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Review article

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Emerging principles in functional representations of touch

Luigi Tamè[1] ✉ & **Matthew R. Longo**[2]

Abstract

The somatosensory system is fundamental to the formation and maintenance of coherent mental representations of the human body. Traditional concepts of somatosensation have been shaped by the principles of somatotopic and hierarchical organization of the primary somatosensory cortex and the motor cortex. However, emerging research has shown that perceptual and neural representations of touch are not fully captured by these principles. In this Review, we critically discuss how newer empirical research has expanded our understanding of touch and body representations. We first consider the role of higher-level categorical information about the body and its parts and the standard configuration of the body. We then discuss empirical evidence showing that functional representations of touch can complement and integrate across topographic organization. Finally, we review how the processing of touch is influenced by the source of the touch (another person or an object), and how the identity of the toucher shapes responses.

Sections

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[1] School of Psychology, University of Kent, Canterbury, UK. [2] Department of Psychological Sciences, Birkbeck, University of London, London, UK. ✉ e-mail: l.tame@kent.ac.uk

Introduction

The operation and coordination of the somatosensory and motor systems enable skilful and efficient interactions with the world and dextrous manipulation of objects[1]. The somatosensory system is a brain network responsible for the processing of tactile information deriving from objects or people and the generation of the sensory feedback necessary to guide motor behaviour. Somatosensation refers to the ability to process and interpret sensations from the body.

Although the somatosensory system is not often in the foreground of mental life, its critical role becomes apparent when it is lost. For example, an individual referred to as I.W. suffered an infection as a young adult that destroyed the majority of sensory fibres in his spinal cord, leaving him without tactile and proprioceptive information from the neck down[2]. Although he was not paralysed (his neuropathy did not affect the motor fibres), in the immediate aftermath of his illness I.W. was almost completely unable to produce skilled actions, such as walking or picking up a pen. I.W. was able to regain an impressive range of function only through continuous visual monitoring of his motor behaviour, requiring constant and taxing attention and vigilance[2]. This striking example suggests that intact somatosensation is essential to the automaticity and seeming effortlessness of everyday actions.

Effective interactions between the somatosensory and motor systems are paramount for performing fine motor behaviour. The classical view is that the somatosensory system is organized by topographic and hierarchical principles (in animals[3–5] and humans[6–9]). Topographic organization refers to the fact that adjacent sensory regions of the brain represent adjacent regions of peripheral receptor surfaces (on the surface of the body). The hierarchical principle refers to an increase in complexity of processing of tactile information from the lateralized response in the primary somatosensory area S1 (and within its four distinct cytoarchitectonic areas[5,10]) to higher-level brain areas such as the bilateral association cortices.

The motor system includes a series of central and peripheral structures responsible for the control of body movements. The primary motor cortex M1 has a somatotopic organization[11] similar to that of S1. However, M1 has larger integrated and overlapped areas compared to S1, which has a more discrete and segregated organization of different body parts[12]. These two systems communicate and interact constantly through an extended network of connections at cortical and subcortical levels[1,13–16]. Moreover, despite their differences in organization[12], they also share several properties and often work in tandem[17,18]. For these reasons, the systems are often considered together.

Newer empirical evidence suggests that the perceptual and neural representations of touch are not fully captured by or reducible solely to the classical view of the topographic architecture of the primary somatosensory cortex and the motor cortex[19–21]. In addition, it has been recognized that the topographic maps in the primary motor cortex are not perfectly defined but rather contain overlaps, reversals, and fractures[22]. Classical views also hold that tactile cortical activations are solely dependent on which mechanoreceptors in the skin are stimulated, known as the stimulus identity independence principle. However, tactile stimuli are processed differently depending on the stimulus identity, namely on whether they are produced by oneself, by another person[23] or by an inanimate object[24]. Thus, the source of touch should be also considered as critical information influencing how tactile stimuli are represented. Overall, newer empirical evidence strongly suggests that the classical view of somatosensory and motor organization is not able to account for the complex processing of tactile stimuli and body representations.

In this Review, we discuss three main aspects of touch processing that complement and extend the principles of topographic and hierarchical representations. First, we explore how high-level categorical information about the body shapes tactile perception. Second, we examine empirical evidence that highlights how functional representations of touch can conflict with the typical topographical organization. Finally, we focus on evidence showing that the processing of touch differs depending on the social identity of who is being touched, even when the stimulation is the same. We conclude that the classical view of tactile processing and body representations needs to include a series of additional rules integrated with the original topographic, hierarchical, and stimuli identity independence principles. We suggest a series of possible studies to further examine how these additional rules can be considered jointly with the classical organization principles of the somatosensory system. In this Review we do not examine proprioception and posture-related processing in detail, as they have been already discussed elsewhere[25,26].

Topographic representations

In the classical view of somatosensation, signals sent to the brain from the periphery and the resulting cortical activations depend on which receptors in the skin are stimulated. These signals project to topographically organized maps in the somatosensory cortex (Fig. 1a). Topographic organization is common across different sensory modalities as well as the motor cortex. In the somatosensory and motor cortices, it is also referred to as somatotopy.

Among the earliest evidence for localization of functions in the brain (in the late nineteenth and early twentieth centuries) were studies using electrical currents to evoke movements from stimulation of the primary motor cortex in animals[27–29]. Some studies attempted to apply this method to humans, with mixed success[30,31]. In 1937, researchers systematically mapped the somatosensory and motor cortices in humans undergoing surgery for intractable epilepsy[32], described the functional anatomy of these brain areas, and emphasized their somatotopic organization and the differential magnification of body parts as a function of their dexterity and sensitivity[6,33].

The primary somatosensory cortex S1 in the postcentral gyrus is organized with a one-to-one representational correspondence of different body parts, in humans and primates. For instance, the fingers are represented from little finger to thumb following a medial-to-lateral distribution symmetrically in the two hemispheres[9]. A similar arrangement is also present in the primary visual cortex V1, which represents the spatial organization of the retina and therefore of the visual field[34]. However, somatosensory maps contain more discontinuity in relation to the receptor surface[35] than retinotopic maps in the visual cortex. The topographic arrangement of somatosensory cortex in monkeys contains several boundaries in which the nearby cortical locations represent different parts of the body surface with non-overlapping receptive fields[36]. For instance, receptive fields abruptly pass from the representation of the face to the arm or from one finger to another. This difference in topographic maps between sensory modalities might derive from a reduced correlation of locally stimulated skin receptor surfaces in the somatosensory system[35]. It also probably reflects the fact that although the retina is approximately circular, the skin has a complex and irregular shape that cannot simply be flattened and mapped directly onto the cortical surface without discontinuities and violations of strict somatotopy.

