.
- Aglioti S, Smania N, Atzei A, Berlucchi G. Spatio-temporal properties of the pattern of evoked phantom sensations in a left index amputee patient. *Behavioral Neuroscience* 1997;111(5):867–872. [PubMed: 9383509]
- Aglioti S, Smania N, Peru A. Frames of reference for mapping tactile stimuli in brain-damaged patients. *Journal of Cognitive Neuroscience* 1999a;11(1):67–79. [PubMed: 9950715]
- Aglioti SM, Beltramello A, Peru A, Smania N, Tinazzi M. Anomalous double sensations after damage to the cortical somatosensory representation of the hand in humans. *Neurocase* 1999b;5(4):285–292.
- Allard T, Clark SA, Jenkins WM, Merzenich MM. Reorganization of somatosensory area 3b representations in adult owl monkeys after digital syndactyly. *Journal of Neurophysiology* 1991;66(3):1048–1058. [PubMed: 1753275]
- Altamura C, Torquati K, Zappasodi F, Ferretti A, Pizzella V, Tibuzzi F, et al. fMRI-vs-MEGf evaluation of post-stroke interhemispheric asymmetries in primary sensorimotor hand areas. *Experimental Neurology* 2007;204(2):631–639. [PubMed: 17291497]
- Avillac M, Deneve S, Olivier E, Pouget A, Duhamel JR. Reference frames for representing visual and tactile locations in parietal cortex. *Nature Neuroscience* 2005;8(7):941–949.
- Azanon E, Soto-Faraco S. Alleviating the ‘crossed-hands’ deficit by seeing uncrossed rubber hands. *Experimental Brain Research* 2007;182(4):537–548.
- Azanon E, Soto-Faraco S. Changing reference frames during the encoding of tactile events. *Current Biology* 2008;18:1044–1049. [PubMed: 18619841]
- Bartolomeo P, Perri R, Gainotti G. The influence of limb crossing on left tactile extinction. *Journal of Neurology, Neurosurgery and Psychiatry* 2004;75(1):49–55.
- Berti A, Oxbury S, Oxbury J, Affanni P, Umiltà C, Orlandi L. Somatosensory extinction for meaningful objects in a patient with right hemispheric stroke. *Neuropsychologia* 1999;37(3):333–343. [PubMed: 10199646]
- Borsook D, Becerra L, Fishman S, Edwards A, Jennings CL, Stojanovic M, et al. Acute plasticity in the human somatosensory cortex following amputation. *Neuroreport* 1998;9(6):1013–1017. [PubMed: 9601659]
- Brown CE, Aminoltejeri K, Erb H, Winship IR, Murphy TH. In vivo voltage-sensitive dye imaging in adult mice reveals that somatosensory maps lost to stroke are replaced over weeks by new structural and functional circuits with prolonged modes of activation within both the peri-infarct zone and distant sites. *Journal of Neuroscience* 2009;29(6):1719–1734. [PubMed: 19211879]
- Clark SA, Allard T, Jenkins WM, Merzenich MM. Receptive-fields in the body-surface map in adult cortex defined by temporally correlated inputs. *Nature* 1988;332(6163):444–445. [PubMed: 3352741]
- Coq JO, Xerri C. Environmental enrichment alters organizational features of the forepaw representation in the primary somatosensory cortex of adult rats. *Experimental Brain Research* 1998;121(2):191–204.
- Coq JO, Xerri C. Acute reorganization of the forepaw representation in the rat SI cortex after focal cortical injury: Neuroprotective effects of piracetam treatment. *European Journal of Neuroscience* 1999a;11(8):2597–2608. [PubMed: 10457159]
- Coq JO, Xerri C. Tactile impoverishment and sensorimotor restriction deteriorate the forepaw cutaneous map in the primary somatosensory cortex of adult rats. *Experimental Brain Research* 1999b;129(4):518–531.
- Craig JC. Anomalous sensations following prolonged tactile stimulation. *Neuropsychologia* 1993;31(3):277–291. [PubMed: 8492881]

- Cramer SC, Crafton KR. Somatotopy and movement representation sites following cortical stroke. *Experimental Brain Research* 2006;168(12):25–32.
