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Bilateral representations of touch in the primary somatosensory cortex

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ABSTRACT

According to current textbook knowledge, the primary somatosensory cortex (SI) supports unilateral tactile representations, whereas structures beyond SI, in particular the secondary somatosensory cortex (SII), support bilateral tactile representations. However, dexterous and well-coordinated bimanual motor tasks require early integration of bilateral tactile information. Sequential processing, first of unilateral and subsequently of bilateral sensory information, might not be sufficient to accomplish these tasks. This view of sequential processing in the somatosensory system might therefore be questioned, at least for demanding bimanual tasks. Evidence from the last 15 years is forcing a revision of this textbook notion. Studies in animals and humans indicate that SI is more than a simple relay for unilateral sensory information and, together with SII, contributes to the integration of somatosensory inputs from both sides of the body. Here, we review a series of recent works from our own and other laboratories in favour of interactions between tactile stimuli on the two sides of the body at early stages of processing. We focus on tactile processing, although a similar logic may also apply to other aspects of somatosensation. We begin by describing the basic anatomy and physiology of interhemispheric transfer, drawing on neurophysiological studies in animals and behavioural studies in humans that showed tactile interactions between body sides, both in healthy and in brain-damaged individuals. Then we describe the neural substrates of bilateral interactions in somatosensation as revealed by neurophysiological work in animals and neuroimaging studies in humans (i.e., functional magnetic resonance imaging, magnetoencephalography, and transcranial magnetic stimulation). Finally, we conclude with considerations on the dilemma of how efficiently integrating bilateral sensory information at early processing stages can coexist with more lateralized representations of somatosensory input, in the context of motor control.

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Introduction

One notion that returns in almost every course on the brain, and every textbook of neuroscience or perception, is that the primary somatosensory cortex (SI) receives stimuli primarily or exclusively from the contralateral side of the body and, by extension, that SI is primarily a relay that represents and processes contralateral stimuli. This well-established notion emerged from the classical studies of Fritsch and Hitzig in dogs (Fritsch & Hitzig, 1870) and from the pioneering studies of Penfield and colleagues in humans (e.g., Penfield & Boldrey, 1937). To some extent, this notion is captured also in one of the most reproduced illustrations of neuroscience, the somatosensory homunculus (Figure 1A). Introduced by Penfield and collaborators in 1937, and revised in 1950 and 1954,

the somatosensory homunculus shows anisotropies in the cortical territory dedicated to different body parts. Furthermore, the equally famous version of a human body draped along the primary somatosensory and motor cortices captures the seminal finding of topographic organization of these regions, in which specific areas of the cerebral cortex are linked with specific parts of the body (Penfield & Boldrey, 1937; Penfield & Jasper, 1954; Penfield & Rasmussen, 1950). Notably, although several versions of the homunculus have been depicted over the years (Schott, 1993), the essential information conveyed remained largely unchanged. In particular, the notion that SI receives and represents only contralateral inputs, represented by showing only a hemisoma over the cortex and by showing the two halves of the body clearly separated by the midsagittal

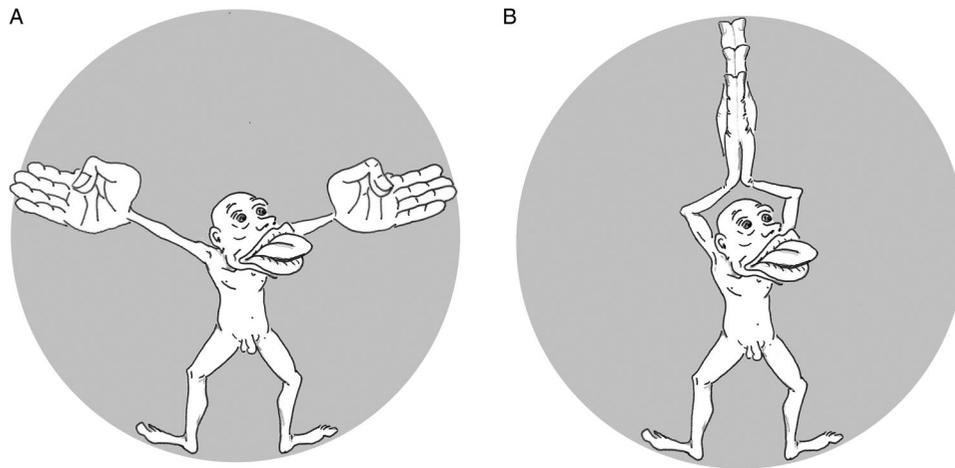


Figure 1. The sensory homunculus representation proposed by Penfield (A) and a new version we propose that highlight the intimate relationships between the two sides of the body (B).

plane (Figure 1A), seems not to be questioned. This depiction reflects and strengthens the notion that interaction of tactile stimuli from the two sides of the body occurs beyond SI, for instance at the level of the secondary somatosensory cortex (SII) or in Brodmann's area 5, areas that are both characterized by dense bilateral afferent projections (Forss, Jousmäki, & Hari, 1995; Hari et al., 1993; Lin & Forss, 2002; Sakata, Takaoka, Kawarasaki, & Shibutani, 1973).

In this paper, we review a series of studies that challenge the notion that SI is uniquely contralateral, and we provocatively suggest that a more appropriate homunculus is the one depicted in Figure 1B, hinting at closer interactions between body sides at processing stages as early as SI, with a particular importance for the hands. We specifically point to the importance of the hands, because the hands are anatomically positioned at the periphery with respect to the body midline and as such have less dense callosal connections relative to the trunk (Iwamura, 2000). Indeed, for other parts closer to the body midline (e.g., the trunk), it is more natural and less surprising, due to denser callosal connections and the presence of bilateral receptive fields, that they show bilateral interactions. Hands, with respect to more central body parts, can move more in space, and can also assume both central and peripheral positions, interact directly with one another, or perform completely different and independent actions.

We begin by describing some of the anatomical bases of interhemispheric interactions, and neurophysiological studies in animals that were the first to suggest bilateral integration of touch in SI. We then

introduce the notion of bilateral tactile interactions, as revealed by behavioural studies of double simultaneous stimulation and sequential stimulation across body sides. Next, we discuss behavioural and neuroimaging evidence that has emerged in the last 15 years in support of the notion that these bilateral interactions occur already in the primary somatosensory cortex. We include contributions from studies of healthy people, neuropsychological patients, and animals. While these studies do not challenge the key notion that SI responds primarily to contralateral stimulation, they call for a new perspective in which SI is seen as a site of integration for bilateral information both at early (i.e., direct ipsilateral thalamo-cortical, and transcallosal cortico-cortical connections) and at later stages (e.g., cortico-cortical interactions with SII) of tactile processing. In the final section, we summarize the ways in which SI can receive ipsilateral afferents from the body, we suggest a possible role of early bilateral integration for behaviour, and we discuss the implications of bilateral tactile representations in SI for the awareness of touch laterality (i.e., knowing which side of the body has been touched). Although we focus on tactile processing, we do not exclude that a similar logic may also apply to other aspects of somatosensation (e.g., pain, heat, or proprioception), and even of movement.

