Review Article

Primary somatosensory cortex organization for engineering artificial somatosensation

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ABSTRACT

Somatosensory deficits from stroke, spinal cord injury, or other neurologic damage can lead to a significant degree of functional impairment. The primary (SI) and secondary (SII) somatosensory cortices encode information in a medial to lateral organization. SI is generally organized topographically, with more discrete cortical representations of specific body regions. SII regions corresponding to anatomical areas are less discrete and may represent a more functional rather than topographic organization. Human somatosensory research continues to map cortical areas of sensory processing with efforts primarily focused on hand and upper extremity information in SI. However, research into SII and other body regions is lacking. In this review, we synthesize the current state of knowledge regarding the cortical organization of human somatosensation and discuss potential applications for brain computer interface. In addition to accurate individualized mapping of cortical somatosensation, further research is required to uncover the neurophysiological mechanisms of how somatosensory information is encoded in the cortex.

1. Introduction

Patients with somatosensory impairments, such as those afflicted with stroke or paralysis, suffer from a degraded ability to manipulate objects, control motor function, and carry out complex, multijoint movements (Flesher et al., 2016; Sainburg et al., 1995; Suminski et al., 2010; Lubin, Strebe and Kuo, 2017; Tabot et al., 2013). A significant component of their rehabilitation is compensating for this lost function, but recently efforts have focused on restoring key somatosensory deficits. Brain computer interface (BCI) is a promising means of restoring function for both motor and somatosensory systems. While efforts have primarily been directed towards the motor component of BCI systems, somatosensory BCI can restore continence, provide feedback on pressure ulcers, improve motor BCI (Akselrod et al., 2017; Lubin, Strebe and Kuo, 2017; Suminski et al., 2010; O'Doherty et al., 2009), or, ultimately, return naturalistic sensations. Electrical stimulation of the primary

somatosensory cortex can produce percepts in specific somatotopic locations, and recent work with this approach has demonstrated reliable, safe operation and robust percepts (Flesher et al., 2016; Armenta Salas et al., 2018). These percepts can exhibit naturalistic characteristics (Armenta Salas et al., 2018; Flesher et al., 2016), and altering stimulation parameters can lead to changes in percept intensity (Lee et al., 2018), frequency (Kramer et al., 2019c; Kramer et al., 2020a), and modality (Armenta Salas et al., 2018). While some growing evidence suggests that microstimulation may offer a promising alternative to large electrode stimulation in improving naturalistic sensation (Flesher et al., 2016; Armenta Salas et al., 2018), artificially mimicking natural sensation remains challenging and requires a detailed understanding of how the somatosensory cortex encodes and communicates information. To achieve this, this review discusses the functional and topographic organization of the primary and secondary somatosensory cortices as possible targets for engineering artificial sensation using somatosensory

BCI systems in the future. This work will primarily focus on human studies given that human subjects can most reliably articulate information about sensation, but we include information from non-human primate studies when pertinent.

2. Somatosensory cortical structure

The somatosensory system receives cutaneous and proprioceptive input from superficial skin receptors and deep receptors within muscles and Golgi tendon organs (Nelson, Blake and Chen, 2009; Kaas, 2015; Kim et al., 2015). As a system, it includes the primary somatosensory cortex (SI), secondary somatosensory cortex (SII), parietal ventral somatosensory area (PV), thalamus parietal association areas, and hypothalamus (for visceral sensation). Regarding cutaneous processing, this system depends on mechanoreceptors to relay information about forces applied on the skin surface. There are four types of peripheral afferents important for tactile perception: slowly adapting type 1 (SA1) fibers that innervate Merkel cell receptors in the epidermis, slowly adapting type 2 (SA2) fibers that innervate Ruffini corpuscles in the dermis, rapidly adapting (QA1) fibers that innervate Meissner corpuscles in the dermal papillae, and Pacinian corpuscle (PC) fibers that innervate Pacinian corpuscles in the deep dermis (Yau et al., 2016; Abraira and Ginty, 2013). SA1 fibers respond to maintained touch or hair displacement, while SA2 fibers react to pressure on the teeth and skin deformations. QA1 afferents respond to low-frequency skin vibration, while PC fibers are receptive to high-frequency vibration (Abraira and Ginty, 2013; Kaas, 2015; Yau et al., 2016; Romo et al., 2000). The rapidly adapting afferents, QA1 and PC, respond transiently at the onset and removal of skin deformation, while the slowly adapting afferents, SA1 and SA2, fire continuously throughout indentation (Yau et al., 2016; Hsiao et al., 2009). SA2 and PC have larger receptive fields than SA1 and QA1 (Yau et al., 2016). SA1 fibers carry spatial resolution higher than QA1 fibers and encode for object orientation and curvature (Khalsa et al., 1998; Yau et al., 2016; Phillips, Johnson and Hsiao, 1988).

Both slowly and rapidly adapting afferents ascend through the dorsal column-medial lemniscus pathway of the spinal cord. The dorsal columns have a somatotopic architecture with more medial fibers carrying afferents from the sacral nerves and more lateral fibers carrying afferents from the cervical nerve roots (Smith and Deacon, 1984). These fibers then synapse in the cuneate (lateral fibers for upper extremity afferents) and gracile (for lower extremity medial fibers for lower extremity afferents) nuclei in the medulla, and project to the ventral posterolateral (VPL) nucleus of the contralateral thalamus. Afferents from the head, face, and mouth ascend to the principal trigeminal nucleus and project to the ventral posteromedial (VPM) nucleus of the contralateral thalamus (Kaas, 2015). Electrical microstimulation of VPL nucleus evokes primarily natural sensation in multiple areas, including across the hand and in the digits. Perceived intensity correlates with stimulation amplitude; as intensity increases, the response is perceived as less natural (Swan et al., 2018). From the thalamus, sensory information projects to SI. Mountcastle (1957) first demonstrated a columnar structure to neuronal architecture in the somatosensory cortex of cats, in which neurons within narrow, vertical columns were activated by the same peripheral receptors (e.g., Meissner's corpuscles or Golgi tendon organs) (Mountcastle, 1957; Horton and Adams, 2005). In rats, the septa between cortical columns are connected to the thalamus, underscoring the close integration between SI and the thalamus (Kaas, 2015; Kim and Ebner, 1999).

The primary somatosensory cortex consists of Brodmann areas 1, 2, 3a, and 3b on the postcentral gyrus. From anterior to posterior, area 3a lies deepest within the central sulcus; area 3b follows, extending onto the postcentral gyrus; area 1 lies on the crown of the postcentral gyrus; and area 2 lies on the posterior bank of the postcentral gyrus, extending into the postcentral sulcus (Kaas, 2015; Roux, Djidjeli and Durand, 2018). Area 3b receives thalamic inputs from VPM and the core regions of VPL (Yau et al., 2016; Kaas, 2015; Cerkevich, Qi and Kaas, 2013).

Neurons in this subregion respond best to cutaneous stimuli (Yau et al., 2016). Area 3a receives proprioceptive information from the shell region surrounding the VPL (Yau et al., 2016) and projects to the motor cortex, premotor neurons in the brain stem and spinal cord (Kaas, 2015), and to areas 1 and 2 (Jones, 1986). Areas 1 and 2 are thought to be responsible for multimodal integration of tactile inputs (Kim et al., 2015). Area 1 receives input from areas 3a and 3b and is presumably important for texture (Kaas, 2015; Jiang, Tremblay and Chapman, 1997; Jones, 1986). Neurons in areas 1 and 3b respond to bars and edges in their receptive fields at preferred orientations and weakly otherwise, suggesting that these areas play a role in the tactile perception of edges (Yau et al., 2016). Area 2 receives cutaneous and proprioceptive input from areas 3b and 1, and the thalamus (Kaas, 2015; Yau et al., 2016), and integrates this information to discriminate object size and shape (Kaas, 2015). Area 2 is densely interconnected across hemispheres. In non-human primates (NHPs), area 2 had dense callosal connections while area 1 had less and area 3b had few callosal connections (Killackey et al., 1983; Iwamura, 2000), which permit the integration of information from both sides of the body and is thought to be important for bilateral coordination (Kaas, 2015). Overall, proprioceptive information from deep receptors generally diverges to neurons in areas 3a and 2, whereas cutaneous information generally transmits to neurons in areas 3b and 1 (Powell and Mountcastle, 1959; Blankenburg et al., 2003). However, a significant proportion of neurons in areas 3a and 3b can respond to both tactile and proprioceptive stimuli, respectively, each with distinct mechanisms for sensory processing (Kim et al., 2015; Trzcinski et al., 2023). Although different neuronal populations in these areas show multimodal response properties, these responses are not distinctly separate (Kim et al., 2015). Area 2 projects to association areas in the posterior parietal cortex and to SII on the upper bank of the lateral sulcus, ventral to SI in the parietal operculum (Yau et al., 2016; Eickhoff et al., 2007). SII receives the majority of its inputs from SI and the thalamus, and projects to the posterior parietal cortex and motor and premotor cortices (Kaas, 2015).