The topographic organization of somatosensory cortex is well captured by one of the most famous illustrations in neuroscience, the somatosensory (and motor) homunculus[37] (Fig. 1b). This illustration

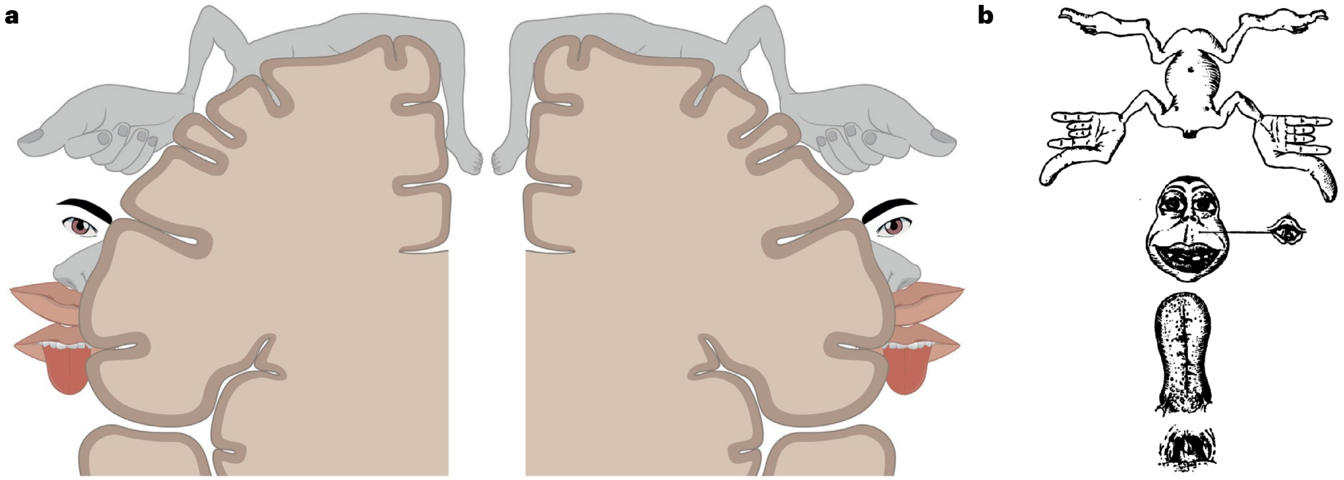

Fig. 1 | Cortical representations of touch. **a**, Coronal view of the primary somatosensory cortex of the two hemispheres with a superimposition of the classical somatosensory 'homunculus' highlighting the magnification factor and topographic organization of body parts. **b**, The somatosensory homunculus representation[32]. Part **a** is adapted from ref. 171, CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/). Part **b** adapted with permission from ref. 32, Oxford University Press.

represents the cortical territory devoted to each body part and the topographic organization in which specific portions of the cerebral cortex are linked with specific parts of the body[6,32,33]. Many researchers have corroborated this notion and confirmed these organizational principles in humans[8,38] and primates[39–41]. Such a spatial representation of touch has also been found beyond the primary sensorimotor cortices, although the relative magnification of different body parts varies across regions[42–44].

In early Nissl staining studies, the primary somatosensory cortex was divided into four distinct subregions (areas 3a, 3b, 1 and 2)[45–48]. This parcellation has been confirmed by neuroanatomical studies[48]; studies using magnetic resonance imaging (MRI) have shown differences between areas in cortical thickness[49], myelinization[50], and population receptive field size[51]. These areas show selectivity for different classes of afferent inputs, such as ones coming from touch (such as vibration or skin stretch) and proprioception[52]. There is evidence for a hierarchically organized flow of information between areas, with areas at the lower levels of the hierarchy processing basic information such as the location and intensity of a stimulus, and higher levels processing more complex information such as texture and shape, from receptive field mapping studies[4,53], lesion studies[54–56] and functional magnetic resonance imaging (fMRI) in humans[51].

This classical characterization of somatosensory system organization does not fully account for circumstances in which tactile coding is based on categorical rather than topographic representations of the body, the functional roles of the body parts and specific task demands. An additional intriguing aspect that might extend the classical principles is coding that represents when touch is produced by oneself, by another person or by an inanimate object. All these aspects will be discussed in the next sections.

Categorical representations

Topographic accounts of touch view tactile representations as essentially continuous, with interactions between skin regions based on their adjacency within somatotopic maps. In this section we discuss evidence for more categorical representations of touch and try to identify the circumstances in which touch is represented using categorical rather than continuous representations. In the visual domain, a fruitful approach towards a better understanding of visual information processing is the study of the dichotomy between categorical and coordinated representations of spatial relations[57]. We start by describing behavioural studies that show that touch is coded using categorical representations and evidence from neuroimaging studies in humans that shows that category boundaries are a basic feature of somatosensory maps. Then we discuss evidence suggesting that touch is represented beyond the homuncular organization through preferential associations of some body parts with certain locations in space.

Categorical perception

One fundamental way in which categories influence cognition is the phenomenon of categorical perception[58], in which stimuli falling on opposite sides of a category boundary are perceived as more different than they really are and stimuli falling on the same side of the boundary are perceived as more similar. Studies have shown that the boundaries between body parts function as categorical borders in this way, leading to overestimation of the distance between two touches when they fall onto different body parts (Fig. 2a). For example, participants judge distances between two touches on opposite sides of the wrist (one on the forearm and one on the hand) as larger than equivalent distances between two touches both located on the forearm or hand[59]. A subsequent study found that this effect depends on the orientation of the stimulus: distances are expanded at the wrist when the touches are oriented with the proximo-distal arm axis (when they cross the wrist), but not when they are oriented with the medio-lateral arm axis (merely near the wrist)[60]. Like adults, children perceive the distance between two tactile stimuli that cross a body boundary (such as the hand and arm) as farther apart than ones that are presented within the same limb[61]. One difficulty in all these studies is that there are probably differences between tactile processing on the hand and forearm, which makes it hard to match the different conditions exactly. Nevertheless,