Basic anatomy and neurophysiology of the interhemispheric transfer

The transfer of the neural signals between the two cerebral hemispheres is a fundamental means by which information from the two halves of the brain and

the two sides of the body is integrated and coordinated. This constant signal exchange occurs through several neural channels. The most prominent is the corpus callosum (CC), the largest fibre tract in the brain. In addition to the CC, other structures at the forebrain level are involved in interhemispheric transfer to different extents—most notably, the anterior commissure and the dorsal and ventral hippocampal commissures (Hoptman & Davidson, 1994). Other structures include connections mediated by hypothalamic, supraoptic, habenular, the massa intermedia, and the posterior and collicular commissures (Hoptman & Davidson, 1994; Lamantia & Rakic, 1990). Here, we briefly describe the main properties of the CC, because of its pivotal role in interhemispheric transfer, and in particular in the interactions between the somatosensory areas that are the focus of the present review.

Although there are no clear boundaries, the CC is typically sub-divided into different functional and morphological regions. Following a rostral to caudal order, they are termed: rostrum, genu, midbody, and splenium. The majority of the fibres connect homologous brain regions of the two hemispheres, though connections between non-homologous areas are also present (Clarke & Zaidel, 1994; Kennedy, Meisler, & Dehay, 1991). The knowledge we have about the functional organization of the CC largely derives from lesion studies on patients that underwent partial callosotomy (Gazzaniga, 2005), a surgical procedure performed for the treatment of seizures to prevent spreading of the epileptic activity from one hemisphere to the other (Van Wagenen, 1940). The anterior part of the CC primarily connects the prefrontal lobes, whereas the middle part (i.e., midbody) connects the primary and secondary auditory, somatosensory, and motor areas. The area between the midbody and splenium (i.e., isthmus) specifically mediates transfer from motor, somatosensory, and primary auditory areas (Aboitiz, Scheibel, Fisher, & Zaidel, 1992; Fabri et al., 2005). Recently, a tractography study has compared the diameter, length, speed, and conduction delay of callosal axons of macaque monkeys and humans. The results showed many similarities in the functional organization of the information transfer in the two species (Caminiti et al., 2013).

The presence of callosal connections between primary and secondary somatosensory cortices has

been reported in several species (Krubitzer, Clarey, Tweedale, & Calford, 1998; Krubitzer & Kaas, 1990). For instance, studies in marmoset and macaque monkeys have shown callosal connections between homotopic regions of SI areas 3b and 1 (Conti, Fabri, & Manzoni, 1986), as well as heterotopic connections between SI and SII (Manzoni, Conti, & Fabri, 1986). Interestingly, there is evidence that callosal connections between the SII hand regions are stronger (i.e., more numerous) than the callosal connections between SII and SI across hemispheres. Connections between SII of the two hemispheres have been shown to be present also in other animals such as cats (Barbaresi, Bernardi, & Manzoni, 1989; Caminiti, Innocenti, & Manzoni, 1979), tree shrew (Weller, Sur, & Kaas, 1987), and squirrels (Krubitzer, Sesma, & Kaas, 1986).

Although several possible callosal routes connect SI and SII of the opposite hemispheres, it is still unclear how the CC mediates the information transfer and what is the nature of the communication. Two accounts have been proposed, one inhibitory and the other excitatory (for reviews see Bloom & Hynd, 2005; van der Knaap & van der Ham, 2011). The inhibitory account proposes that the CC maintains independent processing of information in both hemispheres, preventing spreading of activity across the CC and supporting lateralized representations. Instead, the excitatory account proposes that the CC integrates information between the two hemispheres, decreasing laterality effects by reducing hemispheric differences. Reduced lateralized representation might, for instance, be beneficial in tasks requiring interhemispheric transfer (Clarke & Zaidel, 1994). Generally, one might hypothesize that interhemispheric interactions (i.e., inhibitory or excitatory) vary as a function of task demands (Hellige, 1993). Therefore, depending on task demands, the CC might have in some circumstances an inhibitory effect, whereas in others it has an excitatory function. In this respect, it has been shown that the type of interactions (excitatory or inhibitory) between the human motor cortices (left and right M1) depends on the intensity and latency (transcranial magnetic stimulation, TMS, delivered on the motor cortex of one compared to the other hemisphere) of the TMS (Ferbert, Caramia, Priori, Bertolasi, & Rothwell, 1992). Therefore, some authors suggested that CC is not merely a passive conduit of information, but rather an active structure that contributes to the

exchange of signals of different nature between the hemispheres (Banich, 1995).

Neurophysiological studies in animals have been the first to challenge the notion that neural representations of the body in SI are purely contralateral (Sutherland, 2006), providing support to the idea that integration of touch between the two sides of the body can occur also in primary somatosensory areas. In rats, it has been demonstrated that SI can integrate inputs from the contralateral and ipsilateral whisker pads (Shuler, Krupa, & Nicolelis, 2001). In particular, Shuler et al. (2001) found that the neuronal responses in SI of one hemisphere (e.g., contralateral) after whisker pad stimulation were affected by a previous stimulus that reached the other hemisphere (e.g., ipsilateral). This effect was modulated as a function of the spatial location and the relative timing at which the whisker stimuli were presented. In macaque monkeys (*Macaca fuscata*), bilateral receptive fields have been found in somatosensory area 2, which is considered to be the homologue of Brodmann's area 2 in human SI (Iwamura, Tanaka, Iriki, Taoka, & Toda, 2002; Iwamura, Taoka, & Iriki, 2001). Moreover, interhemispheric interactions (i.e., inhibitory or excitatory) in SI have also been revealed within area 3b of monkeys (Lipton, Fu, Branch, & Schroeder, 2006; Reed, Qi, & Kaas, 2011; Reed et al., 2010). Using functional magnetic resonance imaging (fMRI) and electrophysiology to investigate the hand representation in SI (area 3b) of macaque monkeys, Lipton et al. (2006) found bilateral responses at this early stage of cortical somatosensory processing. In particular, these authors reported a clear haemodynamic response in ipsilateral areas 1, 2, and surprisingly also 3b of SI. Furthermore, they demonstrated that the ipsilateral inputs in SI were mainly inhibitory (Lipton et al., 2006). Callosal connections between the two sides of the body are present mostly in the most proximal regions (e.g., trunk, face), although, to a lesser degree, are also present for the more distal regions of the body such as hands and fingers (Iwamura, 2000; Killackey, Gould, Cusick, Pons, & Kaas, 1983; Lipton et al., 2006).

Interactions between tactile stimuli on the two body sides

The notion that the processing of tactile stimuli delivered to opposite body sides can interact is neither new nor questioned. Studies using paired double

simultaneous stimulation or sequential stimulation across body sides have documented these interactions in healthy humans starting from the 1960s (e.g., Craig, 1968; Gescheider & Wright, 1968; Gilson, 1969; Sherrick, 1964; Uttal, 1960). For instance, using the von Békésy tracking technique to measure vibrotactile thresholds, Sherrick (1964) showed that interference during double simultaneous stimulation within the same hand was greater when the masker and the target were on the same finger (e.g., right index) than when they were on different fingers (e.g., right index and little). Notably, interference was also present when the masker and the target were on fingers of different hands, albeit to a lesser degree (Sherrick, 1964). Later studies provided further support to the notion of competition between tactile stimuli delivered to different hands. Gescheider, Herman, and Phillips (1970) reported masking when fingers of the two hands were stimulated together (Gescheider et al., 1970). Laskin and Spencer (1979), using the method of limits, showed that tactile stimuli delivered to identical sites of the two hands produced a small but reliable interference effect. Importantly, in agreement with an account of interhemispheric interactions that vary as a function of task demands (Hellige, 1993), there is also evidence for between-hands interactions that improve, rather than worsen, tactile performance. For instance, Craig (1985) asked participants to identify a vibrotactile pattern on a series of nine tactile arrays (6 columns \times 24 rows) presented to fingers of the same hand (i.e., middle and index) or fingers of different hands (i.e., right and left index fingers). He found that performance improved when the pattern was presented to different hands, compared to the within-hand condition (Craig, 1985).