3. Somatotopy

3.1. Primary somatosensory cortex

In 1937, Penfield was the first to demonstrate a somatotopic representation of the entire body in SI, termed the homunculus, with each location of the contralateral body surface represented within the cortex. Using direct cortical stimulation in awake neurosurgery patients, he demonstrated that from medial (interhemispheric) to lateral, SI is organized to represent the genitalia, lower limbs, upper limbs, hands, and face (Rasmussen and Penfield, 1947; Penfield, 1937; Kaas, 2015; Kaas, 1983; Kaas, 2012). Structures such as the hand, lip, and tongue are represented in a proportionally larger amount of cortex than larger structures, such as the trunk (Penfield, 1937; Rasmussen and Penfield, 1947). The homunculus appears to be a characteristic feature of the sensory cortices, with SII exhibiting some topographic organization (Penfield, 1937; Nguyen et al., 2004; Disbrow, Hinkley and Roberts, 2003). Still, not all somatosensory regions exhibit the same homuncular properties. Three recent studies using fMRI found that relative overlap between digits was larger in areas 1 and 2 than in area 3b (Krause et al., 2001; Nelson, Blake and Chen, 2009; Pfannmoller et al., 2016). It has been suggested that area 3a's somatotopy is similar to 3b based on its deep receptors, which run in parallel to those of 3b (Kaas, 2004). The somatotopy of area 1 is a mirror reversal of 3b around the medial-lateral axis, flipping the anterior-posterior organization (Kaas, 2015; Nelson, Blake and Chen, 2009; Blankenburg et al., 2003). For example, in area 1, the fingertip is located posteriorly to the palm, whereas the fingertip is located anteriorly to the palm in 3b (Blankenburg et al., 2003). Recent studies have validated the primary selectivity and organization of the somatosensory homunculus but show that the representation of various body parts are distributed throughout, overlapping with regions

selective to other areas (Muret et al., 2022).

3.1.1. Upper Limb

The fingers are represented on the gyrus with digit 5 more medial than digit 1 (Kramer et al., 2020b), and the arm more medial than the hand (Nakagoshi et al., 2005) (Fig. 1), consistent with Penfield's homunculus (Penfield, 1937). Individual digit somatotopy in area 3b has been suggested, as the cortical regions of adjacent digits lie closer together than the representations of digits farther apart on the hand. For example, the cortical distance between the representations of digit 3 and digit 1 is larger than the distance between digit 1 and digit 2 (Pfann-moller, Schweizer and Lotze, 2016; Sathian and Zangaladze, 1996). Medial-lateral and anterior-posterior somatotopy of the hand in area 1 has been shown with little variability in a direct cortical stimulation study on 50 awake operative patients (Roux, Djidjeli and Durand, 2018). Roux et al. (2018) found that fifth digit-first digit somatotopy was medial-lateral on the cortex, as expected, and symmetric across hemispheres. The anterior-posterior somatotopy involved different finger

regions, with the fingertip posterior on the postcentral gyrus to the phalanx, on the anterior bank of area 1 (Roux, Djidjeli and Durand, 2018).

To examine digit somatotopy in area 3b, an fMRI study delivered electrical stimulation to the caput, base of the third metacarpal bone, and third digit distally, medially, and proximally. The fingertip was located most anteriorly in area 3b, with the caput located most posteriorly. In area 1, the caput was located most anteriorly with the fingertip most posteriorly (Blankenburg et al., 2003), consistent with the previous study (Roux, Djidjeli and Durand, 2018). These results support the finding that areas 1 and 3b are mirror reversals of each other around the medial-lateral axis (Fig. 1). Somatotopy could not be determined in area 2, as cortical representations overlapped (Blankenburg et al., 2003).

In an analysis of fMRI images, there was an enlargement of the thumb representation in areas 1 and 2, with a trend towards enlargement in area 3b compared to other digits. This may reflect the importance of sensory integration in the thumb (Martuzzi et al., 2014). Schellekens et al. (2021) recently demonstrated that the cortical
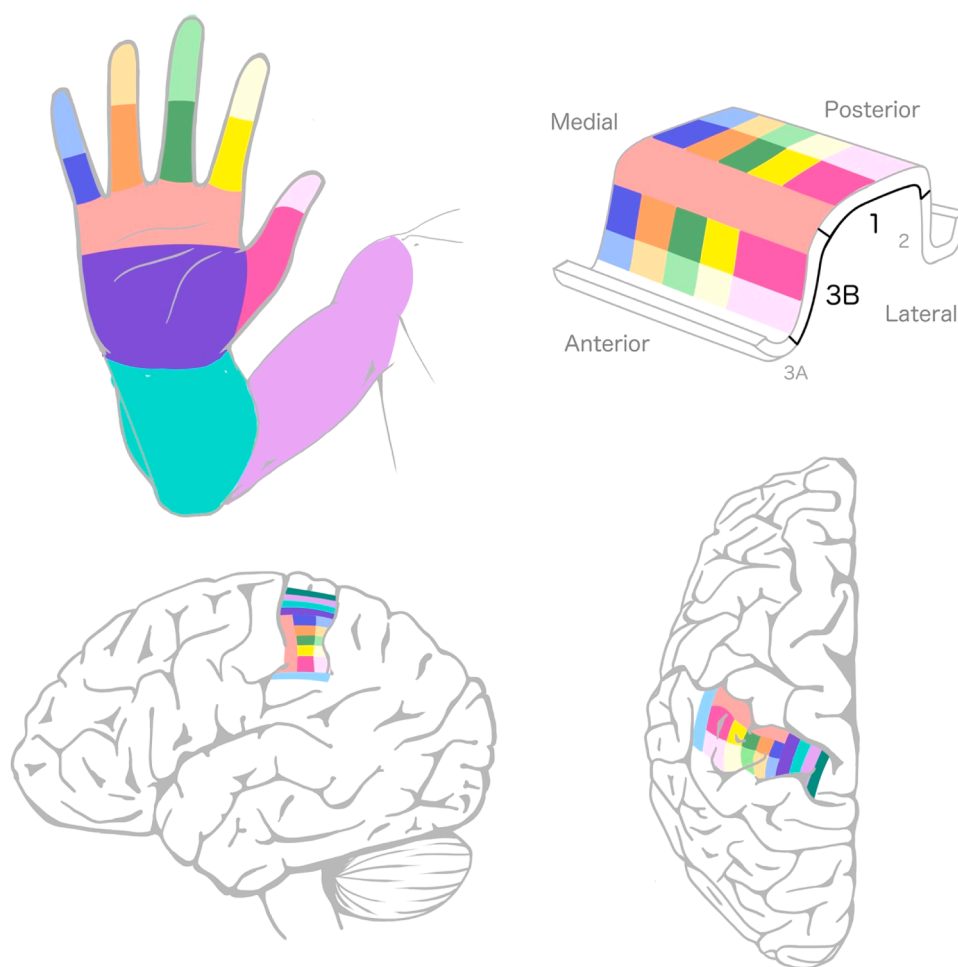