- Cramer SC, Moore CI, Finklestein SP, Rosen BR. A pilot study of somatotopic mapping after cortical infarct. *Stroke* 2000;31(3):668–671. [PubMed: 10700502]
- de Vignemont F. Body schema and body image - pros and cons. *Neuropsychologia*. this issue.
- de Vignemont F, Ehrsson HH, Haggard P. Bodily illusions modulate tactile perception. *Current Biology* 2005;15(14):1286–1290. [PubMed: 16051171]
- Drinkwater H. Obligatory bi-manual synergia with allocheiria in a boy otherwise normal. *Proceedings of the XVIIth International Congress of Medicine* 1913;11:117–124.
- Ehrsson HH, Kito T, Sadato N, Passingham RE, Naito E. Neural substrate of body size: Illusory feeling of shrinking of the waist. *PLOS Biology* 2005;3(12):2200–2207.
- Eimer M, Forster B, Fieger A, Harbich S. Effects of hand posture on preparatory control processes and sensory modulations in tactile-spatial attention. *Clinical Neurophysiology* 2004;115:596–608. [PubMed: 15036056]
- Eimer M, Forster B, Van Velzen J. Anterior and posterior attentional control systems use different spatial reference frames: ERP evidence from covert tactile-spatial orienting. *Psychophysiology* 2003;40:924–933. [PubMed: 14986845]
- Elbert T, Pantev C, Wienbruch C, Rockstroh B, Taub E. Increased cortical representation of the fingers of the left hand in string players. *Science* 1995;270(5234):305–307. [PubMed: 7569982]
- Elbert T, Sterr A, Flor H, Rockstroh B, Knecht S, Pantev C, et al. Input-increase and input-decrease types of cortical reorganization after upper extremity amputation in humans. *Experimental Brain Research* 1997;117(1):161–164.
- Gallace A, Spence C. Visual capture of apparent limb position influences tactile temporal order judgments. *Neuroscience Letters* 2005;379(1):63–68. [PubMed: 15814201]
- Gallagher S. Body image and body schema: A conceptual clarification. *Journal of Mind and Behavior* 1986;7:541–554.
- Gallagher, S. *How the body shapes the mind*. Oxford University Press; Oxford: 2005.
- Gallese V, Sinigaglia C. The body and its selves. *Neuropsychologia*. this issue.
- Gandevia SC, Phegan CML. Perceptual distortions of the human body image produced by local anaesthesia, pain and cutaneous stimulation. *Journal of Physiology - London* 1999;514(2):609–616.
- Godde B, Ehrhardt J, Braun C. Behavioral significance of input-dependent plasticity of human somatosensory cortex. *Neuroreport* 2003;14(4):543–546. [PubMed: 12657881]
- Godde B, Spengler F, Dinse HR. Associative pairing of tactile stimulation induces somatosensory cortical reorganization in rats and humans. *Neuroreport* 1996;8(1):281–285. [PubMed: 9051796]
- Godde B, Stauffenberg B, Spengler F, Dinse HR. Tactile coactivation-induced changes in spatial discrimination performance. *Journal of Neuroscience* 2000;20(4):1597–1604. [PubMed: 10662849]
- Groh JM, Sparks DL. Saccades to somatosensory targets. I. Behavioral characteristics. *Journal of Neurophysiology* 1996;75(1):412–427. [PubMed: 8822567]
- Halligan PW, Hunt M, Marshall JC, Wade DT. Sensory detection without localization. *Neurocase* 1995;1(3):259–266.
- Halligan PW, Marshall JC, Hunt M, Wade DT. Somatosensory assessment: Can seeing produce feeling? *Journal of Neurology* 1997;244(3):199–203. [PubMed: 9050962]
- Halligan PW, Marshall JC, Wade DT. Sensory disorganization and perceptual plasticity after limb amputation - a follow-up-study. *Neuroreport* 1994;5(11):1341–1345. [PubMed: 7919194]
- Halligan PW, Marshall JC, Wade DT, Davey J, Morrison D. Thumb in cheek - sensory reorganization and perceptual plasticity after limb amputation. *Neuroreport* 1993;4(3):233–236. [PubMed: 8477042]
- Head H, Holmes G. Sensory disturbances from cerebral lesions. *Brain* 1911;34:103–254.