The notion that the processing of tactile stimuli across body sides can interact has also been supported by neuropsychological evidence in brain-damaged patients, starting from the 1940s. Clear examples of bilateral interactions in tactile processing are cases of tactile extinction, in which patients are able to detect a single stimulus presented to the ipsilesional or contralesional side of the body, but fail to report the contralesional stimulus when it is paired with a concurrent stimulus on the ipsilesional side (Bender, 1945). Other neuropsychological examples of bilateral tactile interactions have emerged as mislocalization or reduplication phenomena occurring

across body sides when in fact the stimulation was delivered to a single body part. Mislocalization of tactile sensations across body sides has been termed “allochiria” (from ancient Greek “allos” meaning other, and “cheir” meaning hand; i.e., on the other hand), whereas reduplication has been termed “synchiria” (from ancient Greek “synkhoros” meaning at the same time, and “cheir” meaning hand; i.e., at the same time on both hands). Examples of allochiria have been described in arm amputees and brain-damaged patients with hemiparesis and hemisensory loss. These patients can report contralateral referral of tactile sensations to the phantom body part (Ramachandran, Rogers-Ramachandran, & Cobb, 1995) or to the hand rendered anaesthetic by stroke (Sathian, 2000). A striking case of tactile synchiria—a much rarer phenomenon than allochiria—has been reported by Medina and Rapp (2008). They described an individual with left fronto-parietal damage who experienced bilateral tactile sensations after unilateral stimulation (Medina & Rapp, 2008). The authors attributed this phantom sensation to a normal interhemispheric interaction, combined with a deficit of the inhibitory mechanisms that normally impede the bilateral percept. This intriguing interpretation supports the hypothesis that unilateral stimulation may in fact produce bilateral signals, whose ipsilateral component is inhibited under normal circumstances.

Tactile interactions between body sides change along the proximal–distal axis. A recent example of this is provided by Tamè and Longo (2015), who showed that sensorimotor integration is modulated by the body part stimulated, when using the Poffenberger paradigm (Poffenberger, 1912). This classic behavioural paradigm has been employed to quantify sensorimotor transfer between hemispheres. It is based on the fact that people have faster reaction times (RTs) when sensory stimuli (e.g., visual, tactile, or auditory) are presented in the hemi-field or hemi-body ipsilateral (“uncrossed”) to the hand used to respond than contralaterally (“crossed”). It has been proposed that this crossed–uncrossed difference (CUD) reflects the time required for signals to transfer between the two cerebral hemispheres. The logic of the Poffenberger paradigm is that when the sensory stimulus and motor effector are on the same side of the body, sensorimotor information can be integrated and processed within the same hemisphere (uncrossed). By contrast, if sensory input is presented

contralateral to the effector used to respond, the information has to be integrated across hemispheres (crossed). The magnitude of the crossed–uncrossed difference in processing time was larger on the finger (~2.6 ms) and forearm (~1.8 ms) than on the forehead (~0.9 ms). This small but consistent difference is compatible with the distribution of the callosal connections and the density of bilateral receptive fields (RFs) between the regions that represent the body from the periphery to the centre (Caminiti & Sbriccoli, 1985; Iwamura et al., 2001; Pandya & Vignolo, 1969). To date, there have been only a few attempts to extend the study of bilateral tactile interactions to body parts other than the hands (see also the behavioural and neuroimaging studies described in the following sections), and the hypothesis that stronger bilateral interactions should emerge when stimuli are delivered to more medial parts of the body remains largely unexplored. Two recent exceptions are the studies by D’Amour and Harris, which examined bilateral tactile interactions for stimuli delivered to the forearm (D’Amour & Harris, 2014a) or the stomach (D’Amour & Harris, 2014b). Their results, unexpectedly, revealed interactions between body sides when a masker and a target were delivered to opposite forearms, but not when they were delivered to the stomach. This suggests that bilateral interactions may occur differently along the proximal–distal dimension.

For the purpose of the present review, the most relevant issue is the extent to which these bilateral interactions in touch can be attributed to processing occurring in SI, traditionally associated with processing of contralateral touch alone. Although behavioural studies cannot provide direct evidence to answer this question, there is one key feature of tactile processing in SI that has often been used as a signature of its potential involvement, namely somatotopy (Braun et al., 2011). From the pioneering work of Penfield and colleagues to more recent high-field fMRI studies on tactile processing in somatosensory cortices (e.g., Martuzzi, van der Zwaag, Farthouat, Gruetter, & Blanke, 2012; Sanchez-Panchuelo, Francis, Bowtell, & Schluppeck, 2010), strong somatotopic organization has been described in SI more than in SII (e.g., Del Gratta et al., 2002; Ruben et al., 2001). Although the extent to which areas beyond SI actually retain some form of somatotopy is still a matter of debate (Ruben et al., 2001), changes in bilateral

tactile interactions as a function of somatotopy have often been considered a distinctive signature of SI involvement (e.g., Harris, Harris, & Diamond, 2001; Tamè, Farnè, & Pavani, 2011). By contrast, bilateral tactile interactions that are less or not at all somatotopically organized have been conceived as more compatible with bilateral processing occurring in higher somatosensory areas (e.g., SII or Brodmann's area 5). This logic has been adopted in several previous behavioural studies when making inferences about the neural correlates of bilateral interactions in tactile processing (Dempsey-Jones et al., 2015; Harrar, Spence, & Makin, 2013; Harris et al., 2001; Harris, Miniussi, Harris, & Diamond, 2002; Tamè et al., 2012; Tamè, Pavani, Papadelis, Farnè, & Braun, 2015).