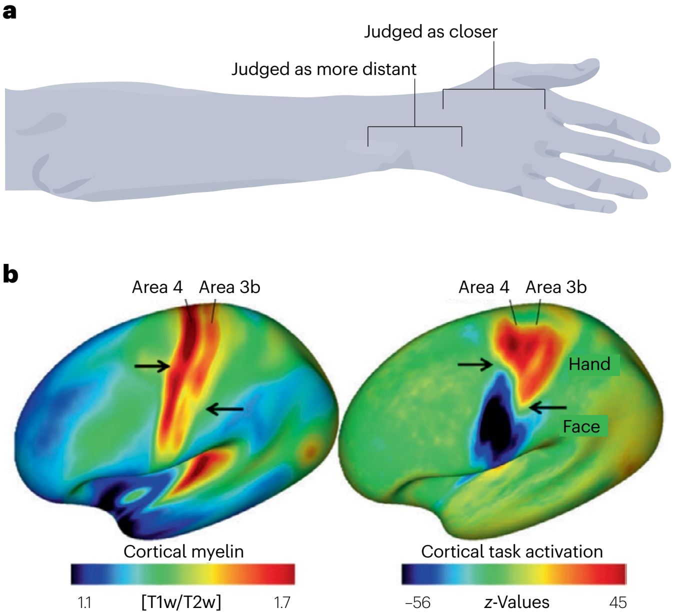

Fig. 2 | Categorical representations. a, Judgements of the distance between two points on the skin when the touched points are within the same body part (hand) or across body parts (hand and forearm). Differences in judgements support the categorical representation of touch. **b**, Relationship between cortical myelination and cortical task activation. Cortical myelin content and activation averaged over a large group sample. Activation is measured as the change in functional magnetic resonance imaging (fMRI) blood-oxygen-level-dependent (BOLD) signal change (*z*-values), with the contrast shown as hand minus [face plus foot], face minus [hand plus foot]). Arrows indicate the S-shaped border separating the hand and face representation areas. T1s, T1-weighted MPRAGE scans; T2w, T2-weighted MPRAGE scans. Part **b** reprinted with permission from ref. 76, Oxford University Press.

these results suggest that perception of tactile distance depends on the categorical segmentation of the body into discrete parts, a classic categorical perception effect. These results make sense given that joints are the 'hinges' that segment the body into parts[62]: the joints both attach parts to the rest of the body and allow them to move independently, analogous to the way a hinge connects a door to a wall.

The neural representations of the body surface as discrete body parts have also been studied using electroencephalograph (EEG) recording. The somatosensory mismatch negativity has been used as an index of categorical body boundaries[63]. Researchers presented pairs of tactile stimuli at equal spatial distances across the wrist or only on the forearm while recording EEG activity. Standard stimuli were presented on the distal part of the forearm, whereas oddballs were presented on the proximal part of the forearm (within the same limb) or on the hand (across the boundary of the wrist), at an equal distance from the standard. The amplitude of the somatosensory mismatch negativity was greater when stimuli were presented across than within the body boundary[63]. This effect was present from early stages of tactile processing (80 ms), suggesting early categorical processing of the body in the somatosensory system. Similar effects have been found across the wrist boundary in 6–7-month-old infants[64]. This evidence from pre-verbal children provides further support to the idea that categorical perception in touch is not due to linguistic labelling of body parts.

Myelinization

Neuroanatomical studies have also provided evidence that category boundaries are a basic feature of somatosensory maps. Despite being folded in complex ways, the cerebral cortex – like the skin itself – is typically studied as a continuous two-dimensional sheet of cells. However, developments in neuroimaging technology permit the investigation of the three-dimensional structure, considering cortical layers[65,66]. For instance, one study used 7T MRI to reveal that the structural boundaries between the hand and the face do not appear between individual finger representations in S1[67].

Within somatotopic maps of the body in somatosensory cortex, boundary regions of comparatively low myelinization, known as septa, form categorical boundaries between regions representing different body parts. In rodents, the somatosensory 'barrel' cortex represents individual whiskers in distinct regions ('barrels') divided by septa with low myelinization[68], reflecting the categorical representation of each whisker. Intriguingly, compared to the barrels themselves, cortical columns in these septal regions receive inputs from different thalamic connections[69], show integration of information over larger spatial areas[70], have different patterns of intracortical inhibition[71], and have denser connections to both primary motor cortex[72] and posterior parietal cortex[73]. These results suggest that in addition to forming categorical body-part boundaries, rodent septa have important functional roles in spatial integration of information and guidance of behaviour. In monkeys, there is evidence for similar septa separating the representations of each finger in primary somatosensory cortex, as well as a septum separating the representations of the hand and face[74].

Septal boundaries were reported in humans more than a century ago on the basis of cadaver studies[75]. Primary motor (area 4) and primary somatosensory (area 3b) cortices are divided by a septum of low myelinization that separates the representations of the hand and face. Although these findings were overshadowed by more influential parcellations of the brain, a neuroimaging study has replicated this main result using MRI-based myelin mapping[76]. An S-shaped region of low myelinization cuts across the primary motor and somatosensory cortices, dividing each of these regions into different cortical fields, each representing a major body part such as the hand and face (Fig. 2b). Moreover, these anatomically defined borders closely align with borders between regions with high levels of functional connectivity, indicating that neurons communicate more strongly with other neurons on the same side of the boundary.

Spatial associations

Another line of evidence for tactile representations beyond the homuncular organization is the presence of preferential associations of some body parts with certain locations in space[77]. In a series of behavioural experiments, stimuli were delivered to the left and right thumb and index fingers. The hands were placed so that one hand was on top and the other on the bottom. Participants were asked to discriminate as quickly as possible whether a tactile stimulus had been presented on a finger that was in a 'top' or 'bottom' position in space, regardless of whether the thumb or index finger had been touched. Participants were faster and more accurate when responding to a touch on the index finger when the finger was located in the top spatial position, and to a touch on the thumb when it was in the bottom spatial position[77] (Fig. 3c).

In a subsequent study, the researchers found faster and more accurate responses to touch on any finger when the finger was located above the thumb rather than below it, suggesting a preferential association between all of the non-thumb fingers and an upper position in space[78].