- Hlushchuk Y, Hari R. Transient suppression of ipsilateral primary somatosensory cortex during tactile finger stimulation. *Journal of Neuroscience* 2006;26(21):5819–5824. [PubMed: 16723540]
- Ho C, Spence C. Head orientation biases tactile localization. *Brain Research* 2007;1144:136–141. [PubMed: 17320836]

- Hodzic A, Veit R, Karim AA, Erb M, Godde B. Improvement and decline in tactile discrimination behavior after cortical plasticity induced by passive tactile coactivation. *Journal of Neuroscience* 2004;24(2):442–446. [PubMed: 14724242]
- Iwamura Y. Hierarchical somatosensory processing. *Current Opinion in Neurobiology* 1998;8(4):522–528. [PubMed: 9751655]
- Jain N, Qi HX, Collins CE, Kaas JH. Large-scale reorganization in the somatosensory cortex and thalamus after sensory loss in macaque monkeys. *Journal of Neuroscience* 2008;28(43):11042–11060. [PubMed: 18945912]
- Janet, P. *Nevroses et idées fixes*. Vol. 1. Felix Alcan; Paris: 1898.
- Jenkins, WM.; Merzenich, MM. Reorganization of neocortical representations after brain injury: A neurophysiological model of the bases of recovery from stroke. In: Seil, FJ.; Herbert, E.; Carlson, BM., editors. *Progress in brain research*. Elsevier; Amsterdam: 1987. p. 249-266.
- Jenkins WM, Merzenich MM, Ochs MT, Allard T, Guic-Robles E. Functional reorganization of primary somatosensory cortex in adult owl monkeys after behaviorally controlled tactile stimulation. *Journal of Neurophysiology* 1990;63:82–104. [PubMed: 2299388]
- Kalisch T, Tegenthoff M, Dinse HR. Differential effects of synchronous and asynchronous multifinger coactivation on human tactile performance. *BMC Neuroscience* 2007;8
- Kennett S, Taylor-Clarke M, Haggard P. Noninformative vision improves the spatial resolution of touch in humans. *Current Biology* 2001;11(15):1188–1191. [PubMed: 11516950]
- Kew JJM, Halligan PW, Marshall JC, Passingham RE, Rothwell JC, Ridding MC, et al. Abnormal access of axial vibrotactile input to deafferented somatosensory cortex in human upper limb amputees. *Journal of Neurophysiology* 1997;77(5):2753–2764. [PubMed: 9163390]
- Knecht S, Henningsen H, Hohling C, Elbert T, Flor H, Pantev C, et al. Plasticity of plasticity? Changes in the pattern of perceptual correlates of reorganization after amputation. *Brain* 1998;121:717–724. [PubMed: 9577396]
- Kobor I, Furedi L, Kovacs G, Spence C, Vidnyanszky Z. Back-to-front: Improved tactile discrimination performance in the space you cannot see. *Neuroscience Letters* 2006;400(12):163–167. [PubMed: 16516383]
- Lackner JR. Some proprioceptive influences on the perceptual representation of body shape and orientation. *Brain* 1988;111:281–297. [PubMed: 3378137]
- Lacquaniti F, Guigon E, Bianchi L, Ferraina S, Caminiti R. Representing spatial information for limb movement: Role of area 5 in the monkey. *Cerebral Cortex* 1995;5:391–409. [PubMed: 8547787]
- Lipton ML, Fu K-MG, Branch CA, Schroeder CE. Ipsilateral hand input to area 3b revealed by converging hemodynamic and electrophysiological analyses in macaque monkeys. *Journal of Neuroscience* 2006;26(1):180–185. [PubMed: 16399685]
- Lloyd DM, Shore DI, Spence C, Calvert GA. Multisensory representation of limb position in human premotor cortex. *Nature Neuroscience* 2003;6(1):17–18.