Studies that took advantage of this distinctive SI feature to explore the interactions between stimulated body sides typically contrasted conditions in which touch occurred on *homologous* versus *non-homologous* body parts across body sides. The left and right index fingers are homologous, whereas the left index finger and right middle finger are non-homologous body parts. This somatotopic aspect of bilateral interactions in touch remained mostly unexplored in the earlier behavioural reports on healthy humans and neuropsychological patients, which tested, almost exclusively, homologous parts of the two sides of the body, but it has been addressed more systematically in the last 15 years (e.g., Harris et al., 2001; Tamè et al., 2011). Other indications of potential SI involvement might emerge when considering the different outcomes of different behavioural tasks. For instance, there is evidence that SI may be more critically involved in tasks requiring tactile frequency discrimination (Hernández, Zainos, & Romo, 2000; Tan, Wühle, & Braun, 2004) than in tasks requiring simple detection of stimuli at threshold (Romo, Lemus, & de Lafuente, 2012). Monkeys who underwent SI ablation can recover detection of tactile stimuli much better than tactile discrimination abilities (LaMotte & Mountcastle, 1979). Similarly, Tamè and Holmes (2016) have shown that, depending on the task demand, TMS over SI in humans affects tactile discrimination, but not tactile detection. In particular, TMS disrupts participants' performance in a tactile detection task when using a one-interval forced-choice (1IFC) design, but not when using a task that is both criterion free and minimally demanding in terms of working memory, such as a two-interval forced-choice (2IFC) design. In the 2IFC task, participants are asked to

detect in which of two successive intervals the near- or supra-threshold target stimulus is presented. This entails a relatively low memory load, as the participant is reminded of the target stimulus in every single trial, and only has to hold information about the (typically very weak) target across the two intervals. By contrast, in the 1IFC task, participants are asked to detect the presence of a stimulus that may or may not occur in each trial. This task potentially entails a higher cognitive load (Harris, Karlov, & Clifford, 2006), may be more influenced by response biases (Campion, Latto, & Smith, 1983), and may rely to a greater extent on memory for what the target stimulus feels like. Near threshold, tactile targets are by definition difficult to perceive, and distinguishing the target from background noise and cardiovascular artefacts requires a clear representation of the target—an "internal standard" (Morgan, Watamaniuk, & McKee, 2000). It has been proposed that SI contributes to 1IFC tasks to a greater extent than to 2IFC tasks (Tamè & Holmes, 2016). Finally, perceptual learning tasks are typically associated with processing occurring in primary sensory cortices (Harris et al., 2001). Therefore, the nature of the behavioural task may also be useful for estimating SI contribution in bilateral tactile interactions.

In the next section we discuss behavioural studies that examined bilateral interactions in touch for homologous versus non-homologous body parts. We consider indirect evidence of SI involvement in those studies in which bilateral tactile interactions were modulated as a function of homology—hence by somatotopy. In addition, with the purpose of facilitating possible links between indirect evidence of SI involvement and the nature of the task, we have grouped the behavioural studies as a function of the complexity of the adopted task (detection, localization, and discrimination).

Indirect evidence for bilateral interactions in SI: Behavioural studies

Tactile detection

The effects of body part homology across different body sides on simple tactile detection have been explored only quite recently (D'Amour & Harris, 2014a; Tamè et al., 2011; Tamè, Farnè, & Pavani, 2013). These studies have adopted one of two approaches: two- or one-interval forced-choice (2IFC

or 1IFC, respectively) detection tasks, also known as alternative forced-choice design.

Using the 2IFC task, Tamè, Moles, and Holmes (2014) investigated whether tactile detection thresholds for stimuli on a pre-specified target finger can be modulated by a simultaneous tactile masker applied on the same hand or on the other hand (Tamè et al., 2014). Importantly, this study aimed to determine whether the interactions between the concurrent touches followed a somatotopic organization, within and between the hands. When stimuli were delivered within the same hand, results showed that detection thresholds increased as a function of the distance between the masker and the target finger. For instance, when the target was at the index finger, a masker delivered at the adjacent middle finger produced more interference than a masker delivered at the ring finger. By contrast, when the target and masker stimuli were delivered one on each hand, the target detection threshold increased regardless of which fingers received the masker stimulation (Tamè et al., 2014). These results indicate that between-hands interactions in the 2IFC task do not follow a somatotopic organization and as such may not be primarily mediated by SI processing.

A 2IFC task was also adopted by D'Amour and Harris (2014a, Experiment 2), who measured tactile sensitivity on the left forearm while the tactile masker (supra-threshold) was applied on a homologous (right forearm) or non-homologous location (wrist, elbow, upper arm) on the right side of the body. Unlike Tamè et al. (2014), they found that tactile sensitivity was strongly reduced when the masker was presented at homologous or near-homologous locations (forearm and elbow), whereas maskers at non-homologous locations (wrist and upper arm) produced much weaker threshold changes (D'Amour & Harris, 2014a). This effect of homology suggests a potential involvement of SI in the interaction, considering that strong somatotopic organization has been described in SI more than in SII (e.g., Del Gratta et al., 2002; Ruben et al., 2001). The discrepancy between these results may derive, at least in part, from the fact that tactile stimuli are interacting differently when occurring on the hands compared to other parts of the body.

Using the 1IFC task, Tamè et al. (2011) asked participants to detect tactile stimuli at a pre-defined target finger that was stimulated alone or concurrently

with another finger, either on the same or on the opposite hand. For instance, when the target finger was the right index, the concurrent stimulation was presented to the middle finger of the same hand, or alternatively to the index or middle finger of the other hand. Results showed interference effects from the concurrent tactile stimulation both within and between hands. Most interestingly, the interference was more dependent upon the identity of the stimulated body-part (i.e., which finger was touched) than body-side (i.e., which hemibody was touched). Interference was comparable when the distracting stimulation was on the non-homologous finger of the same hand, and when it was on the non-homologous finger of the opposite hand with respect to the target. By contrast, when the distracting stimulus was applied to the homologous finger of the opposite hand, the amount of interference was considerably reduced.

Taken together, these studies on simple detection confirm that interactions in tactile processing across body sides can occur both at the hands and at the forearm, with initial indications of a somatotopic organization of this interaction (D'Amour & Harris, 2014a; Tamè et al., 2011, i.e., possible SI involvement). Moreover, the different types of interaction between stimuli on the two sides of the body when a 1IFC compared to a 2IFC design is used suggests that the type of approach adopted can be useful to identify the structures mediating the tactile processing—the level of SI involvement depends upon the specific task demands (Tamè & Holmes, 2016).

Tactile localization

Several studies have examined tactile localization in the context of double simultaneous stimulation or sequential stimulation (Benedetti, 1988; Braun, Hess, Burkhardt, Wühle, & Preissl, 2005; Harris et al., 2006; Harris, Thein, & Clifford, 2004; Schweizer, Braun, Fromm, Wilms, & Birbaumer, 2001; Schweizer, Maier, Braun, & Birbaumer, 2000). Tactile localization within the same hand has been examined using near-threshold tactile stimuli delivered to the fingertips and measuring the pattern of erroneous localization responses (i.e., mislocalizations; Schweizer et al., 2000). Notably, mislocalizations were predominantly to fingers neighbouring the stimulated ones, reflecting the somatotopic organization of SI (Schweizer et al., 2000).

Two studies have examined the extent to which tactile mislocalizations within a hand can be affected by stimuli delivered to the other hand. The first study, conducted by Schweizer et al. (2001), used a tactile training procedure to alter the profile of tactile mislocalization. Participants underwent 20 hours of simultaneous stimulation of the left thumb and left little finger in the context of a perceptual task—the occasional discrimination of tactile stimulus direction. After the training, changes in the profile of mislocalizations were observed only within the trained hand, but not in the untrained hand. A second study used simultaneous bilateral tactile stimulation to investigate whether stimulation delivered to one hand can modify the profile of tactile mislocalization at the other hand. More specifically, Braun et al. (2005) applied supra-threshold interference stimuli on the left thumb or little finger, either 200 or 500 ms prior to presenting a near-threshold test stimulus on the right hand. Results showed that stimuli applied on the left hand strongly interfered with the localization profile of the opposite right hand. Moreover, this interaction occurred in a finger-specific manner. This pattern of results implies that interactions between stimuli on the two hands follow a somatotopic organization, which constitutes evidence for the involvement of SI in the processing of tactile information.