Such preferential associations are specific to the fingers; no analogous associations were found on the toes[79] (Fig. 3c). The researchers suggested that this preferential configuration corresponds to the standard posture of the hand, and is possibly related to hand use, in which hands are naturally presented with the thumb in a relatively lower position and the other fingers in a relative upper position. It is possible that early experiences of active use of the hands include physical and functional constraints that induce the use of the hands with the thumb in a lower position[80].

Spatial prototypes

Another example of categorical information in touch comes from evidence of the use of spatial prototypes for tactile localization. In vision, reproductions of the remembered location of a visual stimulus are based on a weighted combination of actual memory traces with spatial prototypes, which function as Bayesian priors of location within a shape[81,82]. For example, when participants have to remember the location of a stimulus presented within a circle, they implicitly project vertical and horizontal axes onto the circle, and responses are biased towards the centre of mass of each of the resulting quadrants[81,82]. The centre of each quadrant therefore acts as a spatial prototype, pulling responses towards it. There is evidence that similar spatial prototypes are used for tactile localization[83,84]. In one study, participants localized tactile stimuli on their forearm that were either just above the detection threshold (weak stimuli) or well above the threshold (strong stimuli)[83]. Localization of weak stimuli showed greater variability and was biased toward the centre of the forearm, suggesting that the forearm is treated as a single categorical unit with a single spatial prototype in the centre. Moreover, the location of past targets affected the perceived location of current tactile stimulation, suggesting that spatial prototypes can be constructed rapidly on the basis of the immediately preceding history of stimulation. It is unclear from this study[83] whether responses were based entirely on the history of stimulation or whether there are also spatial prototypes based on the geometry of the limbs.

Consistent evidence of the use of spatial prototypes in tactile localization has been found in patients with somatosensory deficits caused by heterogeneous lesions following stroke[85]. Patients performed a tactile detection and localization task on the dorsal surface of the hand. The researchers systematically compared the patients' categorial biases in tactile localization to their degree of basic sensory impairment. Patients with higher tactile detection thresholds (higher levels of basic somatosensory impairment) were more likely to localize the stimulus toward the centre of the hand. Localization uncertainty – rather than increasing error rates – increased the systematic bias towards a certain location on the hand. The centre of the hand therefore acted like a Bayesian prior for localization, suggesting that, like the forearm in the study described above[83], the hand dorsum is treated as a single spatial category with its centre serving as a spatial prototype.

Overall, several behavioural findings and neuroanatomical evidence suggest that the topographic organization of the somatosensory cortex can be complemented and/or extended by forms of representation beyond topographic principles of organization (Table 1). Categorical organization of tactile coding is likely not to be accidental, but might instead have specific functional roles, as we discuss in the next section.

Functional representations

In this section, we discuss to what extent tactile coding is guided by the functional roles of the different body parts and immediate task demands, beyond topographical organization. We will describe the concept of tactile equivalence, how representations can overlap across different body parts, and how tactile representations can follow an organization that reflects the body part's functional use rather than its topographic arrangement.

Tactile equivalence

In the motor system, skilled and purposeful actions tend not to be performed rigidly in the same way upon repeated performance[86]. Rather, behaviours that are recognizably the same action can involve a range of patterns of muscular contractions and kinematic patterns, and even can be performed with different limbs entirely (Box 1). The importance of this motor equivalence is that the internal representation of an action reflects the final state or goal to be achieved, rather than the details of the kinematic motion or muscular contraction required to implement the goal[87,88]. Consistent with this principle, studies with sub-millimetre fMRI have shown that each finger has multiple mirrored representations in M1 that correspond to different finger movements[89].

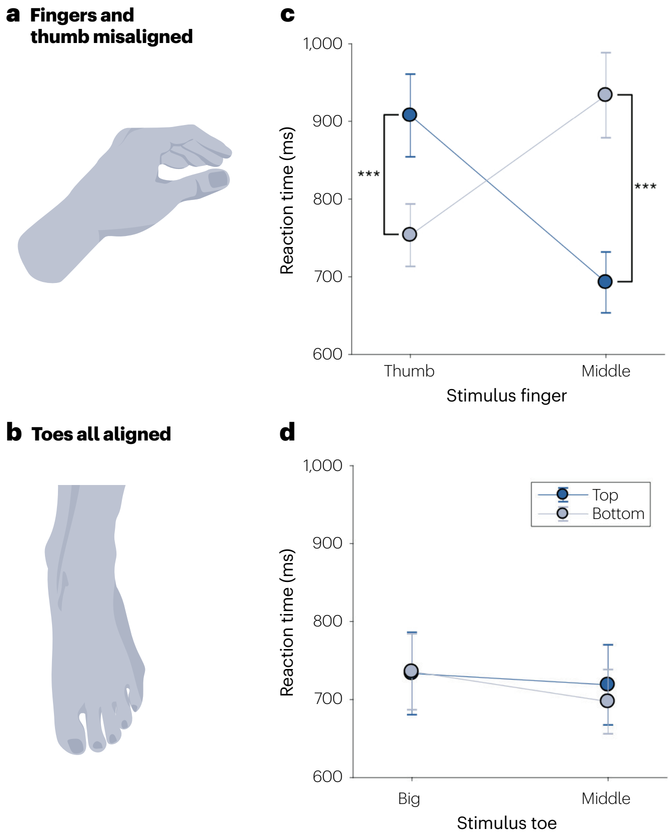

Fig. 3 | Influence of typical postures. a,**b**, The preferential configuration that corresponds to the standard postures of the hand (**a**) and foot (**b**). The typical posture of the hand as depicted (**a**) is characterized by the alignment of the four fingers opposite to the thumb, in contrast with the foot configuration in which all the toes are aligned (**b**). **c**,**d**, Typical pattern from the elevation paradigm for the fingers (**c**) and toes (**d**). **c**, Participants are considerably faster at responding to the fingers when the thumb is in a relatively lower position, and the middle finger in a relatively upper position, than vice versa. **d**, Participants are equally fast at responding to the toes in all locations. Error bars, s.e.m. ***$P < 0.001$. Parts **c** and **d** reprinted with permission from ref. 79, Sage Publications.