- Medina, J.; McCloskey, M.; Rapp, B. Somatotopic and external frames of reference - evidence from the Simon effect. submitted
- Medina J, Rapp B. Phantom tactile sensations modulated by body position. *Current Biology* 2008;18(24):1937–1942. [PubMed: 19062276]
- Merzenich MM, Kaas JH, Wall JT, Sur M, Nelson RJ, Felleman DJ. Progression of change following median nerve-section in the cortical representation of the hand in areas-3b and area-1 in adult owl and squirrel-monkeys. *Neuroscience* 1983;10(3):639–665. [PubMed: 6646426]
- Merzenich MM, Nelson RJ, Stryker MP, Cynader MS, Schoppmann A, Zook JM. Somatosensory cortical map changes following digit amputation in adult monkeys. *Journal of Comparative Neurology* 1984;224(4):591–605. [PubMed: 6725633]
- Mogilner A, Grossman JAL, Ribary U, Joliot M, Volkmann J, Rapaport D, et al. Somatosensory cortical plasticity in adult humans revealed by magnetoencephalography. *Proceedings of the National Academy of Sciences of the United States of America* 1993;90(8):3593–3597. [PubMed: 8386377]
- Moro V, Zampini M, Aglioti S. Changes in spatial position of hands modify tactile extinction but not disownership of contralesional hand in two right brain-damaged patients. *Neurocase* 2004;10(6):437–443. [PubMed: 15788283]

- Moscovitch M, Behrmann M. Coding of spatial information in the somatosensory system - Evidence from patients with neglect following parietal lobe damage. *Journal of Cognitive Neuroscience* 1994;6(2):151–155.
- Paillard, J. Body schema and body image - a double dissociation in deafferented patients. In: Gantchev, GN.; Mori, S.; Massion, J., editors. *Motor control, today and tomorrow*. Akademichno Izdatelstvo; Sofia: 1999. p. 197-214.
- Paqueron X, Leguen M, Rosenthal D, Coriat P, Willer JC, Danziger N. The phenomenology of body image distortions induced by regional anaesthesia. *Brain* 2003;126:702–712. [PubMed: 12566290]
- Penfield W, Boldrey E. Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain* 1937;37:389–443.
- Penfield, W.; Rasmussen, T. *The cerebral cortex of man*. MacMillan; New York: 1950.
- Peru A, Moro V, Sattibaldi L, Morgant JS, Aglioti SM. Gravitational influences on reference frames for mapping somatic stimuli in brain-damaged patients. *Experimental Brain Research* 2006;169(2):145–152.
- Pilz K, Veit R, Braun C, Godde B. Effects of co-activation on cortical organization and discrimination performance. *Neuroreport* 2004;15(17):2669–2672. [PubMed: 15570175]
- Pleger B, Dinse HR, Ragert P, Schwenkreis P, Malin JP, Tegenthoff M. Shifts in cortical representations predict human discrimination improvement. *Proceedings of the National Academy of Sciences of the United States of America* 2001;98(21):12255–12260. [PubMed: 11593042]
- Podoll K, Muhlbauer V, Houben I, Ebel H. Hypnagogic hallucinations presenting as macrosomatognosia and microsomatognosia. *Fortschritte Der Neurologie Psychiatrie* 1998;66(8):338–344. [PubMed: 9741013]
- Podoll K, Robinson D. Macrosomatognosia and microsomatognosia in migraine art. *Acta Neurologica Scandinavica* 2000;101(6):413–416. [PubMed: 10877160]
- Podoll K, Robinson D. Pictorial representations of macrosomatognosia experienced as somesthetic aura in migraine. *Neurology Psychiatry and Brain Research* 2002;10(3):125–128.
- Press C, Taylor-Clarke M, Kennett S, Haggard P. Visual enhancement of touch in spatial body representation. *Experimental Brain Research* 2004;154(2):238–245.