Fig. 1. Cortical SI Representations of the Upper Extremity, Top left, a colored upper extremity matching corresponding cortical areas of somatosensation. Upper extremity somatosensation is separated into the proximal limb (light violet), distal limb (cyan), proximal palm (dark violet), distal palm (red), proximal digits 1–5 (dark shades of pink, yellow, green, orange, and blue), and distal digits 1–5 (light shades of pink, yellow, green, orange, and blue). Top right, a representation of the organization of Brodmann areas 1 and 3b (labeled and underlined in black) on an unfolded portion of cortex. Area 1 somatotopy is mirrored to that of 3b around the anterior-posterior axis. In 3b, representations of distal portions of the digits are located anteriorly on SI within the sulcus, whereas they are located posteriorly in area 1 on the gyrus of SI. Note the larger area of the cortex dedicated to digit 1 somatotopy compared with the other digits. In the cortical representations below (bottom left and right), only area 1 is visible because it sits on the gyrus whereas area 3b is located within the sulcus. Bottom left and right, lateral and superior cortical representations of upper extremity somatosensation. The fingers are represented on the gyrus with digit 5 (dark blue and light blue) more medial than digit 1 (dark pink and light pink) on the cortex, and the cortical representation of the arm (cyan and light violet) more medial than the palm (red and dark violet). Just medial to the proximal upper extremity representation on the cortex is the head representation (colored green-blue to match color schemes in later figures). The lateral border of the hand representation, sitting just lateral on the cortex to digit 1, is the beginning of the face somatotopy (colored baby blue to match later figures).

organization of fingertip somatotopy may reflect processing order by measuring population receptive field size (i.e., the population of neurons responding to a stimulus as measured by fMRI) during vibratory stimulation of the fingertips (Schellekens et al., 2021). The authors found that population receptive field size increased from area 3 to area 1 and was even greater in area 2 (Schellekens et al., 2021), which indicates that spatial information integration increases anterior to posterior. Arbuckle et al. (2022) used fMRI to measure cortical response to multi-finger stimulation in 10 healthy participants (Arbuckle, Pruszynski and Diedrichsen, 2022). They discovered that neuron activity in area 3b represented discrete single finger somatosensation, whereas activity in areas 1, 2, and 4 constituted sensory integration from multiple fingers (Arbuckle, Pruszynski and Diedrichsen, 2022). These results indicate that integration of multi-digit somatosensation takes place in posterior SI (Arbuckle, Pruszynski and Diedrichsen, 2022).

Within-limb somatotopy in SI has also been shown with fMRI. Manual tactile stimulation of four points on the upper limb demonstrated a cortical medial-lateral organization when stimulation occurred proximally to distally on the limb (Nakagoshi et al., 2005). Overall, the upper limb is arranged in a medial-lateral direction on the cortex, with recent studies proposing anterior-posterior somatotopy of the digits (Roux, Djidjeli and Durand, 2018; Blankenburg et al., 2003).

It is worth noting that some recent studies have challenged the traditional view of somatotopic organization. For example, Trzcinski et al. (2023) demonstrated that neurons in 3b can respond to multiple fingers, although the firing rate across these cells was heterogeneous, indicating the presence of a "preferred" digit (Trzcinski et al., 2023). In addition, Hirabayashi et al. (2021) chemogenetically silenced areas of the hand-finger region of SI, which expectedly impaired grasping but also surprisingly directly disinhibited foot activity (Hirabayashi et al., 2021). Their findings indicate that there may be foot representation in the hand region of SI, or more conservatively, a node-node reliance network responsive to inhibition. These studies demonstrate cross-digit integration across SI and challenge the previous simplistic view of
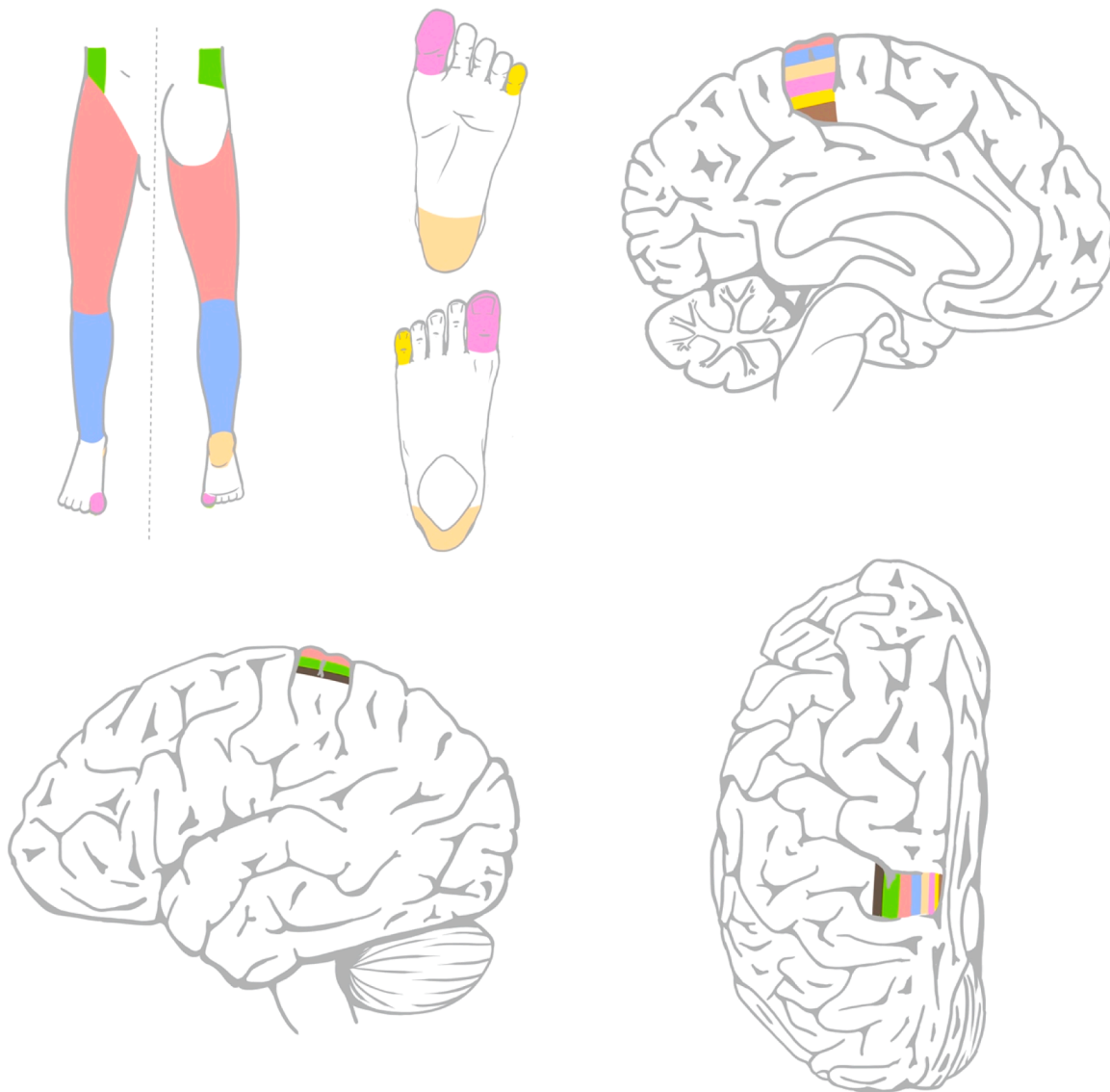

Fig. 2. Cortical SI Representations of the Lower Extremity, Top left, a colored lower extremity matching corresponding cortical areas of somatosensation. Lower extremity somatosensation is separated into the hip (green), proximal limb (red), distal limb (blue), heel (orange), digit 1 (pink), and digit 5 (yellow). The lower extremity is organized with more distal portions of the limb represented more medially on SI cortex. Top right, medial view of cortical representations of the lower extremity. The most medial portion of the lower extremity cortical representation is digit 5 (yellow) with nipple somatotopy representation just medial to it (light brown to match color schemes in later figures). Bottom left and right, lateral and superior views of lower extremity cortical representations. Within the lower extremity, the cortical representation that is most lateral on SI is the hip (green) with the torso representation (dark brown to match later figures) just lateral to it.

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human somatopy, although evidence from these studies suggests that somatopy may be preferably but not exclusively coded to certain regions.