Table 1 | Updated principles of touch

Principle	Summary	Representative finding
Categorical representations		
Categorical perception	Segmentation of the body into discrete parts alters tactile processing	Perceived tactile distance is expanded when two touches lie on opposite sides of the wrist boundary[59–61]
Body-part boundaries	Septa with low myelinization form hard body-part boundaries in S1	S-shaped septum cuts across S1 and M1, separating hand and face representations[76]
Spatial associations and prototypes	Processing of touch is altered by Bayesian priors for body posture and skin location	Tactile processing is faster when fingers are in a 'standard' posture[77,78]
Functional representations		
Tactile equivalence	Tactile processing can be partly independent of which skin region is stimulated	Touch is mislocalized to a body part of the same laterality (left hand to left foot) or limb type (left hand to right hand)[21]
Distributed and overlapping representations	Somatosensory processing of different body parts is distributed and overlapping	Body-part identity can be decoded from widespread regions of S1, not only in the primary region of the homunculus[19]
Functional organization	Some representations are based on the functional role of stimulus or action, not the specific body part	'Hand-like' representations of feet are present in people born without arms[118,120]
Source		
Self-touch	Predictions of sensory consequences of action shape the processing of self-generated touch	Sensory delays lead to rapid recalibration in self-touch, which modulates the ability to tickle oneself[156]
Affective touch	The specialized C-tactile system processes 'affective' touch from other people	Other peoples' forearms feel softer and smoother than ones' own, particularly when touched at velocities optimal for the C-tactile system[24]

S1, primary somatosensory cortex; M1, primary motor cortex.

Whereas motor equivalence has been an influential theoretical concept in motor control, research on touch has been guided by the principle of body-part specificity. However, emerging research has suggested that there might be analogous forms of 'tactile equivalence'. For instance, when one touches an object (such as a phone) it can be recognized regardless of the number of fingers used in the touch (two, three, four or five). It has been also shown that perception of the roughness of a surface is independent of the way it is touched, known as roughness constancy[90]. However, hand movement is necessary to achieve such constancy through the contribution of proprioceptive inputs.

Perceiving the location of a touch is frequently presented as a necessary condition of feeling it at all[91]. However, various tactile mislocalizations have been reported in typical adults, including consistent directional biases[92] and confusions among fingers[93,94] and among toes[94–96]. Some of these mislocalizations are consistent with somatotopic maps. For example, touch on one finger is more often mislocalized to adjacent fingers than to more distant fingers[93,94,97], consistent with levels of overlap in S1[98]. Similarly, people with upper-limb amputation sometimes feel tactile stimuli that are applied to the face on their phantom hand[20,99], consistent with the adjacency of hand and face regions in the S1 homunculus. Similar phenomena have also been found in typical individuals as a result of tactile learning[100]: induced improvement in tactile spatial discrimination is seen not only at the trained body site (such as the index finger), but also on an untrained face region[101]. However, other mislocalizations are harder to explain in terms of somatotopic maps. For example, in some people with upper-limb amputations, referred tactile sensations from stimuli applied to the feet can be elicited on their phantom hand[20,99], despite the foot and hand not being adjacent in S1 somatotopic maps.

One study provided striking evidence for tactile mislocalizations in typical participants that seem to be based on coding of abstract features of limbs rather than adjacency within somatotopic maps. Participants were sequentially touched on two different limbs (for example, right hand and right foot) and judged which limb had been touched first[21]. Remarkably, participants frequently (8% of trials) misattributed touch to a limb that had not been touched and these mislocalizations tended to match the actual stimulation site either in laterality or limb type. If the right foot had been touched, participants tended to mislocalize touch to the right hand (matching laterality) or left foot (matching limb type), but not to the left hand (Fig. 4). This pattern suggests that the felt location of touch was coded in terms of a set of categorical features ('right' and 'foot'), rather than a location within a continuous map.

Another intriguing feature of these mislocalizations links them with the findings on standard postures described in the previous section. For different conditions, participants either kept their limbs uncrossed, with each limb on its usual side of space, or crossed their limbs such that the right limbs were on the left side of the trunk and vice versa. Mislocalizations often corresponded to the correct categorical body part such as type (hand/foot) or side (left/right) only when the body parts were positioned on their typical side of the body. The neurons in the S1 homunculus that receive afferents from the hands and feet are cortically far apart[6], making misrepresentation at this level unlikely. However, hands and feet are represented in close proximity in higher-level areas such as the secondary somatosensory cortex[102,103]. Moreover, the interconnections with other somatosensory areas and subcortical regions might be able to account for such tactile misperceptions[104,105]. Another possibility, in line with evidence reviewed throughout this section and as proposed by the study authors, is that touch location is represented with respect to its categorical affiliation[21] based on limb and side rather than exclusively following the topographic organization.

Distributed and overlapping representations

Traditional approaches to mapping sensorimotor brain areas have identified somatotopic maps by attributing each brain area (neurons in electrophysiological studies; voxels in neuroimaging studies) to the body part that evokes the strongest positive response. This approach has been very helpful in understanding the brain mechanisms underlying touch and has identified somatotopy as a potentially dominant principle of brain organization. However, this winner-take-all approach might have led other features of these maps to have been missed. For example, an fMRI study reported striking patterns of de-activations in S1 following touch on different skin regions[105], which co-existed with the more widely investigated activations. This pattern might reflect a sharpening process based on lateral inhibition, in which focal activations of a preferred body part within a somatotopic map result in de-activation of areas representing other parts.

Even more striking deviations from a purely somatotopic pattern were found in a study of somatosensation during action[19]. In everyday life, tactile stimulation is usually accompanied or caused by action. Indeed, the sensory and motor systems are intimately related, both anatomically and functionally[13,16,106–108], with continuous reciprocal exchange of information and interactions[1,109]. Despite their differences[12], the somatosensory and motor cortices might share some functional organization principles. In one study, participants performed simple movements or object-directed actions with different body parts (such as moving the fingers, part of the face, or squeezing or pushing an object) while lying in the MRI scanner[19]. Using representational similarity analysis, the researchers found that two different movements performed by a single body part (such as the hand) could be distinguished from patterns of activation outside the primary representational brain region for that body part (for instance, hand movements in the foot and face region) within S1. They interpreted these results as evidence for distributed information of the different body parts across S1, rather than the classical topographical organization[19]. Even if somatotopy provides a major, and perhaps dominant, organizing feature of the somatosensory cortex, it co-exists with and is complemented by other types of organization.