In sum, it appears that it is possible to alter the profile of touch localization at one hand by delivering concurrent tactile stimulation at the other hand. This kind of interaction is finger specific and follows a somatotopic organization, suggesting that SI representing the interference stimuli may at some stage be involved in the processing of the near-threshold stimuli applied to the other hand.

Tactile discrimination

Discrimination tasks require participants to report which stimulus was presented, instead of noticing only whether or when it occurred. As such, tactile discrimination tasks entail more complex processing than simple detection tasks (particularly 2IFC detection tasks). A number of studies used tactile discrimination to investigate tactile perceptual learning in humans and other animals (Dempsey-Jones et al., 2015; Harrar et al., 2013; Harris & Diamond, 2000; Harris et al., 2001; Sathian & Zangaladze, 1997). Generally, these reports show somatotopically specific transfer of tactile learning between the two sides of the body.

For instance, Harris et al. (2001) trained human participants to discriminate punctate pressure or roughness stimuli on one finger of the right hand (e.g., the index) and found that training transferred to the first neighbouring finger of the same hand (i.e., the right middle finger) as well as to the homologous finger of the other hand (i.e., the left index finger). Instead, no training transfer emerged for the non-homologous fingers of the opposite hand (Harris et al., 2001; for earlier reports on perceptual learning see Sathian & Zangaladze, 1997, 1998). On the basis of these results showing that tactile learning transfers to the homologous digit on the opposite hand, Allerton and colleagues recently examined whether a 3-s adaptation to a 200-Hz vibrotactile stimulus would also spread within and between hands (Allerton et al., 2016). The QUEST adaptive staircase algorithm was used to measure amplitude discrimination thresholds on four different fingers (for a similar approach see Tamè et al., 2014). Thresholds were measured both with and without a prior vibrotactile adaptation stimulus delivered to the middle finger of one hand. Amplitude discrimination at the adapted site significantly improved after the adaptation stimulus; however, discrimination was significantly *impaired* in the unadapted homologous (middle) finger on the opposite hand and was unchanged in the unadapted non-homologous (ring) fingers on either hand. These results suggest that the areas receiving vibrotactile inputs process information from homologous fingers on the two hands differently over information from non-homologous fingers on the same hand (Allerton et al., 2016). On the same line, Dempsey-Jones et al. (2015) have shown that improved tactile acuity deriving from tactile perceptual learning is transferred differently to fingers that are physically and cortically adjacent to the trained finger (Dempsey-Jones et al., 2015).

A similar protocol was also tested previously in animals. For instance, Diamond, Petersen, and Harris (1999) trained rats to use sensory information from a whisker to perform a behavioural task. Afterwards, they clipped the trained or an untrained whisker and attached a “prosthetic” whisker instead. They found that the rats were able to use the prosthetic whisker immediately when it was attached to the trained, but not if it was attached to the untrained whisker. Moreover, the greater the distance between the trained and the prosthetic whisker, the greater the time needed to re-learn the task. The authors related

this learning transfer between whiskers to the whiskers' representations in SI (Diamond et al., 1999). In a further study, the same authors extended this finding by showing that the transfer of learning occurred also between whiskers located on the homologous part of the opposite side (Harris & Diamond, 2000).

In sum, studies adopting tactile discrimination procedures are consistent in showing interactions between hands that follow a profile indicative of somatotopy. When coupled with the proposal that discrimination tasks may be particularly associated with SI processing (Hernández et al., 2000; Tamè & Holmes, 2016), this body of evidence provides convergent indirect support in favour of the involvement of SI in bilateral tactile interactions.

Neuropsychological studies in extinction patients

Different types of interactions between tactile stimuli on the two sides of the body are also documented in neuropsychological studies on patients showing tactile extinction. For instance, Gainotti, De Bonis, Daniele, and Caltagirone (1989) tested several patients with right and left brain damage. They delivered double simultaneous stimulation both on symmetrical and on asymmetrical parts of the two sides of the body to evaluate contralateral and ipsilateral tactile extinction (Gainotti et al., 1989). Unfortunately, the authors did not report whether the magnitude of tactile extinction varied as a function of body part homology. While the role of homology in tactile extinction remains to be systematically investigated, it is interesting to note that some of the findings from the related phenomenon of cross-modal extinction are somewhat in support of bilateral interactions sensitive to homology of the stimulations.

Mattingley, Driver, Beschin, and Robertson (1997), in three patients with right-hemisphere damage, found that tactile extinction was present also across modalities—namely, vision and touch. Interestingly, the authors used homologous or non-homologous spatial locations for the bilateral stimuli. In both cases, patients exhibited cross-modal extinction, though for the homologous position it was greater. Compatibly, Làdavvas et al. (1998) reported a mild cross-modal extinction for touches at the left-hand effect when the visual stimulus was presented at the level of the patients' right eye (i.e., a non-homologous condition). The issue of homology has been

investigated more systematically both at the unisensory (tactile) and at the cross-modal (visual–tactile) level by Farnè, Demattè, and Làdavvas (2005), though across relatively “distant” body-parts—the hand and the face. Tactile extinction patients were presented with combinations of ipsilesional and contralesional tactile (or visual–tactile) stimuli, both between homologous body parts (i.e., the two hands and sides of the face) and between non-homologous body parts (i.e., right hand & left face; right face & left hand). Tactile extinction was not significantly affected by homology, possibly because the sample of patients was relatively small. Yet, the pattern of visual–tactile extinction observed in the near peripersonal space of homologous body parts was more severe than that obtained between non-homologous body parts. In contrast, cross-modal extinction observed in the far peripersonal space was overall weak and comparable when stimulating homologous or non-homologous body sectors. In addition, a clear near–far modulation of visual–tactile extinction was obtained only when stimulating homologous, but not non-homologous, body parts. Overall, these data on neuropsychological patients converge in suggesting that interactions between stimuli on the two sides of the body can vary as a function of body part homology.

Direct evidence for bilateral interactions in SI: Brain imaging studies

Although several of the behavioural studies described in the previous section are suggestive of a potential SI involvement in bilateral tactile processing, direct evidence in support of this can only emerge from studies that measured neural activity while examining interactions between different body sides.

In humans, neuroimaging studies using fMRI and magnetoencephalography (MEG) have provided evidence of bilateral interactions in SI (Hlushchuk & Hari, 2006; Kakigi, 1986; Kakigi & Jones, 1985; Sutherland & Tang, 2006; Tan et al., 2004; Tommerdahl, Simons, Chiu, Favorov, & Whitsel, 2006). In a recent study, we examined the contribution of SI and SII to the spatial coding of touch at the fingers of the same or different hands, taking advantage of the fMRI adaptation paradigm (Tamè et al., 2012). The adaptation paradigm relies on the hypothesized decrement of a neuronal response that results from the repeated presentation of a stimulus feature to

which the neurons are selective. For present purposes, the first, “adaptor” stimulus could be a touch on the left hand or the right hand, while the second, “probe” stimulus could be a touch on the left hand. Between-hands adaptation would be shown when the response to the probe stimulus is lower if preceded by an adaptor on the other hand than when presented alone.