3.1.2. Lower Limb

Penfield proposed a medial-lateral leg somatotopy with the toes inferior to the leg in the interhemispheric fissure (Penfield, 1937). In his studies, only 10 out of 400 patients described sensation localized to the toes with direct cortical stimulation. Five reported sensations in the hallux, four reported sensations in all lower limb digits, and one reported sensation in digit 5 (Hashimoto et al., 2013; Rasmussen and Penfield, 1947). Since then, fMRI studies have supported Penfield's homunculus, finding a lateral-medial cortical representation of the lower limb as tactile stimulation moves proximally-distally; with the leg more lateral and draping over and into the interhemispheric fissure, ending with the toes more medial and deeper within the fissure (Nakagoshi et al., 2005; Bao et al., 2012; Akselrod et al., 2017) (Fig. 2).

Bao et al. (2012) expanded on this theory, demonstrating inferior-superior somatotopy when tactile stimulation sites were moved from medial to lateral on the lower limb (Bao et al., 2012). For example, stimulation of the medial leg resulted in activation that was inferior to stimulation of the lateral leg on fMRI (Bao et al., 2012). In another fMRI study, the hallux representation was larger than that of the fifth digit, calf, or thigh (Akselrod et al., 2017), similar to the findings of the thumb (Martuzzi et al., 2014). Tactile stimulation of the leg and foot did not result in cross-activation of their cortical representations. For example, the hallux and fifth digit's peripheral stimulation did not result in activation of the leg cortical areas. The total volume of the lower limb representation in area 2 was decreased compared to that in 3b and 1 (Akselrod et al., 2017), similar to findings on the digits of the hand (Martuzzi et al., 2014). While foot somatotopy could not be discerned in this study, in the somatosensory cortex of monkeys, lower limb digits are organized lateral-medial in area 3b and rostral-caudal in area 1 (Akselrod *et al.*). Human lower limb digits may be organized
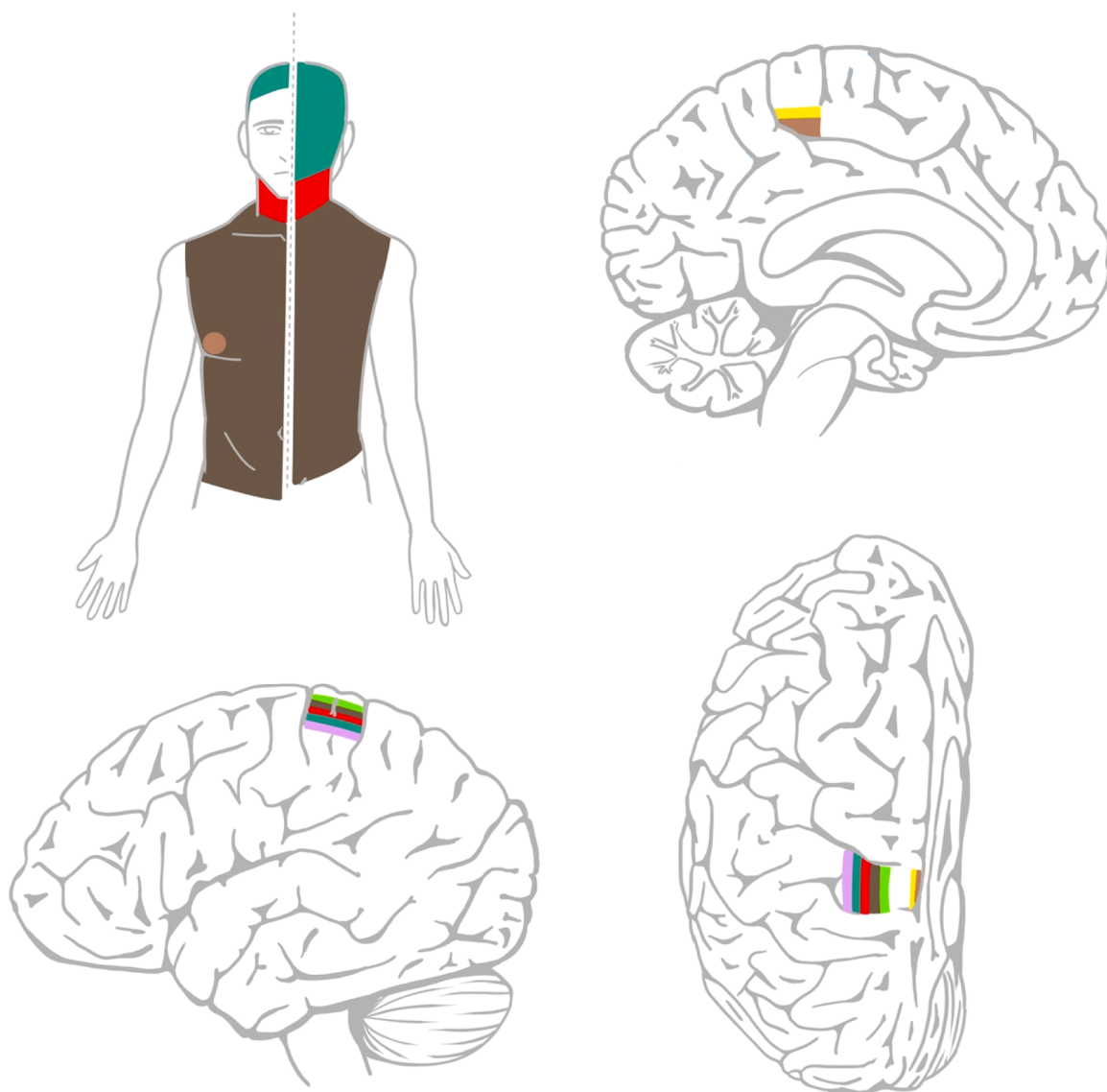

Fig. 3. Cortical SI Representations of the Torso, Head, and Neck, Top left, a colored torso (dark brown), nipple (light brown), head (green-blue), and neck (red) matching corresponding cortical areas of somatosensation. Top right, medial view of the cortex shows the nipple cortical representation (light brown) just medial to the representation of digit 5 of the lower extremity (yellow). Bottom left and right, lateral and superior views of the torso, head, and neck cortical representations. Torso somatotopy representation (dark brown) is located medially to the neck representation (red) and laterally to the hip representation (light green). Nipple somatotopy representation (light brown) is located inferiorly to the lower extremity fifth digit somatotopy representation (yellow). Head somatotopy representation (green-blue) is medial to the proximal upper extremity cortical representation (light violet, same as in Fig. 1).

rostral-caudal (Akselrod et al., 2017; Merzenich et al., 1978; Kaas et al., 1979; Nelson et al., 1980).

A recent MEG study challenged Penfield's homunculus through electrical stimulation of the leg on three different dermatomes based on innervation from lumbosacral roots (Dietrich et al., 2017). The study suggested that dermatomes were separated in SI; specifically, the cortical representation of an S-2 dermatome (back of thigh) was inferior to that of an S-1 dermatome (on the foot), and an L-3 area (front of thigh) was lateral to the S-1 representation (Dietrich et al., 2017). L-3 was lateral on the postcentral gyrus compared to the representations of both S-1 and S-2, which were located just inside the interhemispheric fissure. In the superior-inferior plane, the cortical representation of L-3 was not significantly different from that of S-1. In the medial-lateral plane, the locations of S-1 and S-2 were not significantly different; however, S-2 was significantly more inferior to the S-1 representation in the superior-inferior plane. Overall, L-3 was in a superolateral direction compared to S-2. The location of S-2 inferior to S-1, despite anatomically being more proximal on the actual limb, is consistent with the concept that spinal nerves of a dermatome project to SI in the same order in which they are in the spinal cord (Dietrich et al., 2017). Cortical representations may be organized by dermatomes, in contrast to Penfield's homunculus, which would still follow a thumb representation (C5) lateral to a 5th digit representation (C8/T1). However, other examples such as the neck (C3/C4) are represented in SI medial to the upper limb (Willoughby, Thoenes and Bolding, 2020). Further studies are needed to distinctly map lower limb somatotopy.

3.1.3. Trunk

In Penfield's homunculus, the trunk representation lies medially on the gyrus compared to the neck region and lies laterally on the gyrus compared to the lower limb region (Penfield and Rasmussen, 1950) (Fig. 3). An fMRI study investigated the difference between ventral lateral and medial trunk tactile stimulation. Ventral lateral trunk stimulation between the umbilicus and nipples resulted in contralateral activation in the middle of the postcentral gyrus. Ventral medial trunk stimulation was delivered 2 centimeters away from the midline. It resulted in bilateral SI activation behind the omega-shaped central sulcus in the bank of the anterior postcentral sulcus on fMRI (Fabri et al., 2005).