There is also evidence that the mental representations of the hands and feet overlap in several ways. One line of evidence comes from individuals with Gerstmann's syndrome, a condition that can arise from brain damage and involves a range of symptoms including finger agnosia[110]: the loss of the ability to distinguish, name or recognize the fingers. Intriguingly, finger agnosia frequently co-occurs with toe agnosia[111,112], suggesting functional links between the representations of fingers and toes. This association is particularly informative because it supports the notion that the hands and feet are serially homologous structures that co-evolved[113], resulting in a number of physical similarities (such as both having hairy and glabrous skin on their alternate sides[114], and sharing a qualitatively similar structural plan[115]). Functional links between hands and feet have also been identified in participants without brain damage, who demonstrate similar patterns of mislocalization between the fingers[94,116,117] and toes[94,95], showing a bias for touch to be mislocalized towards the centre of the limb. One study used representational similarity analysis of behavioural judgements of which digit was touched to show that individual differences in the patterns of mislocalization are shared between fingers and toes[96].

Functional organization

The presence of shared representations across hands and feet is also evident in individuals born without upper limbs, who can show a high level of dexterity and perform complex actions with their feet. Several studies have investigated somatotopic and functional representations in these individuals, although with divergent conclusions. In some fMRI studies, it was found that the primary sensorimotor areas that would ordinarily represent the hand were activated by neighbouring body parts, such as the shoulders and torso, but critically not by the feet[118,119]. In sensorimotor association cortices such as the intraparietal sulcus, premotor cortex, and supplementary motor area, representations appeared to generalize across different effectors (the hands and feet). By contrast, another fMRI study used phase-encoded mapping to investigate somatotopic maps of the toes in two individuals born without arms, and found that the ordering and structure of these individuals' toe representations mimics the typical hand representation in regions of the somatosensory cortex (similar to the locations of toe and finger maps in typical individuals)[120].

This latter finding and other results[17] are compatible with the notion that somatosensory representations are shaped not only by their cortical proximity in the somatosensory and motor cortices but also by the body parts' functional use[121]. For instance, in congenital hand absence, the brain regions (in the cerebral cortex and cerebellum) that would represent the hand in individuals born with hands instead process information from multiple body parts[122]. Thus, hand regions can also process information that comes from neighbouring cortical regions.

The relationship between the representations of the functional roles of different body parts has also been investigated in the motor cortex of people with tetraplegia, who do not have the ability to move their upper and lower limbs voluntarily. Multi-unit recordings were made from the hand knob brain area in the precentral gyrus during movements of the face, head, arm and legs[123]. There were strong representations in this 'hand region' for all the movements tested, and a partial compositional neural code was found that linked all the limbs. For instance, a movement coding component was similar when participants grasped with the hand and curled with the toe. These shared representations might facilitate skill transfer across limbs. Shared representations across different limbs have also been reported across hemispheres. Although motor control is clearly lateralized[32], neurons in the ipsilateral motor cortex are active during movements with a single hand and can represent the ipsilateral limb position[124]. For instance, fMRI response patterns in the left and right motor cortices are very similar if the direction of the movement is mirror-reversed across the body midline[125]. This result suggests that there are neurons in the ipsilateral and contralateral motor cortices for both hands that are effector-invariant neurons encoding movements regardless of hand[125]. Effector-independent responses have also been demonstrated

Box 1

Motor equivalence

A central concept in motor control is motor equivalence: the principle that behaviours that can differ substantially in their detailed kinematics are nevertheless represented as the 'same' action. For example, it was shown in classic studies that when someone performs a repetitive movement such as hammering a nail, there is substantial trial-to-trial variability in the exact trajectory of the hand through space[172]. By contrast, there is much less variability in the final position of the hammer on the nail head. This result shows that the action is being coded in terms of the desired end state, with the detailed muscular contractions required to achieve that goal left to be filled in depending on the immediate state of the system as the action is implemented. Similarly, when writing one's name on a sheet of paper or on a blackboard, totally different patterns of hand and arm movement are involved[86]. Nevertheless, the style of text produced is nearly identical[173,174], and similar patterns of brain activity are produced in the motor cortex[175]. Analogous findings are also found for writing with different effectors entirely. Although most people write exclusively with a single preferred hand, writing performed with the other hand or even with a pencil held between one's toes or in the mouth shows a recognizable personal style (even if it is less legible)[87,176].

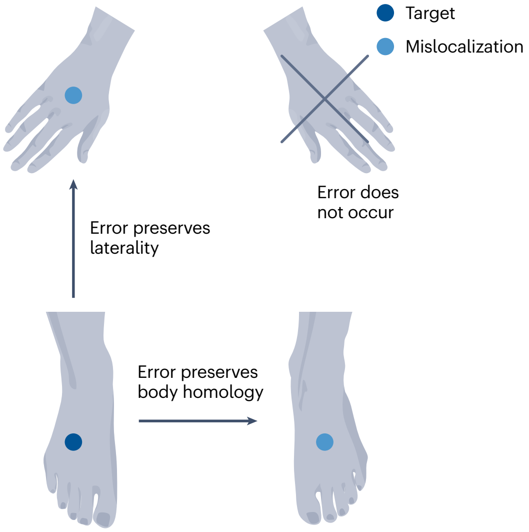

Fig. 4 | Example of the pattern of tactile mislocalizations across hands and feet. In the example, the right foot is touched (dark blue circle). When mislocalized (light blue circles), touch is wrongly attributed to either the homologous limb (the left foot, preserving body homology) or the limb on the same side of the body (the right hand, preserving laterality). Adapted with permission from ref. 21, Elsevier.

in the posterior parietal brain regions when participants perform goal-directed actions[126].

Topographic and non-topographic interactions in the primary somatosensory cortices of the two hemispheres have been demonstrated when touch occurs on the hands both unilaterally and bilaterally[104,127]. In one study, neuromagnetic activity was recoded when a probe stimulus was delivered on a specific finger and an adaptor stimulus was delivered on the same finger as the probe (homologous) or on a different finger (non-homologous)[127]. When the stimuli were on different hands, repetition suppression in S1 was larger for homologous than non-homologous fingers, but only when there was a short delay (25 ms) between the adaptor and the probe[127] (for a detailed explanation of the relationship between topographic organization and repetition suppression in this context, see refs. 104,127,128). Thus, topographical activation in S1 is affected by the characteristics of the stimulus, including the timing between stimuli. Another study used transcranial magnetic stimulation to show that the timing of tactile stimuli can influence the transfer of somatosensory information to the motor cortex and influence corticospinal excitability[128]. When tactile stimuli were delivered to the fingers with a short delay between them, the stimulus location was reflected in corticospinal excitability, but this spatial information was lost when the delay between stimuli was longer[128]. This series of studies suggests that body parts that are positioned at the periphery with respect to the body midline – such as the hands – and have less dense callosal connections relative to the trunk[129] have close interhemispheric interactions at the cortical level, possibly owing to their functional role[129–131]. Moreover, the topographic activation pattern is modulated by the timing between the stimuli. These findings are compatible with the specific structural connectivity architecture of the sensory and motor systems: U-shaped fibres directly connect S1 and the motor cortex[13].