- Ragert P, Schmidt A, Altenmuller E, Dinse HR. Superior tactile performance and learning in professional pianists: Evidence for meta-plasticity in musicians. *European Journal of Neuroscience* 2004;19(2):473–478. [PubMed: 14725642]
- Ramachandran VS. Behavioral and magnetoencephalographic correlates of plasticity in the adult human brain. *Proceedings of the National Academy of Sciences of the United States of America* 1993;90(22):10413–10420. [PubMed: 8248123]
- Ramachandran VS, Hirstein W. The perception of phantom limbs - the D.O. Hebb lecture. *Brain* 1998;121:1603–1630. [PubMed: 9762952]
- Ramachandran VS, Rogers-Ramachandran D, Cobb S. Touching the phantom limb. *Nature* 1995;377(6549):489–490. [PubMed: 7566144]
- Ramachandran VS, Rogers-Ramachandran D, Stewart M. Perceptual correlates of massive cortical reorganization. *Science* 1992;258(5085):1159–1160. [PubMed: 1439826]
- Rapp B, Hendel SK, Medina J. Remodeling of somatosensory hand representations following cerebral lesions in humans. *Neuroreport* 2002;13(2):207–211. [PubMed: 11893911]
- Rasmusson DD, Turnbull BG. Immediate effects of digit amputation on SI cortex in the raccoon - unmasking of inhibitory fields. *Brain Research* 1983;288(12):368–370. [PubMed: 6661627]
- Recanzone GH, Merzenich MM, Jenkins WM. Frequency discrimination-training engaging a restricted skin surface results in an emergence of a cutaneous response zone in cortical area 3a. *Journal of Neurophysiology* 1992;67(5):1057–1070. [PubMed: 1597697]
- Rizzolatti G, Fogassi L, Gallese V. Motor and cognitive functions of the ventral premotor cortex. *Current Opinion in Neurobiology* 2002;12(2):149–154. [PubMed: 12015230]
- Rockstroh, B.; Vanni, S.; Elbert, T.; Hari, R. Extensive somatosensory stimulation alters somatosensory evoked fields; Paper presented at the Tenth International Conference on Biomagnetism; Santa Fe, New Mexico. 1996;

- Rorden C, Greene K, Sasine GM, Baylis GC. Enhanced tactile performance at the destination of an upcoming saccade. *Current Biology* 2002;12(16):1429–1434. [PubMed: 12194826]
- Rossini PM, Dal Forno G. Neuronal post-stroke plasticity in the adult. *Restorative Neurology and Neuroscience* 2004;22(35):193–206. [PubMed: 15502265]
- Rossini PM, Tecchio F, Pizzella V, Lupoi D, Cassetta E, Pasqualetti P, et al. On the reorganization of sensory hand areas after mono-hemispheric lesion: A functional (MEG) anatomical (MRI) integrative study. *Brain Research* 1998;782(12):153–166. [PubMed: 9519259]
- Sakata H, Takaoka Y, Kawarasaki A, Shibutani H. Somatosensory properties of neurons in the superior parietal cortex (area 5) of the rhesus monkey. *Brain Research* 1973;64:85–102. [PubMed: 4360893]
- Sathian K. Intermanual referral of sensation to anesthetic hands. *Neurology* 2000;54(9):1866–1868. [PubMed: 10802803]
- Schaechter JD, Moore CI, Connell BD, Rosen BR, Dijkhuizen RM. Structural and functional plasticity in the somatosensory cortex of chronic stroke patients. *Brain* 2006;129:2722–2733. [PubMed: 16921177]
- Schaefer M, Heinze HJ, Rotte M. Observing the touched body magnified alters somatosensory homunculus. *Neuroreport* 2008;19(9):901–905. [PubMed: 18520990]
- Schicke T, Roder B. Spatial remapping of touch: Confusion of perceived stimulus order across hand and foot. *Proceedings of the National Academy of Sciences of the United States Of America* 2006;103(31):11808–11813. [PubMed: 16864789]
- Schweizer R, Braun C, Fromm C, Wilms A, Birbaumer N. The distribution of mislocalizations across fingers demonstrates training-induced neuroplastic changes in somatosensory cortex. *Experimental Brain Research* 2001;139(4):435–442.