Other investigations have also tried to map nipple and breast somatotopy in both males and females. Komisaruk et al. (2011) investigated nipple self-stimulation and found fMRI activation in both in the interhemispheric fissure at the genital sensory region and laterally on the convexity of SI in the trunk region of Penfield's homunculus (Komisaruk et al., 2011). Another fMRI study investigated the nipple and breast somatotopic organization in both males and females following automatized vibrotactile stimulation (Beugels et al., 2020). Stimulation of the nipple and breast resulted in bilateral activation on the postcentral sulcus convexity in the trunk region described by Penfield (Beugels et al., 2020; Penfield and Rasmussen, 1950), consistent with mentioned studies (Komisaruk et al., 2011). There was no difference between the male and female nipple and breast cortical regions. The nipple representation on SI was larger than the region representing surrounding breast tissue (Beugels et al., 2020), similar to the findings of the thumb and hallux (Martuzzi et al., 2014; Akselrod et al., 2017).

3.1.4. Face

The face is located most laterally in Penfield's homunculus (Penfield, 1937). NHP studies of orofacial somatotopy have demonstrated considerable variability in organization between species and individuals of a single species. However, most studies have mapped orofacial sensation to the lateral portion of area 3b (Dreyer et al., 1975; Cusick, Wall and Kaas, 1986; Cusick et al., 1989; Krubitzer, 1995). Manger et al. (1996) demonstrated that in the macaque, the area innervated by the contralateral trigeminal nerve mapped to area 3b lateral to representation of the hand (Manger, Woods and Jones, 1996). Within this area,

there was expanded representation of the oral region, primarily located in the anteroposterior region (Manger, Woods and Jones, 1996). Dreyer et al. (1975) sought to determine patterns of SI activation depending on the receptive field of trigeminal nerve subdivisions in the macaque (Dreyer et al., 1975). Stimulating areas of the face innervated by the ophthalmic division of the trigeminal nerve activates the junction between areas 1 and 2, while the maxillary distribution activates a circular area that surrounds the ophthalmic field and includes areas 1, 2, 3, and 3a, and the mandibular distribution activates a circular area surrounding the maxillary field (Dreyer et al., 1975). In the spider monkey, Cusick et al. (1986) demonstrated that there are separate representations for the face and head in areas 1 and 3b that are near mirror images of each other (Cusick, Wall and Kaas, 1986). In addition, the authors showed that there was great individual diversity in lip representation between subjects (Cusick, Wall and Kaas, 1986).

In humans, tactile stimulation of the lip and tongue resulted in bilateral activation in areas 3b and 1 on MEG (Disbrow, Hinkley and Roberts, 2003). This represents a divergence from earlier animal studies noting solely contralateral lip activation (Jain et al., 2001; Manger, Woods and Jones, 1995). Another MEG study proposed that the thumb is located superior, medial, and posterior to the lip representation, with the face in the cortical area between the thumb and lip (Nguyen et al., 2004). While there was no consistent organization of various facial regions due to the small cortical area they occupied, midline portions of the face were located more laterally down the SI gyrus compared to less midline structures, which were located more medially up the gyrus (Nguyen et al., 2004). Segmental somatotopy was demonstrated in an fMRI study with brush stimuli (Moulton et al., 2009). Here concentric dermatomal areas were noted to be organized on the SI gyrus (Moulton et al., 2009). The midline structures were located more laterally down the gyrus compared to areas on the upper forehead and lateral cheeks located more medially up the gyrus (Fig. 4) (Moulton et al., 2009). This contradicted the organization of the trigeminal nerve dermatomal regions (Moulton et al., 2009).

3.2. Secondary somatosensory cortex

The secondary somatosensory cortex is likely a higher-order processing center and is less clearly organized than SI. Several studies have used either MEG or fMRI to examine SII, finding large inter-subject variability and no clear topographic organization, although trends have been noted. In general, activations overlapped between body representations, such as between the hand and face areas (Disbrow, Roberts and Krubitzer, 2000). Unilateral stimulation of some body regions, such as the leg and trunk, produced bilateral activation, often broader than that seen in SI (Bao et al., 2012; Eickhoff et al., 2008).

What somatotopy has been shown describes within-limb somatotopy in SII with clear distinction of four leg acupoints. In the contralateral parietal operculum (specifically in the subregion operculum parietal 1 (OP1)), tactile stimulation of more proximal areas on the leg resulted in cortical activation that was medial and posterior to the cortical representations of more distal leg acupoints. Stimulation of the lower limb's lateral portions resulted in cortical activation that was medial and posterior to the activation area of the medial lower limb (Bao et al., 2012). In an MEG study, the lip and tongue representations of SII were found at the intersection of the central sulcus and Sylvian fissure (Disbrow, Hinkley and Roberts, 2003). Interestingly, bilateral tactile stimulation of subjects' lips and tongues increased signal amplitude in SII but not in areas 3b and 1 of SI (Disbrow, Hinkley and Roberts, 2003). In that study, the authors hypothesized that this differential activation of bilateral versus unilateral stimulation might reflect distinct underlying neural mechanisms for sensory integration at the midline mouth (Disbrow, Hinkley and Roberts, 2003).

In contrast to prior studies, Burton et al. (2008) demonstrated that topographic organization is variable and can differ depending on the stimulation (Burton et al., 2008). While vibrotactile and most surface
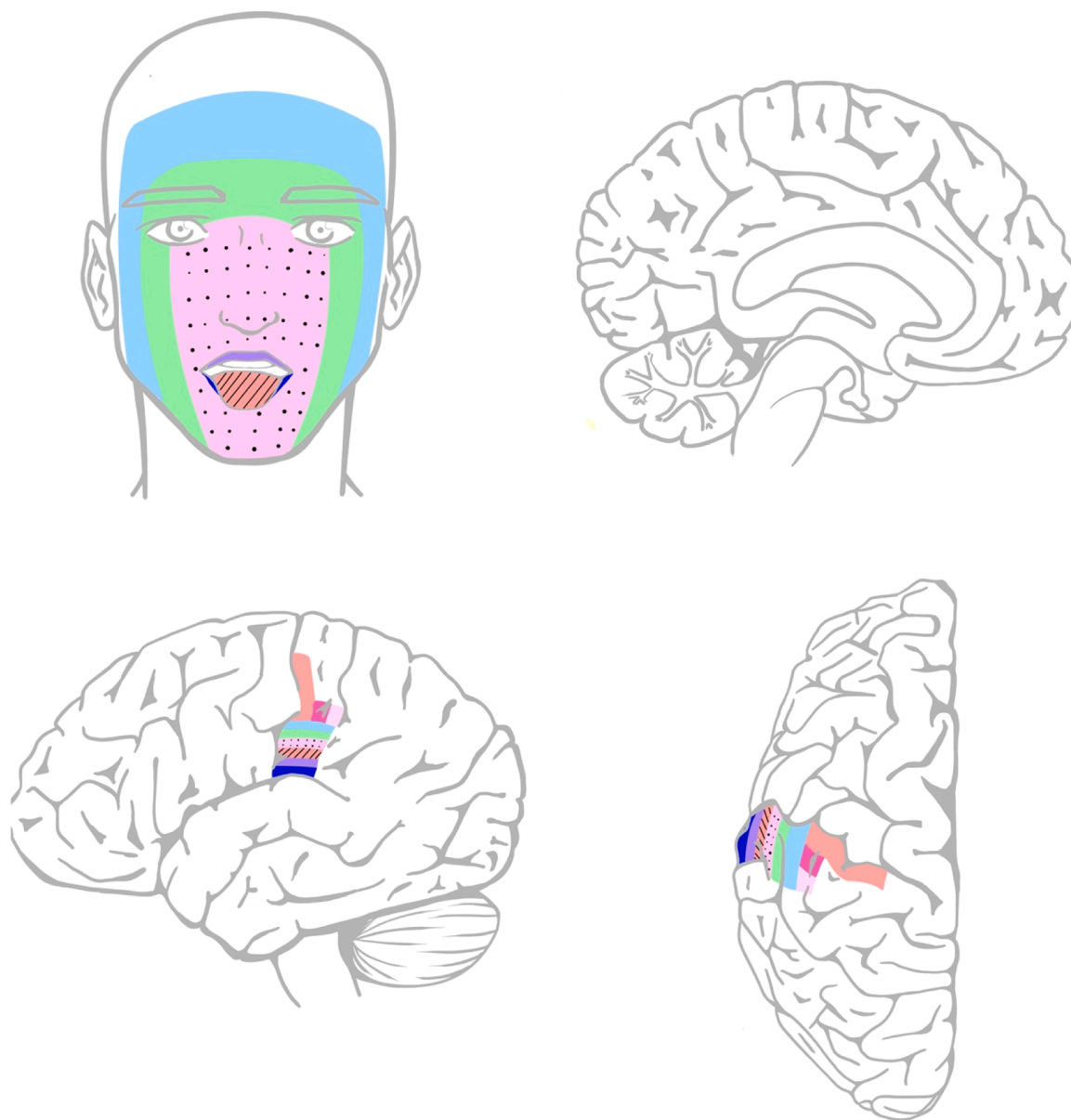
Fig. 4. Cortical SI Representations of the Face, Top left, a colored face matching corresponding cortical areas of somatosensation. The face is separated into the upper forehead and lateral cheeks (baby blue), the lower forehead and medial cheeks (light green), the perioral and perinasal area (pink with black dots), upper lip (light violet), lower lip (dark violet), and tongue (red with black lines). Top right, medial view of the cortex shows the lack of face somatosensation representation in this area. Bottom left and right, lateral and superior views of the face somatosensation cortical representation. Midline facial somatotopy cortical representations (light green and pink with black dots) are located more laterally down the gyrus compared to the upper forehead and lateral cheek representations (baby blue) located more medially up the gyrus. Facial somatotopy cortical representation is located just lateral to the thumb (dark pink and light pink, same coloring as in Fig. 1) and upper palm (red) cortical representations. The upper and lower lip representations are located most laterally on the cortex.