We examined adaptation when successive vibrotactile stimuli were delivered to the same or to different body parts (index or middle fingers), either on the same or on different body sides (left or right hands). We expected finger-specific adaptation in SI, which holds a strong somatotopic representation, and possibly to a lesser extent also in SII. We found that both SI and SII adapted more strongly when the stimulation was applied over homologous than non-homologous fingers, thus showing that both these brain regions can distinguish between the different fingers. Crucially, we found that stronger adaptation to homologous than non-homologous finger stimulation, both in SI and in SII, emerged even when the touched fingers belonged to different hands (Figure 2A). This result implies that both SI and SII can integrate ipsilateral and contralateral signals originating from the hands. Despite the prominent contralateral response of SI, this approach has proven sufficiently sensitive to reveal changes in activity in the somatosensory cortices following bilateral tactile stimulation.

In one study, Tamè, Pavani, Papadelis, et al. (2015) used MEG in the context of the same tactile adaptation paradigm, to overcome the limited temporal resolution of fMRI and to determine whether the integration of contralateral and ipsilateral tactile information in SI occurred at early or late stages of tactile processing. While recording the neuromagnetic activity to a fixed tactile stimulus, we delivered a brief tactile adaptor on the same (i.e., homologous) or different (i.e., non-homologous) finger with respect to the probe. Using a dipole source modelling approach, we characterized the well-known stimulus-specific activity in SI and SII. We then computed the percentage of repetition suppression (i.e., the reduction in activity for the probe relative to the adaptor stimulus) for the different dipole sources as a function of different adaptor stimuli and for different timings of the adaptor relative to the probe. Crucially, the adaptor was delivered on the same hand as the probe (i.e., unilateral stimulation) or on the other

hand (i.e., bilateral stimulation). Adaptor and probe stimuli were either presented simultaneously or with a 25- or 125-ms delay. The results showed that when the adaptor and probe were on different hands, repetition suppression was somatotopically constrained, as it was larger for stimulation of homologous than non-homologous fingers. Importantly, repetition suppression occurred in SI at short delays between adaptor and probe. During bilateral stimulation, repetition suppression emerged when adaptor and probe were separated by 25 ms, but not when they were separated by 125 ms. Because the temporal integration window is short in SI (Mauguière et al., 1997) and long in SII (Wühle, Preissl, & Braun, 2011) Tamè, Pavani, Papadelis, et al. (2015) suggested that selective interaction for short delays is more compatible with interactions occurring within SI, rather than top-down modulations via higher level processing. This temporal profile of the response pattern in SI under bilateral stimulation reveals that, differently from previous reports (Chung et al., 2014; Jung et al., 2012), responses to bilateral touch cannot solely be ascribed to higher stages of processing, such as SII, because the suppression occurs very early in time (i.e., short delay, 25 ms). This result is compatible with the notion that somatosensory inputs from opposite body sides can interact at early stages of tactile processing, most likely through transcallosal pathways connecting SI in the two hemispheres (Figure 2B).

Other studies on healthy humans using electroencephalography (EEG) provided further evidence of early interactions of tactile stimuli from the two sides of the body at the level of SI. For instance, Ragert, Nierhaus, Cohen, and Villringer (2011) proposed the existence of interactions between ipsilateral and contralateral SI after unilateral median nerve (MN) stimulation in an interval ranging between 20 and 25 ms post stimulus (Ragert et al., 2011). In this EEG study, the authors determined SI activity by looking at the effect of an adaptor stimulus on a probe stimulus, delivered on different hands, while varying the inter-stimulus interval. In this way, they were able to estimate the necessary time for the neural activity from one side of the body to reach the other. Having two stimuli on different sides of the body allowed them to estimate the effect of the ipsilateral activity (i.e., adaptor stimulus) on the contralateral activity (i.e., probe stimulus). Moreover, Korvenoja et al. (1995) reported ipsilateral SI activation in five of their 10 participants, in a