The traditional view of brain responses is that each brain area is highly specialized and responds to specific functions. However, several lines of empirical evidence suggest that in the parietal and frontal brain areas, the same neurons respond in a distinctive manner in different contexts (different motor tasks)[132–134]. Thus, areas including the posterior parietal cortex are said to have a mixed-selectivity architecture[132,134–136]. However, this pattern does not imply that posterior parietal cortex is non-topographic, because the presence of somatosensory responses that resemble homuncular organization (with altered body-proportion representations) has been reported in high-level brain areas including the posterior parietal cortex, possibly related to the functional role of the region[42]. Such a mixed-selectivity model could possibly also be applied in the tactile domain[137]. Mixed selectivity is supported by findings of responses in the posterior parietal cortex that generalize across the left and right hands[131] and across hands and feet[126]. Mixed selectivity in the somatosensory system can help to explain the patterns of tactile mislocalization described above that do not follow patterns of somatotopic organization[21].

In summary, the functional relations between body parts have an important organizing role in the somatosensory and motor systems (Table 1). These findings emphasize that topographic representations based on the physical proximity of body parts – as emphasized by the classical view – are an incomplete explanation of the sensorimotor system. Brain regions within the somatosensory and motor systems are instead likely to be organized according to additional principles that reflect their divergent functional roles within larger-scale brain networks. Even within a region, different organizational strategies might be combined onto single neural populations (multiplexed), both for the purposes of computational efficiency and to allow coordinate transformations between different representational modes.

Source of touch

Classical views state that tactile cortical activations are solely dependent on which mechanoreceptors in the skin are stimulated. However, which receptor was stimulated is not the only factor that alters brain responses. Research has identified several situations in which the same physical inputs on the skin are processed differently depending on the 'identity of the stimulus', or whether they are produced by oneself, by another person or persons, or by an inanimate object[138,139]. For instance, touch by one's partner or a stranger in a social context will produce an identical physical signal that is indistinguishable in the afferent responses. However, these touches are probably processed very differently and the perceptual experience can be very dissimilar[23]. Such effects have provided intriguing evidence for deep links between basic aspects of tactile perception and broader brain networks underlying cognition. We will next describe two sources of touch that alter the way in which touch is processed, namely the self and affective touch.

Self touch

One line of evidence for effects of identity of the stimulus on touch comes from patients with somatosensory loss following stroke. In many cases, patients who are unable to detect tactile stimuli applied by an experimenter to their contralesional hand report feeling touch applied by their own other hand[140,141]. One interpretation is that touch is easier to detect when its timing can be predicted. However, another study showed that continuous self-touch of the contralesional limb by the patient also enhanced detection of touches applied by an experimenter[142]. Intriguingly, self-touch appears to have widespread effects, temporarily alleviating not only basic sensory loss, but also feelings of limb disownership[143].

The importance of self-touch can also be appreciated from work on internal models used to anticipate the sensory consequences of actions based on efferent copies of motor commands[144]. According to these models, expected touches resulting from one's own actions should be attenuated, prioritizing perception of unexpected events. Indeed, numerous studies over the past two decades have shown that self-produced touches are perceived as less intense[145,146] and less ticklish[147,148] than equivalent touches delivered by other people.

One set of studies has shown that attenuation occurs only in situations consistent with actual self-touch and is not related more generally to touches caused by movements of one's body. For example, clear attenuation of perceived force is experienced for touches caused by the finger of the contralateral hand touching a force sensor (that controlled the force applied) located immediately above the touched hand. This situation approximates self-touch in that the touching hand is spatially close to the touched hand. However, such attenuation disappears (or even reverses) in situations inconsistent with self-touch, such as when caused by pressing a sensor located farther away from the resulting touch[149,150] or by moving the finger in space without pressing the sensor at all[151]. Another study showed that when the participant's hand was touched by a rubber hand, attenuation of perceived force occurred only when the participant experienced ownership of the rubber hand (induced by a period of synchronous movements of the participant's own hand and the rubber hand)[152]. Other studies have similarly shown that the perceived intensity[153] and the amplitude of somatosensory evoked potentials (measured by EEG)[154] of electrical stimuli are attenuated when triggered by a button pressed by a rubber hand that was experienced as the participant's own hand. Together, these results suggest that tactile attenuation occurs when one touches oneself with what seems to be another part of one's own body. In other situations in which tactile stimuli might be predictably caused by one's own actions, but which cannot be interpreted as self-touch, enhancement of touch is sometimes observed[151], consistent with Bayesian models of perception that emphasize perception of expected, rather than surprising, stimuli[155].

Other research has shown that attenuation effects are adaptively linked to estimates of the temporal delay between initiation of an action and the resulting tactile sensation (which provides feedback to the motor system about the consequences of actions). In one study, delays were introduced between a movement of one hand and the resulting tactile stimulus produced on the other hand[148]. With delays of as little as 100 milliseconds, participants rated the resulting stimuli as more ticklish than the immediate touch, suggesting that attenuation is tightly linked to the expected time of self-touch. In another study, participants pressed a button with their right index finger that caused a touch on their left index finger, located just below the button[156]. Test trials were preceded by an exposure period in which a systematic delay or no delay was introduced between the button press and tactile stimulus. Following exposure to the delay, there was an increase of tactile attenuation for delayed stimuli, as well as a reduction of attenuation for stimuli with no delay. Thus, the sensorimotor system and the internal model used to make predictions about self-touch rapidly recalibrate to account for changes in sensory delays. In a second experiment, the same researchers used this recalibration to influence the ability of participants to tickle themselves[156]. Participants applied self-touch to their forearm via a robot either with or without a delay. Consistent with previous research[148], participants judged the delayed stimulus to be more ticklish than the non-delayed stimulus. However, the bias was substantially reduced following an exposure period to multiple delayed stimuli.