- Schwoebel J, Coslett HB. Evidence for multiple, distinct representations of the human body. *Journal of Cognitive Neuroscience* 2005;17(4):543–553. [PubMed: 15829076]
- Shore DI, Gray K, Spry E, Spence C. Spatial modulation of tactile temporal-order judgments. *Perception* 2005;34(10):1251–1262. [PubMed: 16309118]
- Shore DI, Spry E, Spence C. Confusing the mind by crossing the hands. *Cognitive Brain Research* 2002;14(1):153–163. [PubMed: 12063139]
- Simon JR, Small AM. Processing auditory information - interference from an irrelevant cue. *Journal of Applied Psychology* 1969;53(5):433. &. [PubMed: 5366316]
- Smania N, Aglioti S. Sensory and spatial components of somesthetic deficits following right brain-damage. *Neurology* 1995;45(9):1725–1730. [PubMed: 7675234]
- Sterr A, Green L, Elbert T. Blind Braille readers mislocate tactile stimuli. *Biological Psychology* 2003;63(2):117–127. [PubMed: 12738403]
- Sterr A, Muller MM, Elbert T, Rockstroh B, Pantev C, Taub E. Changed perceptions in Braille readers. *Nature* 1998a;391(6663):134–135. [PubMed: 9428760]
- Sterr A, Muller MM, Elbert T, Rockstroh B, Pantev C, Taub E. Perceptual correlates of changes in cortical representation of fingers in blind multifinger Braille readers. *Journal of Neuroscience* 1998b;18(11):4417–4423. [PubMed: 9592118]
- Taylor-Clarke M, Jacobsen P, Haggard P. Keeping the world a constant size: Object constancy in human touch. *Nature Neuroscience* 2004;7(3):219–220.
- Taylor-Clarke M, Kennett S, Haggard P. Vision modulates somatosensory cortical processing. *Current Biology* 2002;12(3):233–236. [PubMed: 11839277]
- Tecchio F, Zappasodi F, Tombini M, Caulo M, Vernieri F, Rossini PM. Interhemispheric asymmetry of primary hand representation and recovery after stroke: A MEG study. *Neuroimage* 2007;36(4):1057–1064. [PubMed: 17543542]
- Tinazzi M, Ferrari G, Zampini M, Aglioti SM. Neuropsychological evidence that somatic stimuli are spatially coded according to multiple frames of reference in a stroke patient with tactile extinction. *Neuroscience Letters* 2000;287(2):133–136. [PubMed: 10854730]
- Tsumoto T, Hirose N, Nonaka S, Takahash M. Cerebrovascular disease - changes in somatosensory evoked-potentials associated with unilateral lesions. *Electroencephalography and Clinical Neurophysiology* 1973;35(5):463–473. [PubMed: 4126452]

- Turton AJ, Butler SR. Referred sensations following stroke. *Neurocase* 2001;7(5):397–405. [PubMed: 11744781]
- Valenza N, Seghier ML, Schwartz S, Lazeyras F, Vuilleumier P. Tactile awareness and limb position in neglect: Functional magnetic resonance imaging. *Annals of Neurology* 2004;55(1):139–143. [PubMed: 14705125]
- Weber EH. E.H. Weber on the tactile senses. 1834/1996
- Weiss T, Miltner WHR, Huonker R, Friedel R, Schmidt I, Taub E. Rapid functional plasticity of the somatosensory cortex after finger amputation. *Experimental Brain Research* 2000;134(2):199–203.
- Weiss T, Miltner WHR, Liepert J, Meissner W, Taub E. Rapid functional plasticity in the primary somatomotor cortex and perceptual changes after nerve block. *European Journal of Neuroscience* 2004;20(12):3413–3423. [PubMed: 15610174]
- Whiteley L, Kennett S, Taylor-Clarke M, Haggard P. Facilitated processing of visual stimuli associated with the body. *Perception* 2004;33(3):307–314. [PubMed: 15176615]
- Wikstrom H, Roine RO, Salonen O, Lund KB, Salli E, Ilmoniemi RJ, et al. Somatosensory evoked magnetic fields from the primary somatosensory cortex (SI) in acute stroke. *Clinical Neurophysiology* 1999;110(5):916–923. [PubMed: 10400206]
- Wolpert DM, Goodbody SJ, Husain M. Maintaining internal representations the role of the human superior parietal lobe. *Nature Neuroscience* 1998;1(6):529–533.
- Xerri C, Merzenich MM, Peterson BE, Jenkins W. Plasticity of primary somatosensory cortex paralleling sensorimotor skill recovery from stroke in adult monkeys. *Journal of Neurophysiology* 1998;79(4):2119–2148. [PubMed: 9535973]
- Yamamoto S, Kitazawa S. Reversal of subjective temporal order due to arm crossing. *Nature Neuroscience* 2001;4(7):759–765.
- Yang TT, Gallen CC, Ramachandran VS, Cobb S, Schwartz BJ, Bloom FE. Noninvasive detection of cerebral plasticity in adult human somatosensory cortex. *Neuroreport* 1994;5(6):701–704. [PubMed: 8199341]