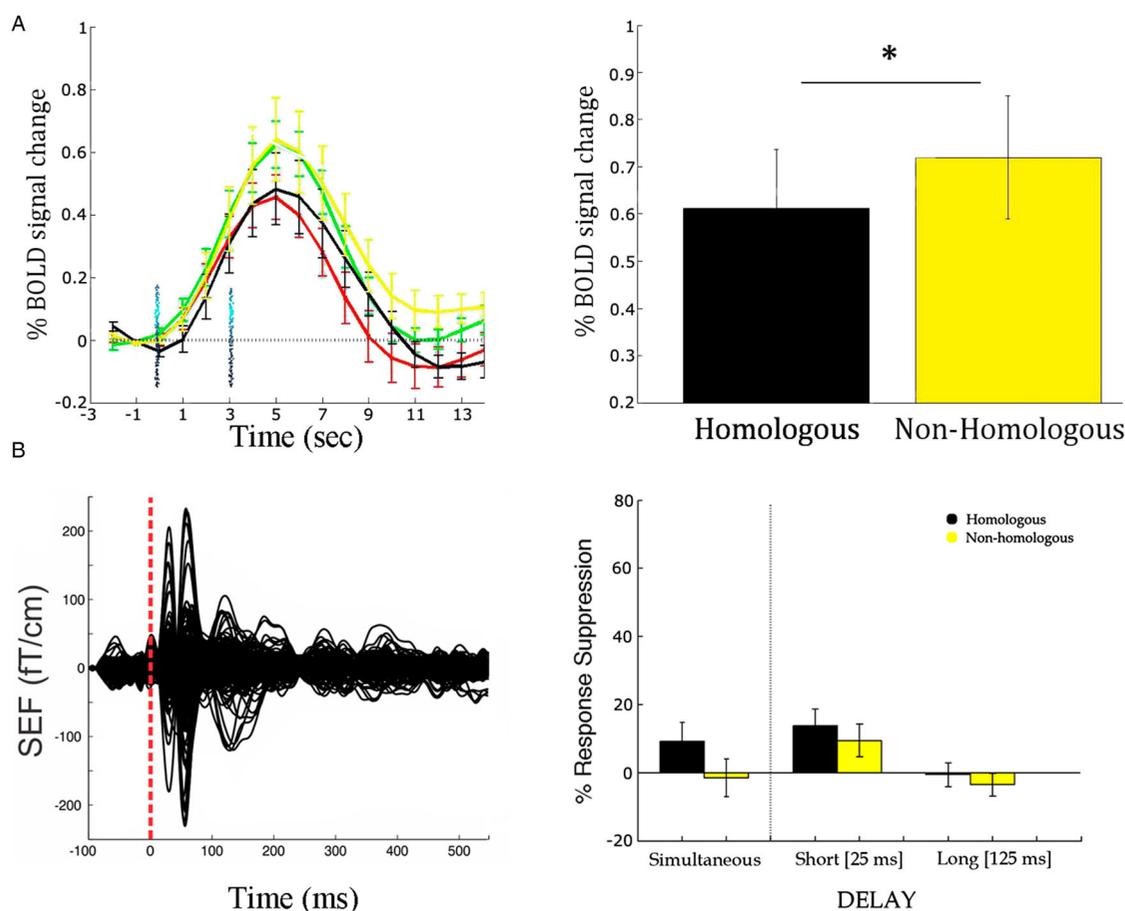


Figure 2. (A) Event-related averaging and the mean percentage of blood-oxygenation-level-dependent (BOLD) signal change from the baseline in the four vibrotactile stimulation conditions in the primary somatosensory cortex (SI). The vertical dotted lines represent the onset time of the first (adaptor) and second (test) stimuli (left panel). Percentage of BOLD signal change of the peak of activation (right panel). Adapted from Tamè et al. (2012). © 2012 by the Massachusetts Institute of Technology. (B) Somatosensory evoked fields (SEF) for the single finger stimulation (150 trials) for the contralateral index and middle fingers (left panel). Percentage of response suppression of the dipole activity in SI when the test stimulus was preceded by an adapting stimulation on the homologous (Ri-Li, black/dark bars) and non-homologous (Rm-Li, yellow/grey bars) finger of the opposite hand simultaneously (Sim), with a short interval of 25 ms (short) and with a long interval of 125 ms (long; right panel). Adapted from Tamè, Pavani, Papadelis, et al. (2015). © 2015 by John Wiley and Sons. Error bars represent the standard errors of the mean ($\pm SEM$). [To view this figure in colour, please see the online version of this journal.]

window of 80 to 300 ms after MN stimulation, although the ipsilateral response was weaker than the contralateral one (Korvenoja et al., 1995). Coherently, neuropsychological studies in patients revealed the presence of ipsilateral neural activity at the level of SI under unilateral tactile stimulation. In this respect, Nevalainen et al. (2012) used MEG to study adolescents with cerebral palsy (CP). CP is a range of permanent movement disorders that occur in early childhood, caused by an early lesion to the developing brain. This condition induces profound reorganization of the motor system that may also extend to the somatosensory system, involving both the ipsi- and contralesional brain. Moreover, alterations in the somatosensory system extend

well beyond the lesioned area, often involving the two hemispheres. Nevalainen et al. (2012) reported the presence of ipsilateral responses in SI more often than in the control groups under MN stimulation. Interestingly, these ipsilateral SI responses emerged with longer latencies than did the contralateral ones (Nevalainen et al., 2012). In a study on two patients with severe left brain damage, Kanno, Nakasato, Nagamine, and Tominaga (2004) reported equivalent current dipoles of ipsilateral responses over the central sulcus after right MN stimulation. The dipole locations for right MN stimulation were adjacent to the location of the N20 in response to left MN stimulation (Kanno et al., 2004). Similarly, Zhu, Disbrow, Zumer, McGonigle,

and Nagarajan (2007), studying the spatiotemporal integration of tactile information using high-resolution MEG in a digit oddball paradigm, reported early ipsilateral responses (i.e., 10 ms later than the contralateral response) in the anterior parietal field (Zhu et al., 2007). This early ipsilateral response suggests that anterior parietal fields can receive tactile input from the ipsilateral hand.

In sum, the direct evidence we described from neuroimaging and neuropsychological research in humans is consistent in supporting the notion of a bilateral integration of tactile stimuli in SI at the early stages of tactile processing.

Discussion

The aim of this review was to present the case for the integration of touch across body sides at the level of primary somatosensory cortex. After a brief review of existing neuroanatomical and neurophysiological studies in animals, we then described indirect behavioural evidence in humans, providing valuable indications about the involvement of the primary somatosensory cortex in the integration of bilateral touch. In particular, we highlighted two features that point to a contribution of SI in bilateral tactile processing. First, we considered the characteristic somatotopic organization of SI, which should modulate bilateral tactile interactions when the homology of stimulation across body sides is considered. Second, we examined the different contributions of SI to different experimental tasks (i.e., detection, localization, and discrimination), which have the potential to distinguish between bilateral interactions involving SI and bilateral interactions that occur at higher stages of the tactile processing (e.g., SII or BA5). Finally, we reviewed the more direct evidence of bilateral tactile integration in SI, coming from neuroscientific studies in humans.

In this concluding section we now discuss two key issues related to the notion of bilateral tactile integration in SI. First, how does SI receive tactile inputs from both body sides? Second, how could a bilateral representation of touch in SI contribute to motor control? In this respect, it is noteworthy that postural changes constitute an important source of variability in bilateral tactile interactions. These postural effects on bilateral integration of tactile stimuli are also discussed below.

Anatomical pathways serving bilateral integration in SI

Multiple anatomical pathways could mediate the integration of tactile stimuli across body sides (Sutherland, 2006). Three possible anatomical pathways—which are not mutually exclusive—are schematically illustrated in Figure 3. A first possibility (direct ipsilateral projections) relies on projections from the receptor surface to ipsilateral SI, which run in parallel to the ones targeting contralateral SI (Kanno, Nakasato, Hatanaka, & Yoshimoto, 2003; Kanno et al., 2004), and which are mediated by uncrossed afferent fibres (Noachtar, Lüders, Dinner, & Klem, 1997). A second possibility (SI–SI transcallosal projections) is that SI receives ipsilateral somatosensory inputs from contralateral SI, via transcallosal fibres (Allison, McCarthy, Wood, Williamson, & Spencer, 1989; Caminiti et al., 2013; Fabri et al., 2005; Fabri et al., 2001; Fling, Benson, & Seidler, 2013). Finally, a third possibility (SII–SII or SII–SI transcallosal projections) is that cortico-cortical modulations of SI could also emerge via transcallosal connections between homologous SII regions or from heterotopic SII and SI regions (Schnitzler, Salmelin, Salenius, Jousmäki, & Hari, 1995; Tommerdahl et al., 2006).

The MEG study by Tamè, Pavani, Papadelis, et al. (2015) may provide initial indications in favour of the second possibility—namely, the SI transcallosal projections. In that study, suppression in contralateral SI in response to bilateral stimulation was weak when the adaptor and probe were delivered simultaneously, emerged very clearly after a short delay (i.e., 25 ms), and vanished at a long delay (i.e., 125 ms). This very fast suppression effect is compatible with the notion that tactile information from the stimulated body side can reach ipsilateral SI via transcallosal connections already at the level of SI (Manzoni, Barbaresi, Conti, & Fabri, 1989; Shuler et al., 2001; Tomasch, 1954). Indeed, the fact that we did not find significant suppression for the bilateral simultaneous stimulation condition suggests that it is unlikely that tactile information reaches ipsilateral SI through direct ipsilateral connections from the spine.