stimuli showed activation in the contralateral SII for the index-finger pad, rubbing embossed capital letters on the skin activated nearly all of contralateral SII and most of ipsilateral SII, suggesting that bilateral processing requires different portions of SII in the hemispheres (Burton et al., 2008). Overall, most surface stimuli elicited greater SII activation than described for hand representations. Additionally, non-painful stimuli were located anteriorly to painful stimuli (Del Gratta et al., 2002; Ferretti et al., 2004), suggesting a more functional organization. Extensive activation was seen in more cognitively demanding tasks, such as letter recognition, potentially due to the need for shape and feature recognition and the recollection of written language. These results underscore the complexity of SII and suggest its role in coding tactile and proprioceptive information to make sense of objects.

4. Visceral sensation

Penfield (1947) first suggested the representation of visceral sensation in SI when direct stimulation at the most lateral, inferior part of the sensory homunculus near the Sylvian fissure elicited an intra-abdominal sensation (Penfield, 1947). Electrical stimulation of rats' vagus nerves showed activation in the parietal granular cortex, consistent with Penfield's homunculus (Ito, 2002), suggesting that visceral sensation in SI is separate from cutaneous sensation.

Expanding upon these results, an fMRI study exposed patients to balloon distension of the distal esophagus and contact heat on the midline chest (Strigo et al., 2003). Balloon distension activated the inferior part of SI, similar to Penfield's intra-abdominal region, and produced subthreshold activation in the trunk representation of SI,

representing esophageal referred chest pain (Strigo et al., 2002; Strigo et al., 2003). Cutaneous pain activated the trunk representation of SI without activating the esophageal visceral region, suggesting that cutaneous pain is not referred to visceral organs (Strigo et al., 2003).

Both visceral and cutaneous pain evoked similar activation in SII (Strigo et al., 2003). In a follow-up fMRI study, visceral sensation was more lateral in the parasylvian cortex, closer to SI than cutaneous pain, suggesting segregation of cutaneous and visceral pain in SII (Strigo et al., 2005). Convergent activation was not seen, indicating that referred pain is more related to SI than SII (Strigo et al., 2005). Future studies are needed to determine whether the separation of cutaneous and visceral representation is correlated to body region, intensity, or modality of stimulation.

5. Genitourinary

Lower urinary tract (LUT) control involves the bilateral prefrontal cortex, insula, anterior cingulate, basal ganglia, and secondary motor cortex, as well as the periaqueductal grey and the pontine micturition center in the brainstem (Griffiths and Fowler, 2013; Leitner, 2016). The somatosensory cortices are hypothesized to play a role in backup continence mechanisms. After patients with incomplete spinal cord injuries with neurogenic LUT dysfunction were stimulated with repeated bladder filling with saline, BOLD imaging demonstrated increased SI and SII activation without periaqueductal grey activation on fMRI compared to healthy controls (Leitner, 2016). This may suggest a compensatory mechanism and supports the theory that extra-spinal pathways are a component of LUT control and can overtake sensory function (Leitner, 2016). Following sacral surface therapeutic electrical stimulation of the bilateral second, third, and fourth posterior sacral foramens, a treatment for urinary incontinence, SI showed MEG activation at the lower limb representation in the interhemispheric fissure and at the trunk representation near the SI convexity outside of the interhemispheric fissure (Matsushita et al., 2008).

Anal and rectal percepts are important in the prevention of fecal incontinence (Whitehead, Engel and Schuster, 1981). An fMRI study investigated the rectum and anal canal's cortical organization following stimulation with balloon inflation (Hobday et al., 2001). Overall, rectal stimulation resulted in activation of SI, SII, the sensory association cortex, anterior cingulate cortex (ACC), periorbital cortex, insular cortex, prefrontal cortex, and the anterior temporal lobe (Hobday et al., 2001). Anal canal stimulation resulted in activation of similar cortical areas, without activation in the ACC (Hobday et al., 2001). Rectal stimulation evoked bilateral activation in the inferior portion of SI, at the previously described visceral area (Hobday et al., 2001). Stimulation of the anal canal elicited activation of the left SI (with bilateral SI activation in some subjects) (Hobday et al., 2001). This activation occurred superior and medial to both the rectal and hand representations in Brodmann areas 1 and 2. Both anal and rectal stimulation resulted in bilateral activation of SII (Hobday et al., 2001).

Pneumatic stimulation of the anal canal elicited activation of the left parietal operculum, left anterior insula, and the ventral midbrain (Eickhoff et al., 2006). Meanwhile, rectal stimulation elicited activation of the left precentral operculum, left anterior insula, ventral midbrain, thalamus, and the pallidum (Eickhoff et al., 2006). However, in contrast to other anorectal studies, they observed no activation of SI, ACC, or the right operculum (Eickhoff et al., 2006). Anal sensations primarily activated SII in the parietal operculum subregion OP4, while rectal percepts were interpreted anterior to SII (Eickhoff et al., 2006).

Male and female genitalia somatotopy have been investigated in other studies. The SI penile representation was located on the convexity of the postcentral gyrus, in an area that overlapped with the lower abdominal wall region and did not extend into the interhemispheric fissure in an fMRI study (Kell et al., 2005). The penile tip and proximal penile shaft were located 1 cm laterally to the SI toe representation (Kell et al., 2005). These results contrast with Penfield's homunculus, where

genital somatotopy is located inferior to the foot in the interhemispheric fissure (Rasmussen and Penfield, 1947), but are in agreement with an NHP study (Rothemund et al., 2002).

Other studies have shown conflicting results on penile somatotopy in SI. An fMRI study showed sexually stimulating pictures to male participants and measured erection with volumetric penile plethysmography (VPP) (Moulier et al., 2006). The group demonstrated two penile representations: one in the interhemispheric fissure, consistent with Penfield's homunculus, and one on the postcentral gyrus' convexity, consistent with the results of Kell and colleagues (Kell et al., 2005). These results indicate the complexity of genital somatotopy and suggest that superficial penile skin stimulation may activate the convexity of SI, while the perception of erection may activate the interhemispheric fissure (Moulier et al., 2006). A similar study demonstrated that activation in area 2 of SI occurred before VPP response, suggesting that SI may help control erection (Mouras et al., 2008).