Attenuation from self-touch has also been seen in differential patterns of brain response to touches from oneself and others. For example, in an fMRI study, participants received gentle strokes to their left forearm performed either by their own right hand or by an experimenter[157]. In comparison to being touched by another person, brain responses to self-touch showed widespread deactivations in numerous brain areas, including S1, the anterior cingulate cortex, and the anterior and posterior insula. Notably, in the self-touch condition there was clear activation in S1 contralateral to the hand that was doing the stroking, but not in S1 contralateral to the arm that was being stroked. This pattern suggests that sensory attenuation in self-touch is specifically linked to the region of skin being touched, not to the body part being actively moved (although it is also possible that such attenuation is masked by activations related to generating the movement). The link between attenuation and the skin being touched makes sense given the importance of tactile feedback from the moving fingers for haptic object recognition[158].

There is also evidence that self-touch results in changes in functional connectivity between brain regions. Both M1 and S1 show increased functional connectivity with the posterior insula during self-touch[157]. Another study found that S1 and S2 showed increased functional connectivity with the cerebellum during self-touch[159]. In addition, the magnitude of these changes was correlated across participants with the amount of tactile attenuation measured in a psychophysical task.

Affective touch

Another line of evidence for differential processing of touch depending on the identity of the stimulus comes from studies of the C-tactile system. C-tactile afferents are a class of unmyelinated afferents found exclusively in hairy skin and that seem to be related to pleasant sensations[160], with signals that project primarily to the insula, rather than to the somatosensory cortex[161,162]. Intriguingly, they show selective responses to specific velocities[163,164] and temperatures[165] that are consistent with social, interpersonal touch. Thus, in contrast to tactile attenuation – which is related specifically to self-touch – the C-tactile system is related specifically to touching other people. In one experiment, fMRI was used to compare brain responses to strokes and taps applied to the forearm either by an experimenter's hand or by an inanimate object (a stick covered in velvet)[138]. For the stick touches, similar brain responses were found for the taps and strokes. By contrast, for the experimenter's hand, stroking produced larger responses than did taps in S1, S2 and the posterior insula.

Another relevant effect is the social softness illusion[24]. In this study, pairs of participants took turns stroking either their own forearm or the forearm of the other person. They were instructed to compare their own skin and the other's person skin in relation to the texture of a felt pad. Participants judged other people's forearms as being softer and smoother than their own arm and the object. In a follow-up experiment, participants were trained to stroke at different velocities. The social softness illusion was largest for velocities that are optimal for activating the C-tactile system[163], and absent entirely for faster stroking and static touch. These results suggest that touching other people's skin elicits a more pleasant experience than touching one's own skin (Fig. 5). The mechanisms mediating this illusion are likely to play a key role in promoting social interactions through the sense of touch as well as reciprocity in giving and receiving affective touch[24].

This illusion was replicated in another study that provided further evidence linking the effect to the identity of the person being touched[154]. In one condition, participants sat next to each other so

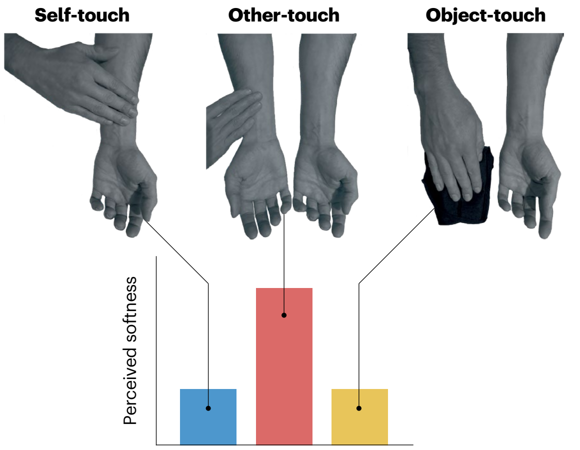

Fig. 5 | Source of touch. Despite having the same or similar effect in terms of the activation of somatosensory receptors, the identity of a tactile stimulus can be substantially different when self-generated, from another person or from contact with an inanimate object. Despite the similar physical input, these touches are processed differently.

that the other's person's arm was in the same posture and orientation as the participant's own arm. In another condition, the participants sat across a table from each other so that the other person's arm was in the opposite orientation. Clear social softness illusions were present in both conditions but had a larger magnitude in the latter condition, in which the distinction between self and other is clearer.

In summary, similar tactile inputs are processed differently depending on whether they are perceived as coming from the self, from another person, or from inanimate objects (Table 1). It is likely that sensitivity for self-related and for other-related touch has different functional roles. Self-touch is important for bodily self-calibration and higher-level aspects of bodily awareness, such as body ownership[152]. Other-touch, by contrast, is likely to have important roles in social bonding and attachment[166,167].

Summary and future directions

Classical approaches to somatosensation emphasized a somatotopic organization in which each brain region has specific links with specific parts of the body. Although these principles are still valid and important, later empirical studies showed that these principles cannot characterize all facets of tactile perception and neural representations. Here, we have discussed empirical data showing that topographic, hierarchical and stimulus identity independence principles are often integrated with and/or complemented by other types of organization.

Higher-level organizational principles help to shape tactile perception and coexist with classical topographic principles. Topographic maps clearly coexist in the brain with other representations based on categorical and functional principles. Which type of organization is adopted probably depends on the type of task required, the agent that produces the stimulation, and to some extent the nature of the stimulus. Different touch processes occur depending on whether they are produced by oneself, by another person or by an inanimate object. A crucial problem for future research is to determine under what circumstances each of these forms of coding is employed and how different representations work together to support complex behaviours.

In the motor system, many neural representations involve mixed selectivity, in which different types of representation and representations of different body parts appear to be jointly represented by the same populations of neurons[135]. It remains uncertain to what extent the same is true of somatosensory representations, and whether sensory and motor representations might themselves be mixed in such populations. The principle of motor equivalence has been a central organizing concept in the study of action (Box 1). It is an intriguing possibility that a similar principle of tactile equivalence might underlie touch, as hinted by some findings[21].

Finally, it will be critical for research to disentangle the representations of touch used for recognizing the physical properties of objects from those involved in self-perception of one's own body and in social perception of affective touch from familiar and non-familiar people. These three forms of touch are likely to involve integration of the somatosensory system with wider brain networks underlying object perception[168], bodily self-awareness[169], and social cognition[170], respectively.

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