A recent tractography study has shown the presence of transcallosal fibre tracts connecting homologous sensorimotor cortical regions (Fling et al., 2013). Earlier bilateral interactions at subcortical and/or spinal cord levels may also be present, as shown

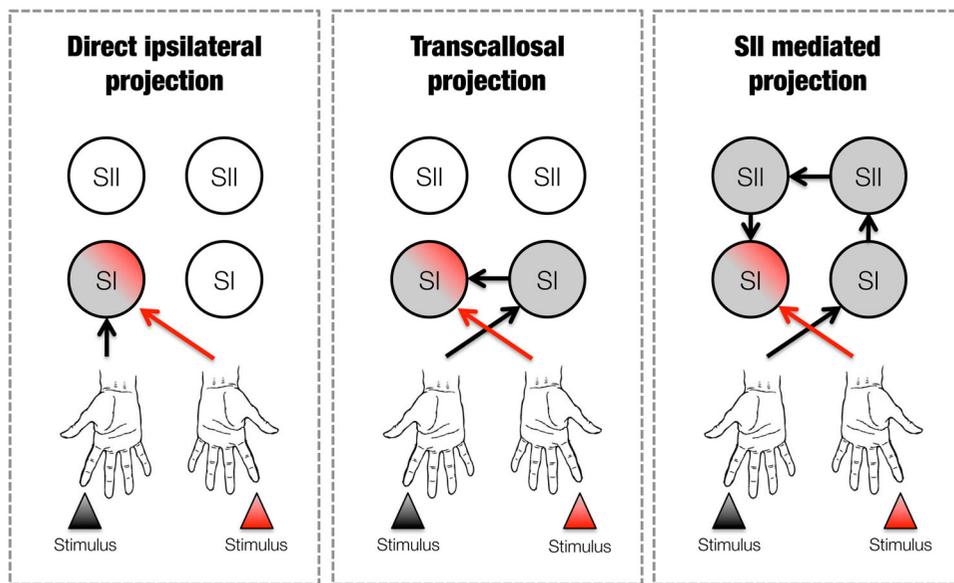


Figure 3. Graphical representation of the possible anatomical pathways mediating the integration of tactile information from the two sides of the body. In this example, the stimulated finger is the right index. Grey circles represent the passage of information through that particular node. SI = primary somatosensory cortex; SII = secondary somatosensory cortex. (A) Direct ipsilateral projections, (B) transcallosal projections, and (C) SII mediated projections. [To view this figure in colour, please see the online version of this journal.]

by reports on patients that underwent callosotomy (Corballis, 1994; Sergent, 1990). Indeed, Sergent (1990) has shown that split-brained patients can make accurate perceptual judgments based on visual stimuli presented simultaneously to the two visual fields (Sergent, 1990). Finally, top-down modulation of contralateral SI by well-known bilaterally organized higher level brain areas (e.g., SII, area 5) is also likely to play some role. It would be of great interest to approach this problem through computational modelling. Even simplified circuits involving SI and SII bilaterally, and taking into account actual transmission times between regions and across hemispheres, could help disentangle the relative contribution of the three different pathways in bilateral tactile integration. In our opinion it is most likely that, as a function of the task demands, SI is recurrently involved in the integration of tactile signals from the two sides of the body from the earliest to the later stages of tactile processing.

Interhemispheric integration and sensorimotor control

In this section we discuss how bilateral integration in SI relates to action. Several studies we described in the previous sections reported modulatory effects on bilateral sensory integration when limb posture (e.g.,

fingers, hands, or arms) changed. The spatial relationship between the parts of the two sides of the body (e.g., whether fingers are aligned or not aligned in space) seems to be of particular importance to determine the way in which bilateral stimuli are integrated (Heed & Azañón, 2014). For instance, in one of our studies described above (Tamè et al., 2011), across conditions participants had the homologous fingers (i.e., left and right index and middle fingers) of their two hands aligned in space (i.e., index-index and middle-middle), whereas in another condition one hand was turned upside down, with the homologous fingers misaligned. Changing the hand posture did not have any impact on the interference for tactile stimuli presented within the hand, but significantly affected participants' performance between the hands. In particular, when performance was assessed while one of the subjects' hands was palm-up, we documented a clear tactile interference for concurrent within-hand stimulation, which was independent of the hand's posture. In contrast, when concurrent stimulation was delivered between hands, no significant interference was observed for either homologous or non-homologous finger stimulation. This posture-dependent modulation indicates a role for non-somatotopic spatial representations for touch, which take into account the overall structure of the body as well as its layout in space. Specifically, it provides an

indication that certain positions (i.e., homologous body parts aligned) may determine whether SI is the primary area mediating the integration.

In everyday life, tactile stimulation is commonly accompanied or caused by action. The sensory and motor systems are intimately related, both anatomically and functionally, with continuous reciprocal exchange of information. In this respect, we combined tactile repetition suppression with the techniques of afferent inhibition (i.e., corticospinal excitability is inhibited when a single tactile stimulus is presented before a TMS pulse over the motor cortex) to investigate whether the modulation of somatosensory activity induced by double tactile stimulation propagates to motor cortex and alters corticospinal excitability in humans. We found that activity in the somatosensory cortices following repetitive (i.e., double) tactile stimulation also elicits finger-specific activation in the primary motor cortex, and this motor modulation varies as a function of the temporal and spatial relationships between the afferent (tactile) stimuli (Tamè, Pavani, Braun, et al., 2015). The two consecutive electrocutaneous stimuli (separated by either 30 or 125 ms) were delivered to either the same or different fingers on the left hand (i.e., the index finger was stimulated twice or the middle finger was stimulated before the index finger). Corticospinal excitability was modulated differently by tactile stimulation of the same and different fingers only when the two stimuli were separated by 30-ms delay. In particular, at short delays, corticospinal excitability reflects information about the presence and location of afferent events, whereas at longer delays the presence of multiple afferent events is communicated to the motor cortex, but location information is lost. The relation between the sensory and motor system is particularly important in haptic tasks, in which we actively explore an object. In this situation our brain is simultaneously receiving sensory signals from, and generating motor signals for, the movements. These inputs have to be combined to perceive the actively explored objects.

Recently, Dupin, Hayward, and Wexler (2015) developed a new paradigm in which they were able to separate the sensory and motor signals typically relating to the same part of the body (e.g., hand), which, when combined, provide the spatial characteristics of an object during haptic exploration, such as shape and size. In their task, participants were instructed to move one hand without receiving any tactile

information, while the other hand felt the consequences of the action without moving itself. The authors found that the sensory and motor signals were combined from the two sides of the body as if they were coming from the same hand. They interpreted this result as evidence that, in haptic perception, the brain combines sensory and motor signals using a simplified representation of the body, in which somatosensory stimulations that are perceived as movement consequences are treated in a body-side-independent manner. Other examples of sensorimotor interactions across the two hemispheres are provided by a series of works by Braun et al. (2001, 2003) as well as by Wühle, Fahlbusch, and Braun (2006) in which they studied the effect of motor tasks on the organization of primary somatosensory cortex. Participants were receiving, unpredictably, a tactile stimulus on the thumb or little finger of one of the two hands, while performing a unimanual motor task that, across blocks, required different levels of dexterity. The results showed that the more dexterous was the action, the larger was the distance between dipoles representing the thumb and little finger in SI. Therefore, finger representations became more segregated when the motor task became progressively more difficult. Although movements were carried out only with one hand, the modulation of SI representation was seen in both hemispheres. These findings show how important the specific type of action that needs to be performed is in determining the interactions at the earliest stages of tactile processing—namely, in SI within and between the hemispheres.

Conclusions

The present review describes recent evidence showing how critical is the primary somatosensory cortex in the integration of tactile stimuli coming from the two sides of the body. We have shown, with indirect and direct evidence, how SI is involved in bilateral integration from the early stages of tactile processing. Moreover, we highlighted how homologous and non-homologous parts of the two sides of the body interact differently as a function of task demands. Our main argument does not intend to challenge the primarily contralateral nature of SI. Instead, we suggest that the dominant perspective of contralateral representation of tactile input in SI should be extended to allow for

more context-dependent early integration of tactile inputs from both body sides.

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