Considerably less research has been done to map female genital somatotopy. Only one female with sensory seizures reported genital sensation in Penfield's works. Based on this patient, Penfield et al. (1937) proposed that the labia, breast, and foot were located in the interhemispheric fissure, similar to the genital area of the man (Penfield, 1937). Since then, studies have challenged this assumption. Bilateral dorsal clitoral nerve stimulation resulted in activation on the convexity of SI on fMRI, without activation in the interhemispheric fissure, contrary to Penfield's homunculus (Penfield, 1937; Michels et al., 2010). The clitoral representation was lateral compared to that of the hallux (Michels et al., 2010), similar to a previous fMRI study on male genitalia (Kell et al., 2005).

Komisaruk et al. (2011) showed activation on fMRI in the interhemispheric fissure following clitoral, vaginal, and cervical self-stimulation, consistent with Penfield's homunculus (Penfield and Rasmussen, 1950). However, there was also activation on the convexity of SI, just outside the interhemispheric fissure (Komisaruk et al., 2011), consistent with the work by Michels and colleagues (Michels et al., 2010). The vagina was most inferior in the interhemispheric fissure, followed by the cervix located superior to the vagina but inferior to the clitoris in the fissure. Knop et al. (2022) recently found clitoral somatosensory activity over the dorsolateral postcentral gyrus of SI in Brodmann areas 1–3 in response to tactile stimulation of the clitoral area (Knop et al., 2022), consistent with the male genital somatotopy findings of Kell et al. (2005) (Kell et al., 2005). Overall, male and female studies have shown similar findings for genital somatotopy with activation areas both in the interhemispheric fissure and on the SI convexity.

A few studies have investigated the SII representation of both male and female genitalia. In males, penile tactile stimulation resulted in bilateral cortical activation in SII with a contralateral emphasis located anterolaterally to the toe representation without overlap (Kell et al., 2005). SII activation was noted before and after VPP response on fMRI (Mouras et al., 2008). Ruesink et al. (2022) found that SII can differentiate affective from discriminative touch of the penile shaft using fMRI (Ruesink et al., 2022). Stroke patients with erectile dysfunction showed that MRI lesions in the left parietal association areas were related to decreased erectile function (Winder et al., 2017); these studies indicate a complicated network for initiating and maintaining an erection. In the SII of females, the cortical representation of the clitoris and the hallux overlapped on fMRI (Michels et al., 2010).

6. Motion and attention

Several NHP studies have demonstrated that motion-related and attentional information is encoded in the somatosensory cortex. Arce et al. (2013) implanted microelectrode arrays in the orofacial sensori-motor cortex of monkeys to record single neuron activity during tongue protrusion, and they found that over 70% of neurons in SI modulated in response to motor planning and execution (Arce et al., 2013). In addition, they found that neuronal populations in SI differentially activated

depending on the direction of tongue protrusion, suggesting that the sensorimotor cortex responds to directionality as well (Arce et al., 2013). Umeda et al. (2019) further sought to determine the temporal evolution of signal integration in SI in response to movement (Umeda, Isa and Nishimura, 2019). To do this, they had monkeys perform a reaching and grasping task and used electrocorticography to study how signals in the SI relate to those in the primary motor cortex and in forelimb sensory afferent neurons, such as including muscle fibers, Golgi tendon organs, and cutaneous receptor (Umeda, Isa and Nishimura, 2019).

Although they found that SI integrated information with both the primary motor cortex and sensory afferents during movement, it only responded to the primary motor cortex before movement initiation (Umeda, Isa and Nishimura, 2019). In addition, in the pre-movement phase, the authors measured SI neuronal activity slightly after primary motor cortex activity but before any afferent neuron activation, suggesting that SI anticipatorily processes the activity of forelimb structures before receiving sensory feedback (Umeda, Isa and Nishimura, 2019). In this way, these studies provided strong evidence for sensory-motor integration involving the somatosensory cortex.

To elucidate the role of the somatosensory cortex in attention, Steinmetz et al. (2000) investigated the synchronous firing of neuron pairs in SII in three monkeys as they switched attention between a visual and tactile discrimination task (Steinmetz et al., 2000). They found that 78% of neurons in SII changed in firing rate when switching between tasks and 66% of the neuron pairs fired synchronously, a known attentional mechanism (Steinmetz et al., 2000). In addition, although the three monkeys completed the same visual task, the tactile discrimination was different, each representing a different degree of attentional effort (Steinmetz et al., 2000). The authors found that the degree of neuron firing synchrony related to the attentional effort required, which, in addition to the other findings, suggested that SII activates during attentional control (Steinmetz et al., 2000).

7. Applications for BCI

BCI has the potential to produce naturalistic sensations in an extremity via intracortical stimulation. One of the seminal works in this field is Romo et al. (1998), who used a brain-machine interface to compare electrical stimulation in the primary somatosensory cortex with sensations in the hand (Romo et al., 1998). In this study, researchers inserted microelectrodes in area 3b in two monkeys and delivered electrical stimuli of varying frequencies. In doing so, they discovered that the monkeys were accurately able to determine if the electrical signal was of a higher or lower frequency than a preceding mechanical one provided to their fingertips. The authors determined that neurons in area 3b are involved in the perception of flutter and furthermore that these neural signals could be manipulated. Fifer et al. (2022) similarly used intracortical stimulation of the somatosensory cortex with electrode arrays in a tetraplegic patient to create finger tactile sensations (Fifer et al., 2022). The patient was able to accurately identify the location of seven different finger percepts. Chandrasekaran et al. (2021) was able to elicit fingertip sensations in two epilepsy patients by using stereoelectroencephalography depth electrodes to stimulate SI sulcal regions (Chandrasekaran et al., 2021). Flesher et al. (2016) induced "possibly natural" and "pressure" sensations in the hand of a tetraplegic subject by stimulation with implanted microelectrode arrays anteriorly on the crown of the postcentral gyrus (Flesher et al., 2016). These results demonstrate that BCI can induce cutaneous sensations, even in tetraplegic patients. However, both proprioceptive and cutaneous sensations are integral in the control of movement.

Proprioceptive percepts provide position information, while cutaneous sensations provide detailed sensory feedback often important for object manipulation (Armenta Salas et al., 2018; Dadarlat, O'Doherty and Sabes, 2015). Armenta Salas et al. (2018) implanted microelectrode arrays more posteriorly on the postcentral gyrus crown in a tetraplegic

individual and reported a mixture of both cutaneous and proprioceptive responses (Armenta Salas et al., 2018). The ability to evoke a specific sensation modality (e.g., proprioceptive versus cutaneous) or quality is possible through proper stimulation parameter settings in addition to accurate electrode placement. In a previous study using electrocorticography (ECoG) arrays, perception intensity increased when stimulation frequency, amplitude, and pulse-width were increased (Lee et al., 2018). This finding is similar to the microstimulation study by Flesher et al. (2016), where amplitude increases correlated with an increase in perceived intensity (Flesher et al., 2016). In determining how to elicit a specific sensation modality, Hughes et al. (2021) used microelectrode arrays and found that both high (100–300 Hz) and low (20–100 Hz) frequencies can produce a stronger percept depending on the stimulating electrode (Hughes et al., 2021). Amputee participants in Page et al. (2021) were able to distinguish proprioceptive and cutaneous location-intensity combinations by differences in stimulation site and parameters (Page et al., 2021). Stimulation parameters can be used in conjunction with electrode location to create distinct naturalistic proprioceptive and cutaneous sensations.

One future direction for BCI applications is determining whether stimulation of higher-order regions of the somatosensory cortex, such as SII, allows for higher-order percepts. For example, Lockwood et al. (2013) applied transcranial magnetic stimulation to the primary and secondary somatosensory cortices and they found disruption of pain intensity perception upon stimulation of SII, although localization of nociceptive stimuli was not affected (Lockwood, Iannetti and Haggard, 2013). Their findings are in line with other studies that similarly used transcranial magnetic stimulation of SII and found altered pain perception (Kanda et al., 2003; Grundmann et al., 2011; Valmunen et al., 2009). Although these studies point to a possible role of somatosensory manipulation in eliciting higher-order percepts, there have been no further studies to our knowledge investigating how stimulation of the higher-order somatosensory cortex affects sensation.

Identifying how sensory input is encoded in the human brain is critical to producing naturalistic BCI-induced somatosensation. To highlight the way SI encodes realistic somatosensory input, neural activity was recorded via ECoG electrodes during mechanical stimulation of the hands, such as soft, light, and deep touch. Signature changes in these signals included increased high-gamma (60–160 Hz) power and decreased alpha (8–15 Hz) and beta (15–30 Hz) power (Kramer et al., 2019a). Deep pressure elicited earlier increases in high-gamma power than light touch (Kramer et al., 2019a), suggesting that a stronger high-gamma response in SI can reflect the sensation of deep pressure. Ongoing studies are expanding upon these results to further understand how to produce reliable somatosensation through BCI.

The ideal electrode configuration for generating somatosensation has not yet been established. Our group found that high-density, "mini"-ECoG (mECoG) grids implanted in the hand area of SI in 13 epilepsy patients provided adequate coverage (63.9% of the hand) with low redundancy and high resolution (Kramer et al., 2020b). We also compared standard ECoG (sECoG), mECoG, and microelectrode arrays (MEA) in the hand region of SI to compare their ability to produce sensory feedback. Overall, sECoG provided the greatest coverage of the hand area (sECoG: 100%, mECoG: 41.7%, MEA: 18.8%) and the lowest resolution. Each electrode's stimulation resulted in sensation in 4.42 dermatomal divisions or boxes for mECoG, 19.11 boxes for sECoG, and 2.3 boxes for MEA. Redundancy, defined as the number of electrodes that generate sensation in the same dermatomal division, was lowest for mECoG (2.65 electrodes) compared to sECoG (3.68 electrodes) and MEA (11.22 electrodes) (Kramer et al., 2019b; Flesher et al., 2016). These results suggest that mECoG arrays may provide the optimal balance between resolution and cortical coverage for BCI systems (Kramer et al., 2020b).

NHP studies have suggested SI reorganization following sensory loss secondary to amputation and spinal cord injury (Jain et al., 2008; Merzenich et al., 1984). However, recent work with humans has

demonstrated retained SI organization despite amputations (Kikkert et al., 2016) or spinal cord injuries (Kikkert et al., 2021) that occurred decades prior. Kikkert et al. (2016) characterized digit topography using high-field neuroimaging in two study participants with unilateral arm amputation experiencing phantom limb sensations (Kikkert et al., 2016). The authors found the missing hand had preserved somatotopy similar to control patients: lateral representation of the thumb to medial representation of the little finger with clear digit preference in the central sulcus and postcentral gyrus. Previous work has shown that in individuals with amputated hands, the cortical representation of the amputated hand is activated during the use of the ipsilateral intact hand (Kikkert et al., 2016; Makin et al., 2013; Philip and Frey, 2014; Raffin et al., 2016). However, this proposed neuroplasticity may reflect the "winner-takes-all" analysis used to map somatosensation. Wesselink et al. (2022) demonstrated that for a single digit in the hand region of SI, the same somatotopy information of the adjacent digits is present when the main digit is blocked with anesthesia and when the digit somatosensory information is simply ignored in analysis (Wesselink et al., 2022). This would indicate that the overrepresentation of the intact hand in the cortex of the amputated hand may not be due to neuroplasticity, but simply due to the lack of sensory input from the amputated hand. Given these results, the functional layout of SI can help determine electrode placement in BCI regardless of a patient's injuries.

It is vital to understand proper SI somatotopy, especially after injury (Kikkert et al., 2021), as specific SI areas can be targeted with intracortical stimulation to provide sensory feedback in a body region. Restoring somatosensory feedback has vast implications for both BCI systems and patient quality of life. An NHP study using a closed-loop BCI system discovered that stimulation of SI evoked artificial tactile sensation and improved motor performance (O'Doherty et al., 2011). Restoration of hand sensation has been shown to improve motor performance in BCI systems (Flesher et al., 2021). Sensory feedback from both the hand and arm may improve reach-and-grasps tasks and manual dexterity (Bockbrader, 2019). In addition, restoration of lower limb sensation via intracortical stimulation may improve gait and coordination. Charkhar et al. (2020) found that sensory feedback enhanced postural stability in unilateral lower-limb amputees with closed-loop neuroprostheses (Charkhkar, Christie and Triolo, 2020). Foot sensation and proprioception are important for proper heel striking in closed-loop exoskeleton walking or preventing ulcers in paralyzed or diabetic patients (Bhattacharya and Mishra, 2015; Hicks and Selvin, 2019; Collinger et al., 2013). Stimulation at changing frequencies (Kramer et al., 2019c; Kramer et al., 2020a) or amplitudes (Armenta Salas et al., 2018; Lee et al., 2018; Flesher et al., 2016) can provide clearly delineated feedback to those areas. For genitourinary dysfunction, stimulation of the correct cortical regions or a combination of regions (such as SI, ACC, and prefrontal cortex) connected to the bladder or rectal stretch sensors may provide closed-loop feedback (Collinger et al., 2013) and help restore function. Similarly, an open- or closed-loop system could restore aspects of sexual dysfunction. Recent fMRI evidence suggests that while somatotopic information for each body part is concentrated in its previously defined region, the information is still present across all of SI at diminished levels (e.g., some foot somatotopic information is present in the cortical region dominated by hand somatotopy) (Muret et al., 2022). While BCI systems will likely focus on targeting SI regions where the desired somatosensory information is most concentrated, future systems may need to consider other SI territories to most emulate naturalistic percepts.

Less is known about SII somatotopy, as it lies in the deeper part of the inferior parietal cortex, making it difficult to investigate (Koch et al., 2010). While the somatotopy remains less clear, it is known that neurons in SII are selective for curvature (Yau et al., 2016) and may be important for higher-order features, such as attention (Burton et al., 1999) and pain (Ferretti et al., 2004; Strigo et al., 2003). Sensory information has also been shown to converge in SII (Carter et al., 2014), alluding to its importance in the integration and processing of higher-order

information that allows us to carry out complex tasks, such as letter recognition. In addition, as anal sensation may be processed in SII (Eickhoff et al., 2006), SII stimulation may play a role in the maintenance of continence. For these reasons, systems of BCI focused on the treatment of pain disorders may be effective in SII but have not been attempted. More naturalistic somatosensory information may be better delivered through stimulation of SII, particularly for closed-loop sensorimotor BCI where object recognition or manipulation are important.

Multiple sensory modalities converge in the parietal cortex. The parietal cortex may be important in attentional control tasks and interpreting tactile information (Macaluso and Driver, 2005; Burton et al., 1999). Parietal lesions have been associated with deficits in attention (Purves et al., 2001) and erectile function (Winder et al., 2017). Single unit activity in the parietal cortex has been shown to reflect different imagined sensations in humans (Bashford et al., 2021). Stimulation of the parietal cortex in BCI may improve erectile dysfunction and produce detailed sensory feedback important for tasks, such as object manipulation. Anal and rectal percepts may also be processed in the parietal association areas (Hobday et al., 2001). Stimulation of these areas may therefore help maintain fecal continence.

Understanding the proper somatotopy of SI and SII may help inform practitioners of the optimal locations to implant electrodes in a BCI system. The field has largely focused on hand and arm regions using intracortical microstimulation in SI of human tetraplegic patients. Future BCI systems should activate a variety of unique percepts across the body by stimulating multiple areas (including SI, SII, and the parietal association areas) and modulating stimulation parameters. Further research is needed to comprehensively map human somatosensation and to determine the optimal parameter settings and electrode configuration for a BCI system.

8. Conclusion

Engineering artificial somatosensation through cortical stimulation is the next step in realizing closed-loop BCIs. To accomplish this, a detailed understanding of cortical somatosensory organization is necessary. Here we provide an updated review of this organization. Overall, SI somatotopy is arranged in a medial-lateral fashion and is relatively discrete, particularly in the hand and face areas. SII organization is less well understood and more diffuse, with greater activation overlap, possibly owing to a functional rather than topographic layout; however, it also follows a medial-lateral trend. Further research in SI is needed to investigate the somatotopy of the lower limbs, particularly the digits of the foot. Future studies should also focus on SII somatotopy of the lower and upper limbs and investigate the higher-level processing that occurs in this region. Finally, somatosensory BCI involving SI and SII has the potential to improve symptoms in sexual dysfunction and incontinence.

CRediT authorship contribution statement

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Declaration of Competing Interest

None of the authors have potential conflicts of interest to be disclosed.

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